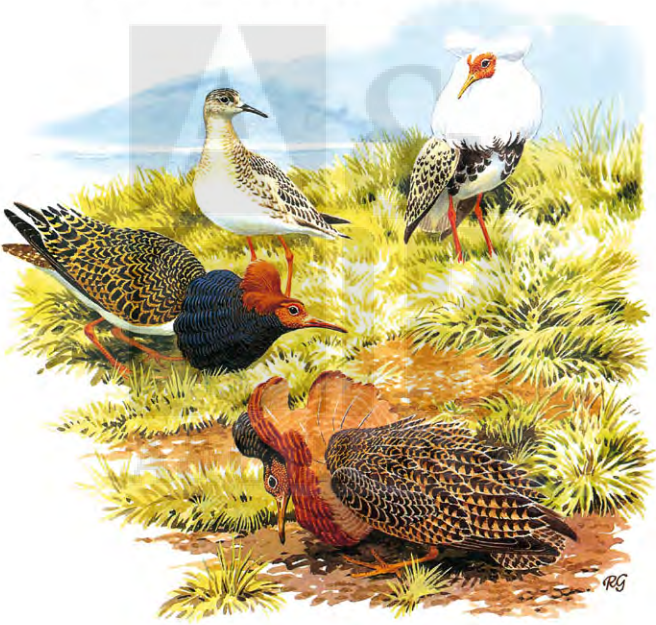
A Dictionary of BIRDS



Edited by **BRUCE CAMPBELL** and **ELIZABETH LACK**

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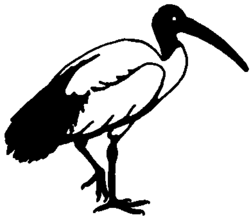
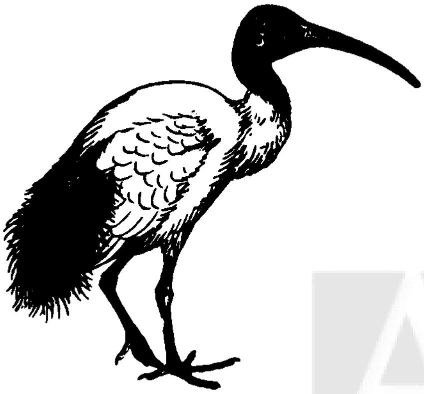


A Dictionary of Birds

Edited by BRUCE CAMPBELL and ELIZABETH LACK

Published for The British Ornithologists' Union



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Contents

Prefaces

By the President of the British Ornithologists' Union

In 1964 the 'New Dictionary', as it became so well known, was termed a comprehensive book of reference on birds on a world-wide basis both by its editor and creator, Sir Landsborough Thomson, and by R.E. Moreau, then President of the BOU. The present volume is no different in this respect, but it has been very widely revised, a great part of it re-written, much fresh material added, and it forms a new and important almost encyclopaedic work, written and illustrated by several hundred experts. Once again the co-operation of authors, artists and photographers has been given unstintedly, nearly all of it in an honorary capacity, and to them all the Union owes much gratitude and praise.

To the great expertise and ability of the senior editor, Dr Bruce Campbell, and to his tireless assistant Elizabeth Lack, has fallen the task of organizing and completing this ambitious work with the help of a panel of advisors, of whom Dr David Snow must be especially mentioned. They have given readily of their time, thought and knowledge for over five years and the Union is indeed grateful. Our publisher also earns generous thanks, for he has given patient and sympathetic help all through and has worked well beyond the limits to which most publishers in his position would go.

A New Dictionary of Birds was in part a tribute to the memory of Professor Alfred Newton F.R.S., whose original *A Dictionary of Birds* was the inspiration behind Sir Landsborough Thomson's project for the Union's Centenary. *A New Dictionary of Birds* has been an important source of reference for 20 years and it so remains. That it needs this new volume to update it in so comparatively short a time is a measure of the immense output of present research into a subject for which Professor Newton did so much to originate respect and esteem. The Union that he helped to found has here been provided with a worthy successor to the two previous works.

J.F. MONK

By the President of the American Ornithologists' Union

The American Ornithologists' Union congratulates the British Ornithologists' Union for the publication of this major new work in our field. The completion in 1985 of *A Dictionary of Birds* continues and extends the service to ornithology provided first in 1896 by Alfred Newton's dictionary and then in 1964 by A. Landsborough Thomson's new dictionary. Because ornithology is expanding and diversifying so fast, the importance of having an up-to-date, comprehensive reference work of its terms is even greater now than it was at the time of Thomson's work. That work was initiated to mark the Centenary of the British Ornithologists' Union. This new dictionary was being prepared at the time that the American Ornithologists' Union celebrated its own centennial in 1983.

We are particularly indebted to the editors and to all the other people involved in its production for the role the dictionary will play in fostering communication among nations. For students it will serve as an entrance to the present status of the field. For scientists it will serve as a research tool and a bridge between disciplines. We are also glad that many of our members were able to serve as contributors to such a worthy cooperative project.

FRANCES C. JAMES

Editorial Introduction

The Dictionary consists of articles on general subjects relating to birds, and on different kinds of birds mainly treated by families.

The arrangement is alphabetical with cross-references in small capitals, so the dictionary constitutes its own index. The short entries define special terms, applications of names, or are merely cross-references to the relevant major article. No attempt has been made to provide a glossary of words that can be found in an ordinary dictionary.

Language. Scientific terms formed from classical languages do not appear as entry headings unless they are in such common use as to be practically anglicized, or unless they have no satisfactory equivalents in common speech. Synonyms in modern foreign languages are also generally excluded.

The English names of birds chosen as entry headings are those in use by British ornithologists; the inclusion of dialect or archaic names is limited to those most widely occurring. North American names and others used in the English-speaking world have also been covered as far as practicable. Scientific names of groups above generic level have been used in headings; families are treated under their English names. Scientific names of genera are not used as entry headings except where they are also the English substantive names.

References. These are generally in English and mainly limited to books, monographs or important papers, which contain fuller accounts of particular subjects. Such publications will usually give references to the international literature. In a few cases we have added references which have been too recently published to be made use of in the articles concerned.

Illustrations. The photographs have been chosen to illustrate different activities of birds. We are indebted to E.J. Hosking for advising us and for his help in collecting suitable subjects from a number of leading photographers. The drawings of birds, normally one to each family, have been assembled for us by Robert Gillmor and executed by 18 artists. The diagrammatic text figures have been supplied mainly by the authors of the articles to which they refer, but a number have been redrawn by J.W.N. Turner. We are very grateful to all of them.

Collaboration. The wide subject cover has been made possible by enlisting contributions from 280 ornithological and other specialists, drawn from every continent and from 29 countries. Artists and photographers bring the total to well over 300. The articles on general subjects are mostly by authors in the UK and the USA; the articles on bird groups are by authors from throughout the world. To all of them we are most grateful.

During the long course of the preparation of the dictionary we have had the assistance of an advisory panel which has met at intervals. Its members were Sir Hugh Elliott, BOU President in January 1979 when the project was begun, S. Cramp (part-time), R. Gillmor (part-time), E.J. Hosking, Dr J.R. Krebs, Dr J.F. Monk (part-time), Dr R.J. O'Connor, P.J.S. Olney (part-time), Dr C.M. Perrins, T. Poyser and Dr D.W. Snow.

Dr D.W. Snow has made an outstanding contribution, not only as the author of 17 articles and numerous short entries, but with invaluable help and advice on the text, and later when reading the proofs.

Drs L.G. Grimes, E.K. Dunn and P.J.K. Burton advised on the revision of many articles, and I.C.J. Galbraith was a generator of several short entries.

We must also make special mention of the part played by Prof. K.H. Voous, whose classification the panel decided to adopt, (though authors have sometimes expressed their own views). Professor Voous wrote or revised all of the relevant articles, and answered many questions from us in his immaculate handwriting.

Many authors, outside the scope of their own contributions, gave us help from time to time and, outside the list of authors, we should like to record our gratitude to Dr N.P. Ashmole, Prof. P.P.G. Bateson, N.J. Ball, A. Bell, Prof. R.J. Berry, Dr L. Birch, Dr R.I. Bowman, Mrs E. Brooks, A.R.M. Campbell, R.N. Campbell, S. Cowdrey, N.C. Davidson, Prof. J. Dorst, S. Digby Firth, Dr J.A. Gibb, Dr J. Horsfall, Dr P. Hudson, Dr I. Keymer, L. Kunzemann, Dr A.J. Lack, C.M. Lack, Dr P.C. Lack, Prof. A.M. Lucas, Dr P. Marler, K.T. Marsland, H. Mayer-Gross, Dr R.V. Melville, P.J.S. Olney, J.L.F. Parslow, Dr M.G. Ridpath, Prof. R.K. Ringer, F.N. Robinson, Dr R. Schodde, Dr J. Sincock, D. Smallwood, Dr H.N. Southern, J.K. Terres, Prof. H.B. Tordoff, M.W. Tweedie, Dr M.A. Vince, P. Ward (died 1979), P. Wayre, M.G. Wilson, I. Wyllie and Dr M. Yasuda.

Dr J.F. Monk, as President of the BOU, gave us welcome support and encouragement in all stages of production, while our publishers, Trevor and Anna Poyser, have continuously helped and co-operated all through our years of work on the dictionary, and we must record our warmest gratitude and thanks to them.

Amendment. In a work of this kind, freedom from error is unobtainable, and it has obviously been impossible to include all new information accruing during the years of preparation. The Editors welcome any intimation of necessary corrections or additions.

Full general references:
Campbell B. & Lack, E. (eds). 1985. A Dictionary of Birds. Calton (Poyser) and Vermillion (Buteo).
Abbreviated references:
Campbell, B. & Lack, E. (eds). 1985. Dict. Birds, Calton & Vermillion.
Reference to a contributed article:
Evans, P.R. 1985. Article 'Migration'. *In* Campbell, B. & Lack, E. (eds). Dict. Birds. Calton & Vermillion.

Note on the Classification Followed

The classification followed in this work, down to familial level, is shown in the succeeding table. It deviates from the classification used in the 1964 *Dictionary*, which for the non-passerine groups was mainly that of volumes 1–7 of the *Check-list of Birds of the World* (1931–1951) by the late J.L. Peters, which itself was essentially based on the well-known Wetmore system. The families of songbirds, by 1964 not yet fully treated by Peters' successors, followed the so-called Basle sequence with 'crows last' (Mayr and Greenway 1956), as opposed to the 'crows first' sequence of Wetmore. The first paragraph of the note on classification followed in the 1964 edition closes with the words: 'It seems likely that the *Check-list*, when completed, will be widely accepted as an international standard for general purposes of ornithology'. This turns out to have been a wish rather than a reality, for suddenly the study of the interrelationships, and hence the sequence of orders and families of birds, has found itself in such a turbulent state of development that at present nobody can foresee where it will all end. This has been caused not only by a general renewal of interest but also by the development of new methods, especially biochemical, a resurgence of morphological studies, and the discovery of new fossil material, with the additional stimulus of the availability of a deductive method known as Hennigian systematics or CLADISTICS (see also CLASSIFICATION).

The use of chemical properties of egg-white proteins throughout the whole class of birds by Charles G. Sibley and collaborators, and of the other biochemical characters by other authors, has revolutionized basic and often traditional thoughts on relationships at the familial level (e.g. Sibley 1970, Sibley and Ahlquist 1972; cf. Voous 1980). The rapids turned into waterfalls after Sibley and his staff started to investigate chemical properties of the genetic material (DNA × DNA hybridization), the first results of which have recently been published and are summarized by Sibley and Ahlquist (1984). Particularly enigmatic have become the relationships of passerine groups endemic to Australia and New Zealand at the generic, familial and near-ordinal levels.

Morphological studies on the bony stapes (ear-bone) in pre-, proto- and recent Passeriformes by Alan Feduccia (1975, 1977) have upset what had been thought well established ideas on the relationships among these birds, including the distinction between non-oscine and oscine songbirds. Careful study of new fossil material has led to noteworthy progress in the understanding of the relationships of certain groups, e.g. the Gruiformes. Other notable contributions to the recognition, sequence and relationship of higher taxa have been included in the table of classification and in the specific articles.

In this situation of uncertainty and hopeful expectation it will be understood that it has not been possible to follow all of the recently proposed changes in the classification of birds. More time is needed for their evaluation, before they are accepted and incorporated into standard lists and handbooks. Here, the starting point has been K.H. Voous's *List of Recent Holarctic Bird Species* (1973, 1977), which was augmented for world-wide use for this occasion. Throughout, Morony, Bock and Farrand's *Reference List of the Birds of the World* (1975) and additions by Bock and Farrand (1980) can be recommended as a sound base for tackling any problems of taxonomy, sequence and literature reference at the specific, generic, familial and ordinal levels relating to the comparative systematics of living birds.

K.H. VOOUS

NOTE: the publication of the *Check-list of North American Birds* 1983 (6th edn) came too late for all pertinent revisions to be incorporated in the articles, but some amendments were made in proof where practicable. (Eds).

Bock, W.J. & Farrand, J. 1980. The number of species and genera of recent birds: a contribution to comparative systematics. Am. Mus. Novit. 2073: 1–29.

Feduccia, A. 1975. Morphology of the bony stapes (columella) in the Passeriformes and related groups: evolutionary implications. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 63: 1–34.

Feduccia, A. 1977. A model for the evolution of perching birds. Syst. Zool. 26: 19–31.

Mayr, E. & Greenway, J.C. 1956. Sequence of passerine families (Aves). Breviora, Mus. Comp. Zool. 58: 1–11.

Morony, J.J., Bock, W.J. & Farrand, J. 1975. Reference List of the Birds of the World. Am. Mus. Nat. Hist., New York.

Sibley, C.G. 1970. A comparative study of the egg-white proteins of passerine birds. Bull. Peabody Mus. Nat. Hist. 32: 1–131.

Sibley, C.G. & Ahlquist, J.E. 1972. A comparative study of the egg white proteins of non-passerine birds. Bull. Peabody Mus. Nat. Hist. 39: 1–276.

Sibley, C.G. & Ahlquist, J.E. 1984. The phylogeny and classification of the passerine birds, based on comparisons of the genetic material, DNA. Proc. XVIII Int. Orn. Congr.

Voous, K.H. 1973. List of recent holarctic bird species. Non-passerines. Ibis 115: 612–638.

Voous, K.H. 1977. List of recent holarctic bird species. Passerines. Ibis 119: 223–250, 376–406.

Voous, K.H. 1980. New developments in avian systematics: a summary of results. Proc. XVII Int. Orn. Congr.: 1232–1234.

See also references under CLASSIFICATION.

Avian Anatomical Nomenclature

The recently published *Nomina Anatomica Avium* (Baumel *et al* 1979) is an annotated, illustrated anatomical dictionary of birds. It is a codification of the names for the anatomical parts of birds which was formulated and agreed upon by some 80 eminent avian scientists from around the world. *NAA* is the first such system of anatomical names to be developed for birds, even though mammalian models have long been in existence.

Avian anatomy has suffered from a diversity of terminologies in the literature. Multiple and inappropriate names for the structures have caused confusion. *NAA* evolved during nearly a dozen years of discussion within the International Committee on Avian Anatomical Nomenclature (ICAAN). The Committee adopted the universally acceptable language of Latin, codifying prevailing usage of satisfactory names, doing away with duplicate terms and defining ambiguous ones. New names were produced where none were previously available or those in use were grossly defective.

The terminology of *NAA* has generally been followed throughout this Dictionary and ornithologists are urged to employ it in their publications. The use of official Latin anatomical terms will help to establish a standard avian terminology.

J.J. BAUMEL

Table of Classification

	Families	*Articles*
ORDER STRUTHIONIFORMES		
Suborder Struthiones	**Struthionidae**	OSTRICH
	Aepyornithidae (extinct)	ELEPHANT-BIRD
Suborder Rheae	**Rheidae**	RHEA
Suborder Casuarii	**Dromaiidae**	EMU
	Casuariidae	CASSOWARY
Suborder Apteryges	**Dinornithidae** (extinct) (incl.. Anomalopteryginae, Dinornithinae)	MOA
	Apterygidae	KIWI
ORDER TINAMIFORMES	**Tinamidae**	TINAMOU
ORDER PROCELLARIIFORMES		PETREL
	Diomedeidae	(Albatross)
	Procellariidae	(Shearwater)
	Hydrobatidae	(Petrel)
	Pelecanoididae	(Diving Petrel)
ORDER SPHENISCIFORMES	**Spheniscidae**	PENGUIN
ORDER GAVIIFORMES	**Gaviidae**	DIVER
ORDER PODICIPEDIFORMES	**Podicipedidae**	GREBE
ORDER PELECANIFORMES		
Suborder Phaethontes	**Phaethontidae**	TROPICBIRD
Suborder Pelecani		
Superfamily Suloidea	**Sulidae**	GANNET
	Phalacrocoracidae	CORMORANT
	Anhingidae	DARTER
Superfamily Pelecanoidea	**Pelecanidae**	PELICAN
Suborder Fregatae	**Fregatidae**	FRIGATEBIRD
ORDER CICONIIFORMES		
Suborder Ardeae	**Ardeidae**	HERON; BITTERN
Suborder Scopi	**Scopidae**	HAMERKOP
Suborder Ciconiae	**Ciconiidae**	STORK
	Balaenicipitidae	SHOEBILL
	Threskiornithidae	IBIS; SPOONBILL
ORDER PHOENICOPTERIFORMES	**Phoenicopteridae**	FLAMINGO
ORDER ANSERIFORMES		
Suborder Anhimae	**Anhimidae**	SCREAMER
Suborder Anseres	**Anatidae**	DUCK

ORDER CATHARTIFORMES	**Cathartidae**	VULTURE (2)
ORDER ACCIPITRIFORMES		
Suborder Accipitres	**Accipitridae**	HAWK; VULTURE (1)
	Pandionidae	HAWK (Osprey)
Suborder Sagittarii	**Sagittariidae**	SECRETARY-BIRD
ORDER FALCONIFORMES	**Falconidae**	FALCON
ORDER GALLIFORMES		
Suborder Galli	**Megapodiidae**	MEGAPODE
	Cracidae	CURASSOW
	Phasianidae	
	Tetraoninae, Odontophorinae	GROUSE
	Phasianinae	PHEASANT
	Numidinae	GUINEAFOWL
	Meleagridinae	TURKEY
Suborder Opisthocomi	**Opisthocomidae**	HOATZIN
ORDER MESITORNITHIFORMES	**Mesitornithidae**	MESITE
ORDER GRUIFORMES		
Suborder Turnices	**Turnicidae**	BUTTONQUAIL
	Pedionomidae	PLAINS-WANDERER
Suborder Grues		
Superfamily Ralloidea	**Rallidae**	RAIL
Superfamily Gruoidea	**Aramidae**	LIMPKIN
	Psophiidae	TRUMPETER
	Gruidae	CRANE
Suborder Heliornithes	**Heliornithidae**	FINFOOT
Suborder Rhynocheti	**Rhynochetidae**	KAGU
Suborder Eurypygae	**Eurypygidae**	SUNBITTERN
Suborder Cariamae	**Cariamidae**	SERIEMA
Suborder Otides	**Otididae**	BUSTARD
ORDER CHARADRIIFORMES		
Suborder Charadrii		
Superfamily Jacanoidea	**Jacanidae**	JACANA
Superfamily Charadrioidea	**Rostratulidae**	PAINTED SNIPE
	Haematopodidae	OYSTERCATCHER
	Ibidorhynchidae	IBISBILL
	Recurvirostridae	AVOCET
	Dromadidae	CRAB-PLOVER
	Burhinidae	THICKKNEE
	Glareolidae	COURSER; PRATINCOLE
	Charadriidae	PLOVER (1)
	Scolopacidae	SANDPIPER; PHALAROPE
	Pluvianellidae	MAGELLANIC PLOVER
Superfamily Thinocoroidea	**Thinocoridae**	SEEDSNIPE
Superfamily Chionidoidea	**Chionidae**	SHEATHBILL

Suborder Lari	**Stercorariidae**	SKUA
	Laridae	GULL
	Sternidae	TERN
	Rynchopidae	SKIMMER
Suborder Alcae	**Alcidae**	AUK
ORDER PTEROCLIDIFORMES	**Pteroclididae**	SANDGROUSE
ORDER COLUMBIFORMES	**Columbidae**	PIGEON
	Raphidae (Dodo, extinct)	DODO
	Pezophapidae (Solitaire, extinct)	
ORDER PSITTACIFORMES	**Psittacidae**	PARROT
ORDER CUCULIFORMES		
Suborder Musophagae	**Musophagidae**	TURACO
Suborder Cuculi	**Cuculidae**	CUCKOO
ORDER STRIGIFORMES	**Tytonidae**	OWL
	Strigidae	
ORDER CAPRIMULGIFORMES		
Suborder Steatornithes	**Steatornithidae**	OILBIRD
Suborder Caprimulgi	**Podargidae**	FROGMOUTH
	Aegothelidae	OWLET-FROGMOUTH
	Nyctibiidae	POTOO
	Caprimulgidae	NIGHTJAR
ORDER APODIFORMES		
Suborder Apodi	**Hemiprocnidae**	SWIFT (Hemiprocnidae)
	Apodidae	SWIFT; SWIFTLET
Suborder Trochili	**Trochilidae**	HUMMINGBIRD
ORDER COLIIFORMES	**Coliidae**	MOUSEBIRD
ORDER TROGONIFORMES	**Trogonidae**	TROGON
ORDER CORACIIFORMES		
Suborder Alcedines		
Superfamily Alcedinoidea	**Alcedinidae**	KINGFISHER
Superfamily Momotoidea	**Momotidae**	MOTMOT
Superfamily Todoidea	**Todidae**	TODY
Suborder Meropes	**Meropidae**	BEE-EATER
Suborder Coracii		
Superfamily Coracoidea	**Coraciidae**	ROLLER
	Brachypteraciidae	GROUND-ROLLER
Superfamily Leptosomatoidea	**Leptosomatidae**	CUCKOO-ROLLER
Suborder Bucerotes		
Superfamily Phoeniculoidea	**Phoeniculidae**	WOOD-HOOPOE
	Upupidae	HOOPOE
Superfamily Bucerotoidea	**Bucerotidae**	HORNBILL

ORDER PICIFORMES

Suborder Galbulae		
Superfamily Galbuloidea	**Galbulidae**	JACAMAR
	Bucconidae	PUFFBIRD
Superfamily Capitonoidea	**Capitonidae**	BARBET
	Indicatoridae	HONEYGUIDE
	Ramphastidae	TOUCAN
Suborder Pici	**Picidae**	WOODPECKER

ORDER PASSERIFORMES

Suborder Deutero-Oscines		
Infraorder Eurylaimi	**Eurylaimidae**	BROADBILL
	Eurylaiminae	
	Calyptomeninae	
	Philepittidae	ASITY
	Philepittinae	
	Neodrepaninae	
Infraorder Furnarii	**Furnariidae**	OVENBIRD (1)
	Furnariinae	
	Synallaxinae	
	Philydorinae	
	Dendrocolaptidae	WOODCREEPER
	Formicariidae	ANTBIRD; GNATEATER
	Rhinocryptidae	TAPACULO
Infraorder Tyranni	**Cotingidae**	COTINGA
	Pipridae	MANAKIN
	Tyrannidae	FLYCATCHER (2)
	Elaeniinae	
	Fluvicolinae	
	Tyranninae	
	Oxyruncidae	SHARPBILL
	Phytotomidae	PLANTCUTTER
Infraorder Pittae	**Pittidae**	PITTA

Suborder Oscines or Passeres

AUSTRALIAN AND NEW ZEALAND PRIMITIVE SPECIALISTS

Scrub Birds and Lyrebirds		
	Atrichornithidae	SCRUB-BIRD
	Menuridae	LYREBIRD
New Zealand Wrens		
	Acanthisittidae	WREN (3)

ISOLATED GROUPS

Larks		
	Alaudidae	LARK
Swallows		
	Hirundinidae	SWALLOW

OLD WORLD INSECT EATERS AND RELATED FAMILIES

Pipits and Wagtails		
	Motacillidae	WAGTAIL
Bulbuls and Allies		
	Campephagidae	CUCKOO-SHRIKE
	Pycnonotidae	BULBUL
	Chloropseidae	LEAFBIRD
Waxwings and Allies		
	Ptilogonatidae	SILKY FLYCATCHER
	Bombycillidae	
	Bombycillinae	WAXWING
	Hypocoliinae	HYPOCOLIUS
	Dulidae	PALMCHAT
Primitive Insect Eaters		
	Cinclidae	DIPPER
	Troglodytidae	WREN (1)
	Mimidae	MOCKING-THRUSH
	Prunellidae	ACCENTOR
	Turdidae	THRUSH
	Turdinae	
	Enicurinae	
	Sylviidae	
	Sylviinae	WARBLER (1); SILKTAIL
	Polioptilinae	GNATCATCHER
	Muscicapidae	FLYCATCHER (1)
	Rhipiduridae	FANTAIL
	Monarchidae	MONARCH FLYCATCHER
	Pachycephalidae	THICKHEAD
	Timaliidae	BABBLER; RAIL-BABBLER; PARROTBILL
	Aegithalidae	TIT, LONG-TAILED
Old Australian Endemics		
	Maluridae	WREN (2)
	Acanthizidae	WARBLER, AUSTRALIAN
	Acanthizinae	
	Mohouinae	
	Ephthianuridae	CHAT, AUSTRALIAN
	Neosittidae	SITTELLA
	Climacteridae	TREECREEPER (2)
Titmice, Nuthatches, and Treecreepers		
	Paridae	TIT
	Sittidae	NUTHATCH
	Tichodromadidae	WALLCREEPER
	Certhiidae	TREECREEPER (1)
	Remizidae	PENDULINE TIT
Uncertain Status		
	Rhabdornithidae	CREEPER, PHILIPPINE
	Salpornithidae	CREEPER, SPOTTED

Old World Nectar Eaters

Nectariniidae		SUNBIRD
Dicaeidae		FLOWERPECKER
	Dicaeinae	
	Pardalotinae	
Zosteropidae		WHITE-EYE (1)
Promeropidae		SUGARBIRD
Meliphagidae		HONEYEATER

CROWS, BIRDS OF PARADISE AND RELATED FAMILIES

Orioles, Shrikes and Allies

Oriolidae		ORIOLE (1)
Irenidae		FAIRY-BLUEBIRD
Laniidae		SHRIKE
	Laniinae	
	Malaconotinae	
Prionopidae		HELMET-SHRIKE
Vangidae		VANGA
Pityriasididae		BRISTLEHEAD
Dicruridae		DRONGO

Australian and New Zealand Crow-like Birds and Crows

Callaeidae		WATTLEBIRD (2)
Grallinidae		MAGPIE-LARK
Corcoracidae		CHOUGH (2)
Artamidae		WOOD-SWALLOW
Cracticidae		BUTCHERBIRD (2); MAGPIE (2); CURRAWONG
Turnagridae		THRUSH, NEW ZEALAND
Paradisaeidae		BIRD-OF-PARADISE
	Cnemophilinae	
	Paradisaeinae	
Ptilonorhynchidae		BOWERBIRD
Corvidae		CROW (1)

Starlings, Weaverbirds and Allies

Sturnidae		
	Sturninae	STARLING
	Buphaginae	OXPECKER
Passeridae		
	Passerinae	SPARROW (1)
	Plocepasserinae	SPARROW-WEAVER AND SCALY-WEAVER
Ploceidae		WEAVER
	Bubalornithinae	
	Ploceinae	
Estrildidae		ESTRILDID FINCH
Viduidae		WHYDAH (1)

NINE-PRIMARIED ASSEMBLAGE			
Vireos			
	Vireonidae		
		Cyclarhinae	PEPPER-SHRIKE
		Vireolaniinae	SHRIKE-VIREO
		Vireoninae	VIREO
Finches and New World Insect Eaters, Fruit Eaters and Granivores			
	Fringillidae		FINCH; DARWIN'S FINCHES
		Fringillinae	
		Carduelinae	
	Drepanididae		HAWAIIAN HONEYCREEPER
	Parulidae		WARBLER (2)
	Coerebidae		CONEBILL; BANANAQUIT
	Thraupidae		TANAGER
		Thraupinae	HONEYCREEPER FLOWERPIERCER SWALLOW-TANAGER
		Catamblyrhynchinae	FINCH, PLUSH-CAPPED
	Emberizidae		
		Emberizinae	BUNTING
		Cardinalinae	CARDINAL GROSBEAK
	Icteridae		ORIOLE (2)

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J.R.J. **Joseph R. Jehl Jr.**, A.B. (Cornell), Ph.D. (Michigan). Assistant Director, Hubbs-Sea World Research Institute, San Diego, California, USA. MAGELLANIC PLOVER.

R.E.J. **Rosemary Elston Jellis**, M.A. (Oxford). Late Senior Producer, British Broadcasting Corporation. Died 1983. MUSIC, BIRDS IN (with J.M. Hall-Craggs).

D.A.J. **Donald A. Jenni**, B.S. (Oregon State), M.S. (Utah State), Ph.D. (Florida). Professor of Zoology, University of Montana, Missoula, USA. JACANA.

A.R.J. **Arthur Ramsden Jennings**, M.A. (Cambridge), D.V.Sc. (Liverpool), M.R.C.V.S. Connel, Argyll, Scotland. DISEASE.

P.A.J. **Paul Austin Johnsgard**, B.S. (North Dakota State), M.S. (Washington State), Ph.D. (Cornell). Foundation Professor of Life Science, University of Nebraska, Lincoln, USA. GROUSE.

E.L.J. **Eric Lionel Jones**, B.A. (Nottingham), M.A., D.Phil. (Oxford). Professor, School of Economics, La Trobe University, Victoria, Australia. UTILIZATION BY MAN.

P.J.J. **Peter J. Jones**, Ph.D. (Oxford). Department of Forestry and Natural Resources, University of Edinburgh, Scotland. CROP MILK; HEAT REGULATION; ITINERANT BREEDING; METABOLISM; NUTRITION; QUELEA CONTROL.

G.C.A.J. **George Christoffel Alexander Junge**, D.Sc. (Amsterdam). Formerly Curator of Birds, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands. Died 1962. NIGHTJAR (with J. Marshall).

J.K.(1) **Janet Kear**, B.Sc. (London), Ph.D. (Cambridge). Assistant Director, Wildfowl Trust, Martin Mere, Lancashire, England. FLAMINGO; FOOD SELECTION; ODOUR.

J.A.K. **James Allen Keast**, B.Sc., M.Sc. (Sydney), M.A., Ph.D. (Harvard). Professor of Biology, Queen's University, Kingston, Ontario, Canada. ADAPTATIONS, ENVIRONMENTAL.

A.C.K. **Alan Charles Kemp**, B.Sc., Ph.D. (Rhodes). Head, Department of Birds, Transvaal Museum, Pretoria, South Africa. HORNBILL (with L.G. Grimes); SECRETARY-BIRD.

R.K. **Robert Kennedy.** Department of Zoology, Washington State University, USA. CREEPER, PHILIPPINE (with R. Orenstein).

R.E.K. **Robert Eyres Kenward**, B.A., D.Phil. (Oxford). Institute of Terrestrial Ecology, Furzebrook, Dorset, England. FALCONRY.

A.K.K. **Angela Kay Kepler**, B.A. (Canterbury, New Zealand), M.S. (Hawaii), Ph.D. (Cornell). Kula, Hawaii, USA. TODY.

C.B.K. **Cameron Bradford Kepler**, B.A., M.A. (California), Ph.D. (Cornell). Biologist-in-charge, Maui Field Station, Patuxent Wildlife Research Center, US Fish and Wildlife Service, USA. HAWAIIAN HONEYCREEPER.

J.K.(2) **Jiro Kikkawa**, D.Sc. (Kyoto). Professor of Zoology, University of Queensland, Australia. WHITE-EYE (1).

A.G.K. **Alan Glasgow Knox**, B.Sc., Ph.D. (Aberdeen). Sub-Department of Ornithology, British Museum (Natural History), Tring, England. KERATIN.

J.R.K. **John Richard Krebs**, M.A., D.Phil. (Oxford), F.R.S. Lecturer, Edward Grey Institute of Field Ornithology, University of Oxford, England. E.P. Abraham Fellow in Zoology, Pembroke College, Oxford. BEHAVIOUR, HISTORY OF; and COUNTING; IMPRINTING; LEARNING; MIMICRY, VOCAL (with W.H. Thorpe).

J.A.K. **James A. Kushlan**, B.S., Ph.D. (Miami). Adj. Associate Professor, University of Miami, Coral Gables, Florida, USA. HERON.

L.L. **Lionel Lambourne**, B.A. (Nottingham). Assistant Keeper, Department of Paintings, Victoria and Albert Museum, London, England. ART, BIRDS IN.

J.H.L. **John Hartley Lawton**, B.Sc., Ph.D. (Durham). Reader in Biology, University of York, England. ECOLOGY.

I.L. **Ingvar Lennerstedt**, Fil.dr. (Lund, Sweden). Department of Zoology, University of Lund, Sweden. FOOT PAPILLAE AND PADS.

J.D.L. **J. David Ligon**, B.Sc. (Oklahoma), D.Phil. (Michigan). Professor, Department of Biology, University of New Mexico, Albuquerque, New Mexico, USA. WOOD HOOPOE.

A.L. **Alan Lill**, B.Sc. (Bristol), Ph.D. (Edinburgh). Senior Lecturer, Departments of Psychology and Zoology, Monash University, Australia. BOWERBIRD (with R.F. Donaghey, C.B. Frith); LYREBIRD.

H.L.	**Hans Löhrl,** Dr. phil. (München). Egenhausen, West Germany. Formerly Vogelwarte Radolfzell. NUTHATCH; WALLCREEPER.
R.L.	**Rosemary Low.** Deputy Editor, 'Cage and Aviary Birds'. New Barnet, Herts, England. AVICULTURE; CAGE BIRD.
J.C.McL.	**John Charles McLachlan,** B.Sc. (Glasgow), Ph.D. (London). Lecturer, Department of Anatomy and Experimental Pathology, University of St. Andrews, Scotland. DEVELOPMENT, EMBRYONIC.
G.L.M.	**Gordon Lindsay Maclean,** B.Sc., Ph.D. (Rhodes), D.Sc. (Natal). Professor, Department of Zoology, University of Natal, Pietermaritzburg, South Africa. COURSER; DRINKING; PRATINCOLE; SANDGROUSE; SEEDSNIPE.
R.McN.	**Raymond McNeil,** B.Sc., M.Sc., Ph.D. (Montreal). Director, Centre de recherches écologiques de Montréal, Université de Montréal, Canada. FOOTEDNESS.
P.H.M.-B.	Sir **Philip Henry Manson-Bahr,** C.M.G., D.S.O., M.D. (London). Died 1966. England. Formerly Chairman, British Ornithologists' Club, and Vice-President, British Ornithologists' Union. MECHANICAL SOUNDS.
S.M.	**Stephen Marchant,** B.A. (Cambridge). Moruya, NSW, Australia. NEST.
M.B.M.	**Miles Berkeley Markus,** B.Sc., M.Sc. (Pretoria), M.Sc., D.I.C., Ph.D. (London). Professor, Department of Zoology, University of the Witwatersrand, Johannesburg, South Africa. FEATHERS, NUMBER OF.
J.M.	**Joe T. Marshall, Jr.** Division of Birds, U.S. National Museum, Washington DC, USA. NIGHTJAR (with G.C.A. Junge).
L.D.M.	**Larry Dean Martin,** B.S., M.S. (Nebraska), Ph.D. (Kansas). Curator, Vertebrate Paleontology, Museum of Natural History, and Professor, Systematics and Ecology, University of Kansas, Lawrence, Kansas, USA. ARCHAEOPTERYX.
G.V.T.M.	**Geoffrey Vernon Townsend Matthews,** M.A., Ph.D. (London). Deputy Director, Wildfowl Trust, Slimbridge, Gloucester, England. HOMING PIGEON; NAVIGATION.
E.M.	**Ernst Mayr,** Ph.D. (Berlin). Alexander Agassiz Professor Emeritus, Museum of Comparative Zoology, Harvard University, Cambridge, Mass., USA. NEARCTIC REGION; NEOTROPICAL REGION.
C.J.M.	**Christopher John Mead,** M.I.Biol. Head of Ringing and Migration Section, British Trust for Ornithology, Tring, England. AGE; PENDULINE TIT; WING FORMULA; WING SPAN.
H.M.	**Heimo Mikkola,** Ph.D. (Kuopio). M.Sc. (Oulu), D.Phil. (Kuopio). Fisheries Specialist, Africa Development Bank, Ivory Coast, Africa. OWL.
P.R.M.	**Philip R. Millener,** B.Sc., Ph.D. (Auckland). National Museum of Natural History, Smithsonian Institution, Washington DC, USA. MOA (with R.J.S. Cassels).
C.D.T.M.	**Clive D.T. Minton,** Ph.D. IMI Australia, Melbourne, Australia. TRAPPING.
D.W.M.	**Douglas Wayne Mock,** B.S. (Cornell), M.S., Ph.D. (Minnesota). Associate Professor, Department of Zoology, University of Oklahoma, Norman, Ok, USA. COLONIALITY.
N.W.M.	**Norman Wilfred Moore,** M.A. (Cambridge), Ph.D. (Bristol). Swavesey, Cambridge, England. Formerly Chief Advisory Officer, Nature Conservancy Council. HABITAT; TOXIC CHEMICALS.
R.A.M.	**Robert Andrew Morgan,** B.Sc. (Wales). British Antarctic Survey, Madingley Road, Cambridge, England. NEST RECORDS; THICKKNEE.
D.H.M.	**Douglas Hathaway Morse,** B.S. (Bates College), M.S. (Michigan), Ph.D. (Louisiana State). Professor of Biology and Chairman, Section of Population Biology and Genetics, Brown University, Providence, Rhode Island, USA. FLOCKING.
G.M.	**Guy Mountfort,** O.B.E. Lyndhurst, Hants, England. Past President B.O.U. BILL.
J.B.N.	**Joseph Bryan Nelson,** B.Sc. (St. Andrews), D.Phil. (Oxford). Reader in Zoology, University of Aberdeen, Scotland. GANNET; GUANO.
I.N.	**Ian Newton,** B.Sc. (London), D.Phil., D.Sc. (Oxford). Institute of Terrestrial Ecology, Monks Wood, Abbots Ripton, Huntingdon, England. FALCON; FINCH; HAWK; IRRUPTIONS.
J-N.N.	**Jean-Noël Neyrolles.** Paris, France. KAGU (with R. De Naurois).
R.J.O'C.	**Raymond Joseph O'Connor,** B.Sc. (National University of Ireland), D.Phil. (Oxford). Director, British Trust for Ornithology, Tring, England. BIOSTATISTICS; EGG; GROWTH; PARENTAL CARE; and DEVELOPMENT, EMBRYONIC (Embryonic thermoregulation).
J.C.O.	**John C. Ogden.** Senior Staff Scientist, Condor Research Center, Ventura, California, USA. IBIS; SPOONBILL; STORK; VULTURE (2).
R.O.	**Ronald Isaac Orenstein,** B.Sc., M.Sc. (Toronto), Ph.D. (Michigan), LL.B. (Toronto). Canada. CREEPER, PHILIPPINE (with R. Kennedy); CREEPER, SPOTTED; ELEPHANTBIRD; EXTINCT BIRDS; SITTELLA; TREECREEPER (2) (with D.L. Serventy).
G.H.O.	**Gordon H. Orians,** B.S. (Wisconsin), Ph.D. (UC, Berkeley). Director, Institute for Environmental Studies, and Professor of Zoology, University of Washington, Seattle, Washington, USA. ORIOLE (2).

M.O. **Myrfyn Owen,** B.Sc. (Wales), Ph.D. (Leeds). Assistant Director (Research), The Wildfowl Trust, Slimbridge, Gloucestershire, England. WILDFOWL.

R.S.P. **Ralph S. Palmer,** B.A. (Maine), Ph.D. (Cornell). Research Associate, Smithsonian Institution, Washington, DC, USA. CARDINAL GROSBEAK; COLOUR STANDARDIZATION; LIMPKIN.

S.A.P. **Shane Alwyne Parker,** B.Sc. (Adelaide). Curator of Birds, South Australian Museum, Adelaide, South Australia. CHAT, AUSTRALIAN; FANTAIL; MONARCH FLYCATCHER; WARBLER, AUSTRALIAN; WREN (2).

K.C.P. **Kenneth Carroll Parkes,** B.Sc., M.Sc., Ph.D. (Cornell). Chief Curator, Life Sciences, and Curator of Birds, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA. WARBLER (2).

D.T.P. **David Thomas Parkin,** B.Sc. (Durham), Ph.D. (Manchester). Senior Lecturer, Department of Genetics, University of Nottingham, England. GENETICS.

C.P. **Colin Patterson,** B.Sc., Ph.D. (London). Senior Principal Scientific Officer, Department of Palaeontology, British Museum (Natural History), London, England. CLADISTICS.

R.B.P. **Robert Berkeley Payne,** B.S. (Michigan), Ph.D. (University of California, Berkeley). Museum of Zoology and Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan, USA. CUCKOO; WHYDAH (1).

C.J.P. **Colin James Pennycuick,** M.A. (Oxford), Ph.D. (Cambridge). Maytag Professor of Ornithology, University of Miami, Florida, USA. FLIGHT.

C.M.P. **Christopher Miles Perrins,** B.Sc. (London), D.Phil. (Oxford). Director, Edward Grey Institute of Field Ornithology, University of Oxford, England. BREEDING SEASONS; CLUTCH-SIZE.

D.E.P. **Derek Edmund Pomeroy,** M.A. (Cambridge), Ph.D. (Adelaide). Professor of Zoology, Makerere University, Uganda. BILL ABNORMALITIES.

A.P. **Adolf Portmann,** Ph.D. (Basel), Dr. h.c. (Aix-Marseille; Freiburg i Br.). Formerly Professor, Director, Zoological Institute, University of Basel, Switzerland. HATCHING (with W.H. Stingelin).

W.F.P. **William Frank Porter,** B.A. (Northern Iowa), M.S., Ph.D. (Minnesota). Associate Professor, Department of Environmental and Forest Biology; Director, Adirondack Ecological Center, State University of New York, Syracuse, New York, USA. PARTHENOGENESIS; TURKEY.

I.P. **Ian Prestt,** M.Sc., (Liverpool), F.I. Biol. Director, Royal Society for the Protection of Birds, Sandy, Bedfordshire, England. CONSERVATION.

J.P. **Jesu Prévost,** Ph.D. Professor, Faculty of Sciences, University of Limoges, France. PENGUIN (*Aptenodytes*).

R.P.P.-J. **Robert Parton Prŷs-Jones,** B.Sc. (Nottingham), D.Phil. (Oxford). Research Officer, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa. BUNTING.

E.P. **Erkki Pulliainen,** Ph.D. Professor of Zoology, University of Oulu, Finland. WAXWING.

J.D.P. **John David Pye,** B.Sc. (Wales), Ph.D. (London). Professor of Zoology, School of Biological Sciences, Queen Mary College, Mile End Road, London, England. ECHOLOCATION; (MECHANICAL SOUNDS).

D.A.R. **Derek Almey Ratcliffe,** B.Sc., D.Sc. (Sheffield), Ph.D. (Wales). Chief Scientist, Nature Conservancy Council, Peterborough, England. EGGSHELL THINNING.

J.M.V.R. **Jeremy Mark Verrinder Rayner,** M.A., Ph.D. (Cambridge). Department of Zoology, University of Bristol, England. FLIGHT, SPEEDS OF.

R.E.R. **Reginald Elson Rewell,** M.D. (London), M.R.C.P. Formerly Pathologist, Zoological Society of London, England. BLOOD.

J.F.R. **John Frank Reynolds,** M.A. (Oxford). Head of Biology, Rastrick Grammar School, Yorkshire, England. BELLY-SOAKING.

A.S.R. **Andrew Stephen Richford,** B.Sc. (Edinburgh), D.Phil. (Oxford). London, England. PAINTED SNIPE.

M.R. **Mark Ridley,** M.A., D.Phil. (Oxford). New College, Oxford. ALTRUISM; E.S.S.; FACILITATION, POSTURAL; FACILITATION, SOCIAL; FITNESS; SEXUAL DIMORPHISM; SOCIOBIOLOGY.

M.W.R. The Hon. **Matthew White Ridley,** B.A., D.Phil. (Oxford). Science editor, The Economist, London, England. PHEASANT (with J.T. Delacour).

S.D.R. **S. Dillon Ripley,** K.B.E., Sc.D. Secretary, Smithsonian Institution, Washington, DC, USA. RAIL; THRUSH.

R.B.R. **Richard B. Root,** B.S. (Michigan), Ph.D. (Berkeley). Professor, Section of Ecology and Systematics, Cornell University, Ithaca, New York, USA. GNATCATCHER.

I.C.R.R. **Ian Cecil Robert Rowley,** B.Agr.Sci. (Melbourne). Senior Principal Research Scientist, CSIRO, Helena Valley, Western Australia. CHOUGH (2).

F.S. **Finn Salomonsen,** Ph.D. (Copenhagen). Formerly Keeper of Bird Department, Zoological Museum, Copenhagen, Denmark. Died 1983. FLOWERPECKER; HONEYEATER (with H.A. Ford).

L.S. **Luc Schifferli,** Lic. Zool. (Basel, Switzerland), D.Phil. (Oxford). Schweizerische Vogelwarte (Swiss Ornithological Institute), Sempach, Switzerland. GRIT.

R.P.S. **Roberto Pablo Schlatter,** Med. Vet. (U. de Chile, Santiago), Ph.D. (Johns Hopkins, USA). Professor, Institute of Zoology, Faculty of Sciences, Universidad Austral de Chile, Valdivia, Chile. PLANTCUTTER.

J.S. **J. Schwartzkopff,** Professor Dr. Ruhr-Universität Bochum, Germany. TOUCH.

D.K.S. **Dafila Kathleen Scott,** B.A. (Oxford), Ph.D. (Cambridge). Scientist at the Wildfowl Trust, Welney, Norfolk, England. RECOGNITION, INDIVIDUAL.

P.S. Sir **Peter Markham Scott,** K.B.E., D.S.C., M.A. (Cambridge). Founder and Director, Wildfowl Trust, Slimbridge, Gloucestershire, England. DECOY; DUCK; GAMEBIRDS.

D.L.S. **Dominick Louis Serventy,** B.Sc. (W. Australia), Ph.D. (Cambridge). Formerly Principal Research Officer, CSIRO Division of Wildlife Research, Nedlands, Western Australia. AUSTRALASIAN REGION (with H.A. Ford); FROGMOUTH; OWLET-FROGMOUTH; TREECREEPER (2) (with R. Orenstein).

J.T.R.S. **John Timothy Robin Sharrock,** B.Sc., Ph.D. (Southampton). Managing Editor, 'British Birds', Blunham, Bedford, England. ATLAS.

L.L.S. **Lester LeRoy Short,** B.Sc., D.Phil. (Cornell). Chairman and Curator, Ornithology Department, American Museum of Natural History, and Professor, City University of New York, USA. HYBRID; HYBRIDIZATION, ZONE OF SECONDARY; INTROGRESSION; WOODPECKER.

A.S. **Aharon Shulov,** D.Sc. Nat. (Naples). Emeritus Professor of Zoology, Hebrew University of Jerusalem, Israel. Founder and first Director of Jerusalem Biblical Zoological Garden. BIBLE, BIRDS OF THE.

C.G.S. **Charles Gald Sibley,** Ph.D. (California). William Robertson Coe Professor of Ornithology; Curator of Birds, Peabody Museum of Natural History, Yale University, New Haven, Conn. USA. DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA.

H.S. **Helmut Sick,** Ph.D. (Berlin). Academia Brasileira de Ciências, Rio de Janeiro, Brazil. CURASSOW; HOATZIN; SERIEMA; TAPACULO; TINAMOU.

W.R.S. **Walter Roy Siegfried,** B.Sc., Ph.D. (Cape Town). Director, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa. HAMERKOP; OXPECKER (with R.K.Brooke); SUGARBIRD.

K.E.L.S. **Kenneth Edwin Laurence Simmons,** M.Sc., Ph.D. (Bristol). Honorary Visiting Fellow, Department of Psychology, University of Leicester, England. ANTING; COMFORT BEHAVIOUR; DISTRACTION BEHAVIOUR; DUSTING; GREBE; SMOKE BATHING; SUNNING, and PARENTAL CARE (Protection of eggs).

S.S. **Sverre Sjölander,** Dr. Zoologiska Institutionen, University of Stockholm, Sweden. DIVER.

A.F.S. **Alexander Frank Skutch,** A.B., Ph.D. (Johns Hopkins University). San Isidro de El General, Costa Rica. JACAMAR; MOTMOT; PUFFBIRD; SHRIKE-VIREO; SILKY-FLYCATCHER; SUNBITTERN; TANAGER; TOUCAN.

T.S. **Tore Slagsvold,** D.Phil. Zoologisk Avdeling, University of Trondheim, Norway. NEST SITE SELECTION.

P.J.B.S. **Peter James Bramwell Slater,** B.Sc., Ph.D., D.Sc. (Edinburgh). Professor of Natural History, University of St. Andrews, Scotland. DISPLACEMENT ACTIVITY.

G.T.S. **Graeme Talbot Smith,** B.Sc., Ph.D. (ANU). Senior Research Scientist, Division of Wildlife and Rangeland Research, CSIRO, Midland, Western Australia. SCRUB-BIRD.

N.G.S. **Neal Griffith Smith,** D.Phil. (Cornell). Smithsonian Tropical Research Institute, Balboa, Panama. NESTING ASSOCIATIONS; SHARPBILL.

B.E.S. **Bertram Evelyn Smythies,** B.A. (Oxford). Merstham, Surrey, England. Formerly Forest Service in Burma and Sarawak. CUCKOO-SHRIKE; WOOD-SWALLOW (with P.J.K. Burton).

B.S. **Barbara Katherine Snow,** B.Sc. (Reading). Wingrave, Bucks, England. Formerly of Trinidad. HUMMINGBIRD.

D.W.S.(1) **David William Snow,** M.A., D.Phil., D.Sc. (Oxford). Wingrave, Bucks, England. Formerly Senior Principal Scientific Officer, British Museum (Natural History). BANANAQUIT; CHARACTER DISPLACEMENT; COEVOLUTION; CONEBILL; COTINGA; FINCH, PLUSH-CAPPED; HONEYCREEPER; HYPOCOLIUS; LEK; MANAKIN; MATING SYSTEM; OILBIRD; PEPPER-SHRIKE; POLYANDRY; POLYGYNY; SEED DISPERSAL; SWALLOW-TANAGER.

E.J.L.S. **E.J. Lawson Soulsby,** M.A. (Cambridge), Ph.D., M.R.C.V.S., D.V.S.M. (Edinburgh). Professor of Animal Pathology and Head, Department of Clinical Veterinary Medicine, University of Cambridge, England. ENDOPARASITE.

R.S. **Robert Spencer,** B.A., M.Sc. (Durham). Cockermouth, Cumbria, England. Formerly head of Ringing and Migration Section, and Director of Services, British Trust for Ornithology, Tring, England. MARKING.

D.W.S.(2) **David William Steadman,** B.Sc. (Edinboro State College), M.Sc. (Florida), D.Phil. (Arizona). Research Associate, Division of Birds, Smithsonian Institution, Washington, DC, USA. FOSSIL BIRDS.

W.H.S. **Werner Hugo Stingelin,** Ph.D. (Basel). Zoological Institute, University of Basel, Switzerland. HATCHING (with A. Portmann).

B.S. **Bernard Stonehouse,** B.Sc. (London), M.A., D.Phil. (Oxford). Scott Polar Research Institute, Cambridge, England. FRIGATEBIRD; SHEATHBILL; TROPICBIRD.

R.W.S.	**Robert W. Storer,** A.B. (Princeton), M.A., Ph.D. (California). Professor of Zoology and Curator of Birds, Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA. SWIMMING AND DIVING.
J.G.S.	**Joseph G. Strauch, Jr.** Ph.D. Adjoint Curator, University Museum (Zoology), University of Colorado, USA. SKELETON, POST-CRANIAL.
D.S.-S.	**James Denis Summers-Smith,** B.Sc. (Glasgow), Ph.D. (Reading). Guisborough, Cleveland, England. SPARROW (1).
A.L.T.	Sir **(Arthur) Landsborough Thomson,** C.B., D.Sc. (Aberdeen). President XI Orn. Int. Congr., Basel 1954. Editor, A New Dictionary of Birds, 1964. London, England. Died 1977. AVES; CONGRESSES (with B. Campbell); CROCODILE-BIRD; FAMILY; NAME, ENGLISH; NOCTURNAL HABITS; NOMENCLATURE; TAIL (with J.J. Baumel); SHOEBILL (with A. Guillet); TAMENESS; TAXONOMY; TOPOGRAPHY; YOUNG BIRD.
W.H.T.	**William Homan Thorpe,** M.A., Ph.D., Sc.D. (Cambridge), F.R.S. Emeritus Profesor of Animal Ethology, University of Cambridge, England; Past President, British Ornithologists' Union; Past President, Association for the Study of Animal Behaviour. COUNTING; IMPRINTING; LEARNING (all with J.R. Krebs); (MIMICRY, VOCAL).
N.T.	**Nikolaas Tinbergen,** Ph.D. (Leiden), M.A. (Oxford), F.R.S. Oxford, England. Formerly Professor of Experimental Zoology, University of Leiden, Netherlands; Formerly Reader in Animal Behaviour, University of Oxford, England. RECOGNITION; REDIRECTION; SIGN STIMULUS.
S.R.T.	**Susan Rhonda Tingay,** B.A. (Adelaide), Ph.D. (Western Australia). Stoneville, West Australia. MAGPIE-LARK.
L.T.	**Ludwik Tomiałojć,** B.Sc., Dr., Dr. habil. (Wrocław). Museum of Natural History, University of Wrocław, Poland. URBANIZATION.
S.G.T.	**Stephen Graham Tullett,** B.Sc., Ph.D. (Bath). Senior Scientific Officer, Department of Reproductive Physiology, Agricultural and Food Research Council's Poultry Research Centre, Roslin, Midlothian, Scotland. INCUBATION; LAYING.
D.A.T.	**Donald Arthur Turner.** East African Natural History Society, Nairobi, Kenya. TURACO (with L.G. Grimes).
G.E.S.T.	**Geoffrey Eric Slade Turner,** M.A. (Oxford). Formerly Secretary, Science Area Delegacy, University of Oxford, England. Died 1984. (FOLKLORE); (OMENS, BIRDS AS); ORNAMENTATION, BIRDS IN HUMAN.
E.K.U.	**Emil Karl Urban,** B.Sc., Ph.D. (Wisconsin), M.A. (Kansas). Professor and Chairman, Department of Biology, Augusta College, Augusta, Georgia, USA. PELICAN.
G.F.v.T.	**Gerard Frederick van Tets,** B.A., M.A., Ph.D. (British Columbia). Principal Research Scientist, CSIRO Division of Wildlife and Rangelands Research, Canberra, Australia. CORMORANT; DARTER.
H.G.V.	**Henry Gwynne Vevers,** M.B.E., M.A., D.Phil. (Oxford). Formerly Assistant Director of Science, The Zoological Society of London, England. COLOUR.
K.H.V.	**Karel Hendrik Voous,** D.Sc. (Amsterdam). Emeritus Professor of Systematic Zoology and Zoogeography, Free University, Amsterdam; Formerly Deputy Director, Zoological Museum, University of Amsterdam, Netherlands. CLASSIFICATION; ORDER; PALEARCTIC REGION.
F.V.	**François Vuilleumier,** Lic. ès sciences naturelles (Geneva), Ph.D. (Harvard). Curator, Department of Ornithology, American Museum of Natural History, New York, USA. ZOOGEOGRAPHY.
J.W.	**John Warham,** B.Sc. (Durham), Ph.D. (New Zealand). Reader, Department of Zoology, University of Canterbury, Christchurch, New Zealand. PENGUIN (*Eudyptes*).
K.E.W.	**Keith Edward Webster,** B.Sc., Ph.D., M.B., B.S. (London). Professor of Anatomy, King's College, University of London, England. NERVOUS SYSTEM.
M.W.W.	**Milton W. Weller,** A.B., M.A., D.Phil. (Missouri). Professor, Caesar Kleberg Chair in Wildlife Ecology, Texas A & M University, College Station, Texas, USA. SCREAMER.
D.R.W.	**David R. Wells,** Ph.D. (Malaya). Department of Zoology, University of Malaya, Kuala Lumpur, Malaysia. BROADBILL; FAIRY-BLUEBIRD; LEAFBIRD.
G.R.M.	**Gordon R. Williams,** B.Sc. (Sydney), M.Sc. (New Zealand), Ph.D. (Canterbury). Formerly Professor of Entomology, Lincoln College, Canterbury, New Zealand, and Director of New Zealand Wildlife Service. Died 1983. KIWI.
E.O.W.	**Edwin O'Neill Willis,** B.S. (Virginia Polytechnic Institute), M.S. (Louisiana State), Ph.D. (California). Professor Colaborador, Departamento de Zoologia, Universidade Estadual Paulista, São Paulo, Brazil. ANTBIRD.
R.F.W.	**Raffael Felix Winkler,** Dr. Phil. (Basel). Curator of Birds, Natural History Museum, Basel, Switzerland. PNEUMATIZATION OF BONE.
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ABDOMEN: the 'belly', being the part of the body containing the excretory, reproductive, and main digestive organs (see ALIMENTARY SYSTEM; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; EXCRETORY SYSTEM); applied also to the ventral surface of the same region (see TOPOGRAPHY).

ABDUCTOR: see MUSCULATURE.

ABMIGRATION: an anomalous migratory movement of a particular type (see MIGRATION).

ABNORMALITIES: see BILL ABNORMALITIES; PLUMAGE, ABNORMAL.

ABRASION: the effect of wear on the vane of a feather, involving some reduction of the tips of the barbs or their barbules; where these tips are coloured differently from the rest of the vane, their loss may substantially change the pattern and hue of the plumage generally (see PLUMAGE).

ABUNDANCE: see NUMBERS.

ACANTHISITTIDAE: a family of PASSERIFORMES, suborder Oscines; alternative name for the Xenicidae; see WREN (3).

ACANTHIZIDAE; ACANTHIZINAE: a family and subfamily of PASSERIFORMES, suborder Oscines; WARBLER, AUSTRALIAN.

ACCENTOR: former generic name used as substantive for most species of Prunellidae (Passeriformes, suborder Oscines); in plural, general term for the family, which comprises 12 species placed in the single genus *Prunella*.

Characteristics. They are small birds (14–18 cm) with rufous or brownish-grey upperparts, streaked in most species; and with greyish underparts, usually marked in places with rufous. The general size and appearance are like those of a sparrow *Passer*, but the bill is more slender and pointed. The sexes are similar in plumage but males have longer wings and are heavier. Anatomically the Prunellidae have the fringillid character of a true crop and a muscular gizzard, adapted to a diet of seeds at some seasons. Their systematic position among the Oscines had been long debated, but recent evidence from DNA-hybridization indicates that they are closest to the ploceine weavers (see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA). (Sibley and Ahlquist 1981).

Distribution and habitat. The family is exclusively Palearctic, widely distributed from western Europe to Japan. The Alpine Accentor *P. collaris* is the most widespread species, its disjunct occurrence in high mountains having resulted in the evolution of many races; 8 subspecies are currently recognized. The Himalayan Accentor *P. himalayana* breeds as high as 5,000 m. The Robin Accentor *P. rubeculoides* is also found at high altitudes in central Asia, showing a preference for dwarf rhododendrons and other scrub, or for willows and sedges in damp meadows. The Siberian Accentor *P. montanella* breeds in the Siberian mountains and also along the lower courses of the Siberian rivers well north of the Arctic Circle. The best-known species, the Dunnock (formerly Hedge Sparrow) *P. modularis*, breeds mainly in mountains in central and eastern Europe, but is a familiar bird of gardens and cultivation, as well as woodland and scrub, in the west.

Movements. Some accentors are migratory, while others move to lower altitudes in winter. The Dunnock is sedentary in mild parts of its range, migratory in the north, and makes altitudinal movements in mountains.

Food. Accentors are unobtrusive ground feeders, often creeping about with a mouse-like action. They are mainly insectivorous in summer, and in winter subsist largely on seeds. In winter quarters some accentors regularly forage in flocks.

Behaviour. The Dunnock, the only species investigated in detail, has a complex and highly variable social organization (Birkhead 1981; Davies and Lundberg 1984, Snow and Snow 1982). Female ranges are largely exclusive. Males set up song territories in spring and compete to monopolize females. Depending on their ability to monopolize one or more females, the resulting mating systems range from polygyny (a male with two or three females) through simple pairs to polyandry (a female with two or three males) or even 'polygynandry' (several males associated with several females). The commonest mating systems are pairs and 'trios' (a female with two males). When two males share a female, one is dominant and the other subordinate. The dominant male guards the female closely, and the subordinate male may or may not succeed in mating. Only if he does, does he help in feeding the young. The likelihood that a similar social system may occur in other species is suggested by the report of two males and a female feeding the young in an Alpine Accentor nest (Dyrcz 1977).

The Dunnock's precopulatory display and method of mating are most unusual. The male pecks the female's cloaca for up 2 minutes before mating, which he does with extraordinary rapidity, jumping towards her at a slight angle and making cloacal contact for only a fraction of a second. During the precopulatory display the female's cloaca makes strong pumping movements and sometimes, at least, she ejects a small droplet of sperm. The male is very interested in the droplet, looks at it, and then immediately copulates. In view of the complex mating system, often including polyandry, this display may have evolved because it increases the male's chances of paternity (Davies 1983). From the little evidence available it seems that the Alpine Accentor's mating behaviour is similar.

Voice. The Dunnock has a complex song consisting of a succession of rapid modulated notes and trills. Males include in their songs extensive passages copied exactly from their neighbours. Females very occasionally sing. The Alpine Accentor has a longer song of similar structure and regularly sings in flight. Other calls include sharp high-pitched alarm and contact notes (Dunnock) and a rippling trill (Alpine Accentor).

Breeding. The nest, built by the female, is an open cup of plant fragments and moss, lined with hair, wool or feathers, and placed in low tree branches, shrubs, rock crevices, or on the ground. The 3–6 unmarked eggs range from blue to light bluish green. Two or three broods are normal for the Dunnock, two for the Alpine Accentor. Incubation is by the female alone in the Dunnock, but both sexes are reported to incubate in the Alpine Accentor. The incubation and fledging periods are each about 12–13 days in the Dunnock, but probably average somewhat longer in the high montane species. M.E.B.

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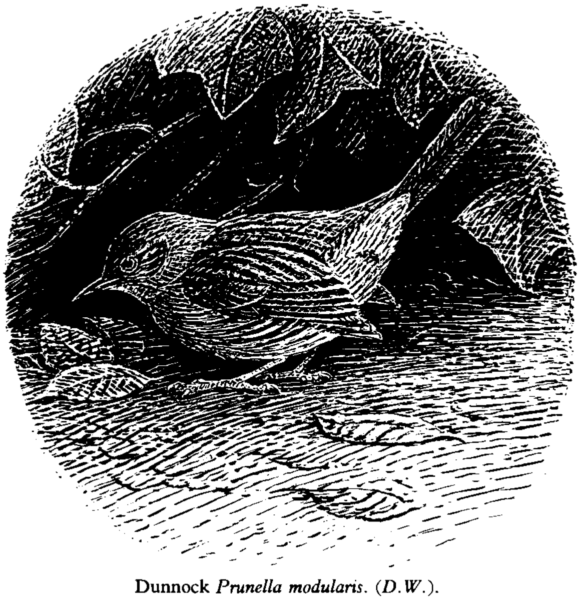

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ACCIDENTAL (SPECIES): see VAGRANT.

ACCIPITER: sometimes used in North America as a vernacular term for *Accipiter* spp., 'hawk' having there a wider connotation than in Britain (see HAWK).

ACCIPITRES: alternative ordinal or subordinal name (see ACCIPITRIFORMES).

ACCIPITRIDAE: see ACCIPITRIFORMES; HAWK.

ACCIPITRIFORMES: an order, alternatively 'Accipitres', comprising 2 suborders: Accipitres, Sagittarii; 3 families: Accipitridae (HAWK), Pandionidae (OSPREY), Sagittariidae (SECRETARY-BIRD).

The order is a cosmopolitan one and contains all birds-of-prey in the strict sense, such as hawks, kites, harriers and eagles, but not the cathartid vultures (see VULTURE (2)) and the falcons and caracaras (see FALCONIFORMES). The Old World vultures, sometimes treated as Aegypiinae, are included in the Accipitridae, whereas the Osprey *Pandion haliaetus* is given family rank Pandionidae, as in Wetmore's system.

All species are generally characterized by hooked beak and sharp curved claws, used as talons in seizing living prey. The large number of species have developed an astonishingly wide ecological radiation and an impressive variety of wing shapes and flight methods, depending on habitat and hunting techniques. The order includes the largest known fossil and Recent flying land birds, some of the former with enormous wingspan. Food ranges from small insects to relatively large terrestrial and arboreal mammals, such as small deer, sloths, and monkeys. Some have turned to feeding on carcasses of large ungulates, others to plant material including oily fruits.

ACCLIMATION: the process of adjusting to changed environmental circumstances, often with respect to temperature. Often used as a synonym of acclimatization but strictly refers to experimentally induced changes whilst the latter term is appropriate to natural change.

ACETABULUM: the hollow in the pelvic girdle, on each side, into which the head of the femur fits (see SKELETON, POST-CRANIAL).

ACQUIRED CHARACTERS: those arising during the life of the individual as the result of environmental or functional influences, as distinct from those expressing genetic constitution (see EVOLUTION; NATURAL SELECTION).

ACROMION: anterior projection of the scapula (see SKELETON, POST-CRANIAL).

ACROMYODI: see PASSERIFORMES.

ACROPODIUM: the dorsal surface of the toes.

ACROTARSAL: pertaining to the anterior surface of the tarsus.

ACUTIPLANTAR: having the hinder aspect of the tarsus coming to an angle (applied to oscine Passeriformes); opposite of LATIPLANTAR (in general, see LEG).

ADAPTATION: the production of fitness for a particular function, the term being also applied to a character (structure, behaviour, etc.) specially providing such fitness (see EVOLUTION; NATURAL SELECTION). 'Adaptive radiation' denotes divergence in the characters of related forms that enables them to exploit different kinds of opportunity. 'Convergence' denotes the adaptation of unrelated forms to similar functions, often giving rise to superficial resemblance (see CONVERGENCE). The term 'pre-adaptation' is used in cases where, coincidentally, a character existed in advance of the opportunity to which it proved particularly suited.

ADAPTATIONS, ENVIRONMENTAL: the production of fitness for particular functions.

The make-up of the bird, especially warm-bloodedness and capacity for flight, pre-adapt it for certain ways of life, ecological roles, life-zones, and habitats. Warm-bloodedness and feathery insulation permit birds to thrive at high latitudes and altitudes, fly annually to exploit habitats thousands of kilometres apart, utilize temporary habitats, as well as patchily distributed resources, and feed at different levels. Many seeming adaptations are thus really pre-adaptations.

Every aspect of the bird's life is adaptive: adaptations to the physical environment, habitat, prey and predators, and other bird species. Adaptations to the various aspects of reproduction alone are bewildering in their diversity and complexity. In this broad review it is not possible to cite the cross references involved.

Within the avian framework some of the most important adaptations to different living areas involve modification to the annual cycle: the more or less stereotyped annual sequence of breeding—moulting—outward migration—moulting—return migration—breeding. Basically the annual cycle is structured around reproduction in the spring, this usually being the time of optimum food resources. In those parts of the world with significant annual day-length changes, breeding is initiated by the changing photoperiod, a threshold being passed in the lengthening process that, via the pituitary pathway, triggers enlargement of the reproductive organs. Other phases of the annual cycle, moulting and migration, are also linked in most species to the changing photoperiod.

Each phase of the annual cycle represents a major energy drain on the bird, and may be the basis of adaptive modification. Breeding entails the setting up and defence of territory, courtship, nest-building, incubation, and the raising of the young. The moult (Payne 1972) represents the massive replacement of the body and flight feathers. Migration (Berthold 1975) may entail flights of thousands of kilometres: it is characteristically preceded by the laying down of layers of body fat (premigratory fat) to be used as fuel during the flight.

Breeding and moulting are almost invariably sequential and do not overlap. In high latitude breeding species the former commonly occupies 4–8 weeks. Erratic and unpredictable environments may necessitate modifications to the control and timing of breeding and moulting (Serventy 1971; Immelmann 1971). For example, in the interior of Australia breeding may be linked with rainfall, and only partly to the photoperiod. In such an environment, when conditions are optimal for only a brief period, there may be some overlap of breeding and moulting, and moulting may be very protracted so that it never represents a major energy-drain (Keast 1968).

Migration is, of course, very much a feature of the higher latitudes and altitudes. Whilst in most species the moult precedes migration, in a minority it is post-migratory. Presumably in such cases better resources are available in the wintering ground; or it is advantageous to leave the breeding grounds early. An alternative to the north-south (or south-north) migration of the higher latitude birds is the seasonal nomadism found in many inhabitants of warmer savanna and desert areas. Nomadism is a more random form of seasonal movement than 'true' migration and is of shorter amplitude. It brings the birds to areas where resources improve seasonally (e.g. winter rainfall areas, areas of fruiting or flowering), with the end point of the movement varying somewhat from year to year. Nomadic journeys may have a directional component (as in some African hawks and Australian interior birds) so that whether a movement be regarded as nomadic or migratory is a matter of choice. Presumably nomadic movements are usually less demanding on the bird than a 1,000 km migratory journey.

There may be one, or two, moults. Most bird species have only one, the 'complete' moult of late summer or early autumn. This post-reproductive moult entails a complete replacement of the flight, tail, and contour feathers. In a minority of species, mostly those with distinct breeding plumages, there is a prenuptial moult that is partial, involving the body feathers only. These different patterns of moulting are doubtless adaptive. Just as some races of species, but not others, are migratory so there may, or may not, be a prenuptial moult.

The component parts of the avian annual cycle are under neurendocrine control. As yet, however, despite intensive research, most of the finer control mechanisms remain unknown. The control of breeding (and of the various aspects of breeding behaviour) is well understood, but the same is not true of the moult. Whilst the thyroid is clearly linked to the moult in many species, in others this link is much less clear-cut. Little is known of the antagonistic/synergistic effects of the hormones on the pituitary, reproductive organs, and thyroid, in the control of the moulting process.

The link between hormones and migration is also inadequately understood.

Species inhabiting extreme environments often share common adaptations to those environments. Those of Arctic birds include migration, heavy body insulation, and sometimes white winter plumage. The small minority of species that over-winter in the far north commonly avoids freezing by spending the night in hollows (sometimes communally), or by burying themselves in the snow. Desert adaptations include nomadism; breeding after rain; avoiding breeding in bad years; breeding at an early age (permitting rapid population build-up); mechanisms for restricting water-loss; evaporative cooling, and modifying the effects of heat; ability to survive on a minimum of water or to drink semi-saline water; and being cryptically coloured (Serventy 1971; Immelmann 1971; Dawson 1980). Gloger's Rule (that races living in arid areas are pale-coloured) has wide application in birds, as does Bergmann's Rule (races occupying colder latitudes are larger than those inhabiting warmer areas).

At the finer level, within avifaunas and bird communities, it is now appreciated that individual species show complex ecological, behavioural, and structural adaptations for specific ways of life. These also serve to channel species within communities into different roles, thus permitting a diversity of different species to live together. There is a general link between body and bill size, and prey or food particle size (e.g. Hespenheide 1971). Migratory races of species have longer and more tapering wings than resident ones. Species living close to the ground or in thickets (e.g. quails) have rounded wings, a shape presumably linked to rapid vertical take-off. In warblers, minor differences in tarsal structure have been shown to be related to different perching habits (Leisler 1980; Osterhaus 1962). Species interactions could be a significant factor in consolidating ecological specializations.

Recent studies on migration (e.g. papers in Keast and Morton 1980) reveal not only a great diversity of adaptations associated with overwintering patterns but also a high adaptational plasticity amongst the migrants. These birds not only occupy different habitats in winter and summer but some may change their diets (e.g. from insect-eater to frugivore). Again, they are able to operate effectively in quite different bird communities in summer and winter. J.A.K.

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ADAPTIVE RADIATION: denotes divergence in the characters of related forms that enables them to exploit different kinds of opportunity (see ECOLOGY).

ADDLED: term applied to egg in which the developing embryo has died, as opposed to an infertile egg in which no development has taken place.

ADDUCTOR: see MUSCULATURE.

ADENOSINE TRIPHOSPHATE (ATP): the source of energy for, *inter alia*, muscular contraction (see METABOLISM).

ADJUTANT: also 'Adjutant-bird' or 'Adjutant Stork', substantive name of species of *Leptoptilos* (see STORK).

ADRENAL GLAND: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

ADULT: theoretically, a bird that has reached its fullest development; in practice, however, a term difficult to define precisely. Size is no criterion, as a bird is virtually full-grown at a very early age (see also YOUNG BIRD). The implication is that the bird has attained, appropriately to season, definitive plumage (see PLUMAGE; MOULT); and also that it is capable of breeding (see MATURITY). For most purposes, plumage provides the only practicable criterion. Difficulties are that many species breed, some even more than once, before acquiring their best plumage; and that others do not breed in the first year of wearing it (see AGE).

ADVERTISING DISPLAY: see DISPLAY.

AEGITHALIDAE: see under PASSERIFORMES, suborder Oscines; TIT, LONG-TAILED.

AEGITHOGNATHOUS: see PALATE.

AEGOTHELIDAE: see CAPRIMULGIFORMES; OWLET-FROGMOUTH.

AEGYPIINAE: see VULTURE (1).

AEPYORNITHIDAE: see under STRUTHIONIFORMES; EARLY EVOLUTION OF BIRDS; ELEPHANT BIRD; EXTINCT BIRDS.

AERATION: see RESPIRATORY SYSTEM.

AETHINI: see AUK.

AETIOLOGY: the science of causation, especially the causes of disease (see DISEASE).

AFFERENT: carrying inwards i.e. towards the centre; applied especially to nerves, in respect of the direction in which they transmit impulses—contrasted with EFFERENT (see NERVOUS SYSTEM).

AFRICA: see AFROTROPICAL REGION (for Africa south of the Sahara); PALEARCTIC REGION (for North Africa); MALAGASY REGION (for Madagascar).

AFROTROPICAL REGION: one of the six major zoogeographical regions (see DISTRIBUTION, GEOGRAPHICAL), consisting essentially of Africa south of the Sahara but excluding Madagascar (see MALAGASY REGION) and the Comoro Islands while including the islands of Zanzibar, Pemba, Mafia and the Gulf of Guinea. Previously known as the Ethiopian Region until the former state of Abyssinia changed its name to Ethiopia and necessitated a revision of the regional name. In the north it abuts the southern border of the Palearctic Region, which runs from about 21°N in the west to $22\frac{1}{2}$°N at the Red Sea, skirting to the south of the Ahaggar and north of the Air and Ennedi massifs. The south-west corner of Arabia has sometimes been included; it contains enough Palearctic elements to exclude it from the Afrotropical Region but enough Afrotropical elements to exclude it from the Palearctic. The total area of the region is about 21 million km^2 of which about $1\frac{1}{4}$ million km^2 are south of the tropics; the southern limit is at about 35°S.

The distribution of Afrotropical birds is closely related to that of vegetation types, which in turn are influenced by climate and topography, and, within a vegetation type, to its history. A useful account of the habitats of Africa, with special reference to birds, is given in Brown *et al* (1982). The most recent authoritative study of the vegetation is incorporated in the map by White (1982), which recognizes 18 floristic divisions and about 75 vegetation types. An important feature is the extent of vegetation types that are transitional between others, or are a mosaic of different types existing side by side; together, transitions and mosaics account for about 36% of the area of the Afrotropical region. The most conspicuous avifaunal changes coincide approximately with the boundaries of major vegetational types. Bird distribution patterns analyzed by Crowe and Crowe (1982) could be divided into 31 avifaunal zones, arranged in a 3-tier hierarchy from sub-regions through provinces to districts; of these, the boundaries of the 10 provinces coincide most closely with the boundaries of phytochoria (floristic zones) in White's map. The most important distinction in the avifauna remains that between forest and non-forest species, as stressed by Moreau (1966), even though more forest species are now known to occur in other habitats as well.

The geographical pattern of vegetation types is essentially a series of latitudinal belts becoming progressively more arid and open away from the Equator. This basic pattern is complicated by topography; east of 30°E and south of about 8°S, much of the land surface is 1,000 m or more above sea level and is too cool and dry for the development of the lowland rain-forest that is found at lower altitudes. On these raised plateaus, woodland, savanna and grassland or scrub replace the forest found further west and north. About 37% of the Afrotropical Region lies at altitudes of 1,000 m or more, compared, for example, with less than 17% of the Neotropical Region; the relatively small proportion of lowland must go some considerable way towards explaining the impoverishment of the Afrotropical Region compared with other parts of the tropics.

Lowland rain forest occupies the equatorial lowlands to about 10° north and south, and east to about 28°E; it is bordered broadly by a transitional zone consisting of a mosaic of woodland, forest and grassland maintained by the burning and stock-grazing activities of man. The zone as a whole is characterized by high rainfall—150 cm a year or more—and the lack of a marked dry season; but few if any parts of the Region receive the high and dependable rainfall found in many parts of the lowland rain forests of South America or South-East Asia. There is little or no undisturbed primary rain-forest remaining in Africa, but those areas that approach this condition most nearly are dominated by tall trees with few side branches beneath the canopy at 30–50 m, festooned with epiphytes and lianes. Below these tall emergent trees are several layers of tree canopy that between them shade the ground so darkly that the vegetation there is a sparse one of scattered herbs and saplings with very few grasses. Natural breaks in the canopy, caused by falling trees, watercourses or landslips, are important because they admit the light to lower levels and so allow the growth of a dense luxuriant undergrowth. This understorey is characteristic of much African forest where man has crudely mimicked the effects of natural breaks in the canopy. Rich forest extends also along rivers, whose water allows the trees to survive far outside the climatic limits of forest set by rainfall; these 'gallery' or riverine forests are often only a few trees deep but may be important dispersal routes for forest birds.

The stratification of the forest plants into layers is often confused; the ground layer, understorey and uppermost canopy are clearly recognizable but it is often impossible to distinguish other separate strata. Characteristic birds of the ground layer and understorey are thrushes and babblers; the upper layers are far richer, abounding in cuckoos, turacos, trogons, hornbills, barbets, starlings and weavers. Flycatchers, warblers and bulbuls range widely at all levels of the forest.

Woodlands and grasslands. Beyond about 8° north and south of the Equator, the transitional mosaic of forest, woodland and grassland gives way to more uniform expanses of woodlands and wooded grasslands. The chief distinction between these and the forest habitats is that here the trees are often more widely scattered, are deciduous and have a lighter, more airy canopy, allowing enough light to reach the ground to support a luxuriant growth of perennial grasses. The term 'savanna' is often used for some of these habitats but for a variety of reasons is now to be avoided. A wide belt between about 8°–10°N and 10°–16°S is dominated by the wettest of these habitats, a closed deciduous woodland consisting chiefly of *Brachystegia* spp., *Julbernardia* spp. and, especially north of the Equator, *Isoberlinia* spp.; much of this, especially in the south, is often referred to as MIOMBO. The grassier, more open habitats are characterized by frequent dry-season fires; the trees are characteristically thick-barked and fire-resistant, the grasses grow in dense clumps with roots and stems protected deep in the soil. The characteristic birds of the grassier habitats are grass-warblers *Cisticola*, weavers (Ploceidae) and estrildid finches (Estrildidae).

Semi-arid bushlands and deserts. Drier vegetation with small scrubby trees and bushes, and scattered annual herbs and grasses, dominate three areas—a belt along the southern edge of the Sahara (the Sahel), a block in the north-east from the Gulf of Aden to northern Tanzania, and another block centred on Namibia in the south-west. Trees and shrubs are predominantly species of *Acacia* and *Commiphora*, while baobab trees *Adansonia* are conspicuous at low altitudes in the east. The vegetation is so sparse that for most of the year the appearance of the landscape is dominated by the colour of the soil. Characteristic birds are coursers, bustards and larks, but the avifauna of the trees is also quite rich and these habitats support many Eurasian migrants. The birds show a variety of adaptations to the extreme conditions, including paler plumage than relatives in moister environments, and less sedentary behaviour; some species undertake regular migrations of many hundred kilometres south from the Sahel, notably Abdim's Stork *Ciconia abdimii* and the Grasshopper Buzzard *Butastur rufipennis*. True desert is found in the Sahara, in the Chalbi Desert of northern Kenya, along the shore of the Red Sea and in the Namib Desert of the south-west.

Montane regions. Between about 1,000 m and 3,500 m, the forest on most African mountains changes continuously in its species composition and in the growth form of its trees. The sharp division between lowland and montane forest so firmly stressed by Moreau (1966) and others is less widely accepted now (Diamond and Hamilton 1980). On isolated small mountains, and those near the coast (such as the Usambaras where Moreau worked), vegetation changes occur at lower altitudes, and possibly more sharply, than in forests nearer the centre of the continent. Above the tree-line there is often a zone of heathy bushes and low trees which merges into a more open moorland community of tussock-grasses, rushes, and, on the highest mountains, giant lobelias and ragworts. The 'Afromontane' zone of White (1982) contains many endemic plants and is recognized as a distinct floristic division, occurring on the scattered mountains of the Region in an archipelago-like distribution. Many bird species are common to this zone wherever it occurs, except in Ethiopia where the montane forest avifauna is notably depauperate. Moreau (1966) interpreted the disjunct distribution of these montane species as indicating that montane forest was previously much more widespread, but present historical evidence does not support this (see below).

History. Two major historical phenomena have shaped the present Afrotropical avifauna. Widespread volcanic and tectonic activity in the Miocene period, ending about 7 million years ago, raised the eastern and southern parts of the continent a thousand metres or so and generated most of the volcanic massifs there; it also broke the previous connection between the forests of Africa and those of Asia, a connection that is reflected in the affinities of the non-passerine forest avifauna (Snow 1980). The Quaternary period, from about 2 million years ago, has shown continued volcanic activity but has also suffered dramatic climatic changes related to the ice ages at higher latitudes. The classic description of the effects of these changes on the Afrotropical avifauna by Moreau (1966 and references therein) needs to be modified in at least two chief respects. First, the assumption that the distinction between lowland and montane forest is determined by temperature did not take into account the very major influence of moisture; second, the cold periods coinciding with the glacial maxima of the ice-ages were not also wet in Africa, as Moreau supposed—the so-called 'pluvials'—but extremely arid. The combined effects of these two points lead to the conclusion, which is supported by a variety of evidence from deep-sea cores to pollen diagrams, that montane forest was not continuous over much larger areas of Africa than it is now, as Moreau supposed was necessary to explain the occurrence of similar species on widely-separated mountains, but is probably as extensive now (apart from its recent reduction by man) as at any time in the last hundred thousand years (Diamond and Hamilton 1980 and references therein). The increased aridity of glacial periods confined forests to the most climatically stable areas; these 'refuges' are identifiable now as centres of endemism and species diversity within areas of apparently homogeneous habitat. During arid periods, the Sahara desert extended as far as 500 km south of its present boundary, and the Kalahari Desert occupied most of the area now occupied by the lowland rain-forest of Zaire and reached as far east as Victoria Falls as recently as 10,000 years ago.

Characteristic forms. Endemic Afrotropical taxa are few above the generic level: they include one order, the mousebirds, and 5 families—Hamerkop, Secretary-bird, guineafowl, turacos and wood-hoopoes, as well as the Ostrich (Struthionidae) which has become endemic, as it were, only by recent extinction elsewhere. The Region is particularly rich in francolins, bustards, barbets, honeyguides, larks, grass-warblers *Cisticola*, helmet-shrikes, shrikes and estrildid finches (Ploceidae and Estrildidae). The 2 species of oxpecker (Buphaginae) are of special interest because they have evolved as symbionts of the spectacular African fauna of large herbivorous mammals. On the other hand, the Region is poor in parrots and woodpeckers, and the number of species in the Region as a whole is substantially fewer than in the Neotropical Region.

One of the most dramatic features of the Afrotropical avifauna is the enormous influx of migrants from the Palearctic region in the northern winter (Moreau 1972). About a third of all Palearctic species winter wholly or mainly in the Region, occupying every habitat except lowland rain-forest and some reaching as far south as the Cape. Several species occasionally breed in their African 'winter' quarters, and the close affinity of many species of the southern grasslands with Palearctic species suggests that other African taxa may have originated in this way (Snow 1980). See also MIGRATION. A.W.D.

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AFTERFEATHER: (also called aftershaft). This is a structure resembling a feather in miniature attached to the underside of a feather at the superior umbilicus. Six types may be recognized of which the most developed is that found in Casuariiformes, where the afterfeather closely resembles the main feather, so that each feather appears double. In its simplest type the afterfeather lacks an aftershaft (hyporachis) and merely consists of a row of barbs (an aftertuft) attaching to the rim of the superior umbilicus. It is found in the New World vultures (Cathartinae). Several groups entirely lack afterfeathers, e.g. Ostrich *Struthio*, pigeons, cuckoos and swallows. Most workers assume that the function of afterfeathers is to increase the thermal insulating property of the feathers. This is supported by the facts, (1) that they nearly always have a downy structure, (2) that they are best developed on body feathers, especially down and semiplumes, but small or lacking on remiges and rectrices, and (3) that some birds, e.g. ptarmigans *Lagopus*, have larger afterfeathers in the winter than in the summer plumage. See FEATHER; FEATHERS, NUMBERS OF.

AGAMI: *Agamia agami* (see HERON).

AGE: elapsed time, since hatching, of a live bird. Analogous to age in human beings but only able to be measured accurately for birds for those individually marked as nestlings (see MARKING). In studies of populations (see ECOLOGY) the age of first breeding is particularly important: for small temperate zone passerines it is generally during the first summer but may be deferred for several years in larger species (averages ninth year for Fulmar *Fulmarus glacialis*). Even when breeding has started, age may have a significant effect on productivity as demonstrated by Coulson and White (1958) for the Kittiwake *Rissa tridactyla*. Older Kittiwakes were generally in better condition, returned to the colonies earlier in the breeding season, occupied the 'best' sites, laid larger eggs and produced bigger clutches which gave rise to more and healthier young than recent recruits to the breeding population. Such age-effects have now been demonstrated for a wide variety of birds, including small passerines, and are a very significant feature in the population ecology of many species.

The age composition of any population of birds depends on the species' mortality which is the fractional part of the population alive at the beginning of a period but dead by its end. Similarly the survival is the fractional part still alive at the end of the period, and so $S = 1 - M$ where S and M are the survival and mortality rates expressed as proportions. In many studies these figures are calculated over a year but they may also be calculated monthly or over a particular phase of the bird's life e.g. breeding season mortality. The earliest calculations of mortality were made by Lack (1943), who used reports of birds ringed so long before the analysis that no further reports could be expected; this is known as the Lack or complete data method. Later Haldane (1955) devised a maximum likelihood analysis allowing for the effects on the mortality estimate of ringed birds which were still alive: this enables the incomplete data to be included in the calculation. Both methods assume that the annual mortality rate of adult birds remains constant from year to year. Later methods, often involving detailed modelling and computer analysis, have attempted to allow both for variation in mortality rates from year to year (for instance changes related to the severity of winter weather) and for variation with the age of the bird.

Wandering Albatross *Diomedea exulans* male 30 years old. (*Photo: J.P. Croxall*).

The sample of dead birds found is much more likely to include birds dying through inexperience (e.g. dead on road, brought in by cat or stunned against a window) than those dying under more natural circumstances (e.g. egg-bound on the nest, at a secluded roost or on migration). In fact most birds die through inexperience, for they are constantly at risk from predators, disease, accident and food shortage. Newly independent fledglings are at greatest risk and mortality gradually decreases as the birds become more experienced. For many species mortality seems to be least just after the birds have bred for the first time, and is fairly constant thereafter. The two graphs (Fig. 1) show the gradual loss of individuals from a cohort of youngsters reared in the same year—one species (solid line) is long-lived with a delay of several years before breeding and the other (broken line) is a short-lived passerine breeding in its first summer. A few analyses show that particularly old birds are less likely to survive: this was first demonstrated for the Common Tern *Sterna hirundo* with increased mortality from the 19th year onwards. Where the species concerned has been studied intensively, the results of mortality analyses can be compared with known productivity and population figures. Mortality estimates computed from dead ringed birds are often high when related to such figures although survival estimates, from repeated sightings of live marked birds, are often compatible with productivity and population figures. Hence the sample of dead birds found is probably biassed towards younger rather than older individuals.

Mortality may vary between the sexes. Females are particularly at risk during the breeding season when they must produce and lay the clutch and generally undertake the major share of incubation duties. On the other hand, in some species the males have 'dangerous' displays, including conspicuous song-flights and the regular use of song-posts which may put them at risk; and territorial chases may result in their death from traffic accidents or other collisions. In species with marked sexual dimorphism, size or colour differences may also be responsible for differences in mortality.

If a steady annual adult mortality is assumed it is possible to calculate the Expectation of Further Life of an adult bird. The simplest formula is $2 - M/2M$ where M is the annual adult mortality. This gives the expected further life-span of a bird on reaching adulthood. However, for many

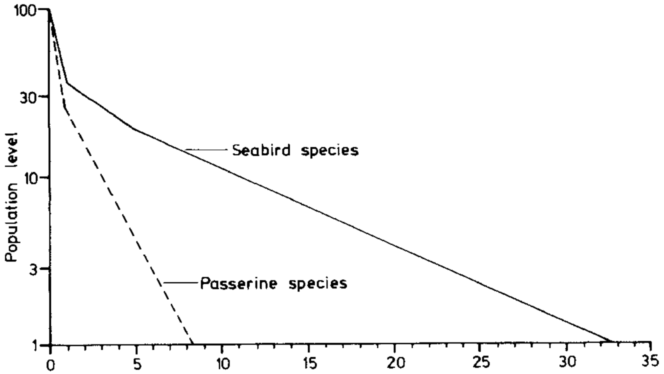

Fig. 1. The decay of two bird populations of 100 individuals at fledging. The solid line is of a seabird with 65% first year mortality, 15% *p.a.* for 4 pre-breeding years and 10% *p.a.* thereafter. On average one bird will live to 32 years of age. The broken line is for a passerine with 75% first year mortality and 35% *p.a.* thereafter: one of these would, on average, last into its ninth year. N.B. the vertical scale (population) is logarithmic.

small passerine species in the northern temperate regions, 90% or more of all eggs laid may fail to produce young that attain adulthood. Indeed, for a bird population to remain stable, each adult that breeds needs only to replace itself. Thus each adult needs, on average, only to rear two young to maturity during its life as a breeding bird—two need to be reared as each breeding attempt involves an adult of each sex. The huge changes in life expectation as mortality rates vary are evident from the following examples:

Bird	*Annual adult mortality*	*Expectation of further life of an adult*
Small passerine	70%	0.9 year
Woodpigeon *Columba palumbus*	40%	2.0 years
Swift *Apus apus*	20%	4.5 years
Yellow-eyed Penguin *Megadyptes antipodes*	10%	9.5 years
Royal Albatross *Diomedea epomophora*	3%	32.8 years

Longevity records (examples of extreme old age) provide concrete evidence of age-span but may be difficult to interpret. Species for which many recoveries have been reported are more likely to include a particularly old individual rather than those rarely marked or from parts of the world where ringing has only recently been introduced. The two tables of longevity records show the maximum recorded elapsed time between ringing and recovery of wild birds. Most have been taken from Rydzewski (1978, 1979) with additional data from British ringing files. The tables are in descending order of age and include, if available, one record (maximum three) for each main family or group. Clearly the larger birds can be expected to live longer than the smaller ones when species are compared. Lindstedt and Calder (1976) investigated the relationship between longevity records (4.08–38 years) and body mass (3.5–12,200 g) of 152 species in the wild. They obtained a good correlation between the two and showed that longevity was roughly proportional with the fifth root of body mass—$L = 17.6\,M^{0.20}$ where L is longevity in years and M body mass in kg. Thus, on average, a doubling of body mass would lead to 15% greater longevity and body mass has to increase 32-fold for a doubling in longevity (e.g. Blue Tit *Parus caeruleus* to Tawny Owl *Strix aluco*). The non-passerine list shows that waders and terns survive well despite being relatively light species. Ducks, game-birds and kingfishers mostly appear in the lower part of the table and generally lay large clutches. Among the passerines the larger temperate species head the list because very large files of recoveries are available, but it is likely that tropical passerine species will eventually be shown to be much longer lived than temperate ones (Fry 1980). Extreme longevity is symptomatic of K-SELECTION and poor longevity of R-SELECTION (see also ECOLOGY).

The records from bird collections and zoos show that captive birds live much longer than those in the wild. London Zoo in 1982 had two birds in its collections which had been resident for 50 years: a Common Caracara *Polyborus plancus* since 1932 and a Sulphur-crested Cockatoo *Cacatua galerita* since 1925. The cockatoo had been with its previous owner since about 1902 and was certainly more than 80 years old. This may be the oldest bird ever reliably recorded. Also 75% of London Zoo's Night Herons *Nycticorax nycticorax* were still alive at an age (about 8 years) when 99% of wild Grey Herons *Ardea cinerea* would have died (no data were available for Night Herons in the wild).

In normal circumstances there is no possibility of accurately measuring the age of a wild bird without marking it but instances exist of individually recognizable birds, e.g. albino waders, frequenting the same place for a decade or more. Detailed work on Bewick's Swan *Cygnus columbianus* has shown that individuals can be recognized, over periods of many years, by their bill patterns (see DUCK). One individual, Lancelot, was recorded over 19 winters. However it is often necessary to describe the age of a bird in the field or in the hand, in so far as it can be assessed. For nestlings growth is so rapid that measurements of bill, tarsus and primaries may often be used to estimate the age to within a day or so from hatching (see GROWTH) but, after fledging, a bird's age can usually be estimated only within broad limits, generally on the basis of age-specific plumages (see PLUMAGE; MOULT), from the colour and growth of the bare parts or, for young birds, from the incomplete ossification of the skull. Birds pass through a sequence of plumages and age has normally been recorded by a simple description of the bird's current plumage phase. The progression for a northern temperate passerine is as follows:

Month 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5
Moult Major Minor Complete Minor
Juvenile *First winter* *First summer* *Adult*

First winter and first summer may be combined into *First year.*

Adult is used for the rest of the bird's life as it has reached its definitive adult plumage.

These simple descriptions of age for free-flying birds are liable to confusion, especially between different groups of workers, and are, in any case, not adequate for large non-passerine species with a long sequence of identifiable immature plumages spanning several years. Bird ringers, in the Holarctic, now use a precise code based on the calendar year:

Longevity records—Non-passerines	*years*
Oystercatcher *Haematopus ostralegus* +	36.0*
Royal Albatross *Diomedea epomophora* +	35.9
Arctic Tern *Sterna paradisaea* +	33.9*
Guillemot *Uria aalge*	32.1*
Black-headed Gull *Larus ridibundus*	32.1
Osprey *Pandion haliaetus*	31.2
Mallard *Anas platyrhynchos*	29.0*
Honey Buzzard *Pernis apivorus*	28.9*
Spoonbill *Platalea leucorodia*	28.2*
Long-eared Owl *Asio otus*	27.7*
Black-throated Diver *Gavia arctica*	27.0
White Stork *Ciconia ciconia*	26.2*
Manx Shearwater *Puffinus puffinus* +	26.0
Purple Heron *Ardea purpurea*	25.5*
Northern Fulmar *Fulmarus glacialis*	23.0
Blue-faced Booby *Sula dactylatra*	22.9*
Pink-footed Goose *Anser brachyrhynchus*	22.1
Mute Swan *Cygnus olor*	21.7
Swift *Apus apus* +	21.1*
Shag *Phalacrocorax aristotelis*	20.6*
Red-bellied Woodpecker *Melanerpes carolinus* +	20.4
Leach's Petrel *Oceanodroma leucorhoa*	19.9
Little Blue Penguin *Eudyptula minor* +	18.9*
Coot *Fulica atra*	18.3
Arctic Skua *Stercorarius parasiticus* +	18.1*
Mourning Dove *Zenaida macroura*	17.1*
Kestrel *Falco tinnunculus*	16.2*
White Pelican *Pelecanus erythrorhynchus*	16.1*
Kea *Nestor notabilis*	14.1
Little Grebe *Tachybaptus ruficollis* +	13.1
Cuckoo *Cuculus canorus*	12.9*
Kookaburra *Dacelo novaeguineae* +	12.3
Capercaillie *Tetrao urogallus*	9.3*
Quail *Coturnix coturnix*	7.6
Ruby-throated Hummingbird *Archilochus colubris* +	5.0

Ringer's age categories	*European code*	*American code*
Free flying: age unknown	2	U (Unknown)
Hatched this year	3	HY (Hatching Year)
Hatched before this year	4	AHY (After Hatching Year)
Hatched last year	5	SY (Second Year)
Hatched before last year	6	ASY (After Second Year)
Hatched the year before last	7	TY (Third Year)
Hatched earlier still	8	ATY (After Third Year)

Important manuals containing age (and sex) information on northern hemisphere birds are Svensson (1984) for European passerines, Wood (1981) for North American species and Prater, Marchant and Vuorinen (1977) for Holarctic waders. C.J.M.

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AGGRESSION: threatening behaviour and attack. Overt aggression, in the form of pure physical assault, is usually intermingled with or overlain by a variety of postures, movements and vocalizations which serve as threat, repelling or intimidating the opponent without actual combat. A general term for this mixture of attack, threat and withdrawal is 'agonistic behaviour'. Certain behaviour must be distinguished from true aggression or the category becomes so diffuse as to be useless. For example, bird song may induce withdrawal and thus make unnecessary the physical defence of a territory, but its motivation is distinct from that of attack or threat. Raptorial killing is separated from true aggressive behaviour for similar reasons. Whilst most aggressive behaviour occurs within a species, true aggressive behaviour does occur between members of different species where these compete for resources.

Longevity records—Passerines	*years*
Blackbird *Turdus merula*	20.3
Starling *Sturnus vulgaris*	20.0
Rook *Corvus frugilegus*	19.9*
Bullfinch *Pyrrhula pyrrhula*	17.5
Swallow *Hirundo rustica*	16.0*
Great Tit *Parus major*	15.0
Golden Oriole *Oriolus oriolus*	14.9*
Common Grackle *Quiscalus quiscula* +	14.7
Red-winged Blackbird *Agelaius phoeniceus*	14.2*
Cardinal *Cardinalis cardinalis* +	13.5*
Brown-headed Cowbird *Molothrus ater* +	13.0
Robin *Erithacus rubecula*	12.9*
White-crowned Sparrow *Zonotrichia leucophrys*	12.8
Waxwing *Bombycilla garrulus*	12.6
White-browed Babbler *Pomatostomus superciliosus* +	12.1
House Sparrow *Passer domesticus*	12.0
Brown-throated Sunbird *Anthreptes malacensis* +	11.7
Olive-winged Bulbul *Pycnonotus plumosus* +	11.7*
Black and White Warbler *Mniotilta varia*	11.1
Reed Warbler *Acrocephalus scirpaceus* +	11.0
Silvereye *Zosterops lateralis* +	10.7
Skylark *Alauda arvensis*	10.1*
Warbling Vireo *Vireo gilvus* +	10.0
Pied Wagtail *Motacilla alba* +	9.9
Blue-gray Tanager *Thraupis episcopus*	9.4
White-breasted Nuthatch *Sitta carolinensis* +	9.4
Pied Flycatcher *Ficedula hypoleuca* +	9.2*
Dunnock *Prunella modularis*	9.0
Dipper *Cinclus cinclus* +	8.4*
Long-tailed Tit *Aegithalos caudatus* +	8.1
Bay-backed Shrike *Lanius vittatus* +	7.9
Wood Thrush *Hylocichla mustelina*	7.8
Goldcrest *Regulus regulus*	7.0
Treecreeper *Certhia familiaris*	6.8*
House Wren *Troglodytes aedon* +	6.2

Great Skua *Stercorarius skua* aggressive display. (*Photo: E.J. Hosking*).

In wild birds, fighting is rarely prolonged and threat is often used rather than overt fighting. This is because fighting involves costs: physical combat is exhausting, carrying a risk of injury and an increased risk of predation. Set against these costs are the benefits of gaining or owning the contested item. The theory of natural selection indicates that the level of aggression shown will depend on the balance between these benefits and the costs involved. Although it is difficult to quantify these it has, for example, been possible to measure the greater yield of flowers within the territory of sunbirds *Nectarinia reichenowi* compared with the undefended flowers outside.

Aggressive interactions may lead to the formation of a DOMINANCE hierarchy, within a group of birds, although species differ in the readiness with which this occurs. The hierarchy is best regarded as a way of reducing the detrimental effects of frequent aggressive interactions, rather than a desirable feature of social structure, but its presence may have important implications for population dynamics (see ECOLOGY). In some species, dominance rank in winter flocks is related to earlier territorial boundaries,

White-billed Diver *Gavia adamsii* aggressive display. (*Photo: A.V. Krechmar*).

Pheasant *Phasianus colchicus* two males fighting. (*Photo: F. Pölking*).

an illustration of the links between aggression in different contexts.

Aggression has sometimes been regarded as an inborn drive which must be suppressed or re-channelled for successful social life. But since it enables birds to compete for food, nesting and roosting sites and mates, and spaces them out appropriately, its occurrence can be better understood in most instances in terms of the benefit it brings to the individual involved. Aggression cannot be a unitary phenomenon across such a wide range of contexts, but it appears to share causal factors in different contexts, so that its subdivision into several distinct categories is inappropriate. Outside the reproductive season, one common factor is physical proximity. Factors such as hunger, which increases fighting over food, produce this effect by bringing birds together rather than by increasing their aggressiveness. Whilst most non-reproductive fighting can thus be explained in terms of defence of the individual distance (a small defended area, centred on the bird), reproductive fighting may involve defence of a larger, fixed territory. In the Chaffinch *Fringilla coelebs*, intermediate stages between defence of the individual distance and defence of the territory can be found. The gradual modification of the defended area in this species, under the influence of androgens and experience during the spring, demonstrates close links between reproductive and winter fighting. But in the weaver bird *Quelea quelea*, the hormone which stimulates individual distance fighting (luteinizing hormone) is not the same as that which stimulates fighting over nest materials (testosterone). Thus the control of aggressive behaviour may differ in detail in different contexts, and generalizations must be made with due care. Androgens such as testosterone are important in the control of aggression in many species, and female phalaropes *Phalaropus* spp., which set up and defend the territory whilst the males incubate, have high levels of androgen. Other hormones which modify aggressive and defensive behaviour in various species are oestrogens, progesterone, prolactin and follicle stimulating hormone (FSH), but the details of such hormonal effects will probably depend on the reproductive cycle of the species concerned.

Although most aggressive behaviour can be understood in terms of benefit to the individuals involved, the effects of pain and frustration (which increase the probability of aggression) have not yet been explained in this way. Demonstrations of this effect of frustration in pigeons *Columba livia*, hens *Gallus gallus*, and Quail *Coturnix coturnix* have all involved frustration of feeding, and so it is possible that the effect could be understood in terms of the tactics of feeding in a flock. Some examples of the 're-direction of aggression', for instance where a Chaffinch which has just lost a fight attacks a feeding subordinate without provocation, may also be explicable in this way, rather than implying that aggression must be discharged once it has been aroused, as the term 're-direction' suggests. In a reproductive context, behaviour which was once described as re-directed 'aggression' (the 'swoop and soar' performance of the Black-headed Gull *Larus ridibundus*) has proved to be purely sexual in motivation, and need not be explained in terms of the re-channelling of aggressive motivation aroused by the mate.

Most aggressive behaviour is triggered by external stimuli. Despite the fact that fighting cocks will work for the opportunity to threaten a rival in the laboratory, there is little evidence that wild birds show appetitive behaviour for fighting, except as a consequence of learning. The European Robin *Erithacus rubecula*, for instance, will go specifically to places at which it has recently had fights when patrolling its territory, and may even

Snow Goose *Anser caerulescens* aggressive display. (*Photo: A.V. Krechmar*).

Galapagos Hawks *Buteo galapagoensis* fighting. (*Photo: F. Pölking*).

attack an imaginary opponent if the effect of previous experience is very intense. External stimuli from the territory, the mate and the family may all play a part in triggering aggression in different species, but stimuli from the opponent are of greatest importance. Many aspects of the form, posture and bearing of a bird determine whether it will be attacked, but some features are so important that they are termed RELEASERS, for instance the red breast of the European Robin. (Some features, such as the nape band of the Kittiwake chick *Rissa tridactyla*, have the opposite effect, inhibiting attack). Such badges on the plumage also modify the way in which birds respond to aggression by the bearer. In the Red-winged Blackbird *Agelaius phoeniceus* experimental concealment of the male's red epaulets reduced the ability of the subjects to win contests and retain their territories, since their opponents refused to submit.

Birds use a variety of postures in threat; in many species these contain intention movements of attack, and have evolved from behaviour reflecting ambivalence towards the opponent. The effect of threat postures has been analysed by noting what posture is shown in an interaction, and correlating this with the opponent's response, and also by presenting dummies mounted in a particular posture and noting the response. Threat postures may produce withdrawal without the need for physical attack. There has been dispute over whether they do this by providing information about the signaller's intention to attack (statements of intention would be open to cheating), and the processes involved in the interaction are not yet understood. Aggressive elements are also visible in the form of many courtship and parental displays in birds, but the role of aggression in courtship is not fully understood (see AMBIVALENCE).

House Martin *Delichon urbica* attacking Swallow *Hirundo rustica* when collecting nest material (mud). (*Photo: H. Schouten*).

The development of aggression has been studied in detail in only a few species, including the Junglefowl *Gallus g. spadiceus*. Its adult aggressive behaviour is only gradually built up from components which appear independently in the young bird. Although the process appears to allow opportunities for learning in the integration of these motor components, isolation during rearing disturbs not the form of the motor patterns, but rather the way in which the aggressive behaviour is used. For example, isolation-reared cocks do not switch from aggression to sexual behaviour when the hen crouches. This evidence that individuals require social experience during rearing to show normal aggressive behaviour parallels that for many higher animals, but we cannot yet explain the details of its pattern of development. See photo DISPLAY. P.G.C.

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AGONISTIC: term applied to behaviour relating to combat (see AGGRESSION).

AIGRETTE: see PLUME.

AILUROEDINAE: see BOWERBIRD.

AIR-PASSAGES; AIR-SACS: see RESPIRATORY SYSTEM.

AIR SPEED: see FLIGHT, SPEEDS OF.

AKALAT: substantive name used in West Africa for *Malacocincla* ('*Illadopsis*') spp. (for subfamily see BABBLER), and in East Africa for chats of the genus *Sheppardia* (for subfamily see THRUSH).

AKEPA: *Loxops coccinea* (see HAWAIIAN HONEYCREEPER).

AKIALOA: *Hemignathus obscurus*, also called 'Sicklebill' (see HAWAIIAN HONEYCREEPER).

AKIAPOLAAU: *Hemignathus wilsoni* (for family see HAWAIIAN HONEYCREEPER).

ALA MEMBRANA: the wing membrane, on the posterior margin of the forewing and manus, from which the remiges grow (see WING).

ALAR: pertaining to the wing.

ALARM: expressed, like WARNING, either visually or vocally, with the distinction that there is not necessarily a warning function, although this may be the effect on other individuals.

Great Spotted Woodpecker *Dendrocopos major* juvenile showing alarm. (*Photo: A.T. Moffett*).

ALA SPURIA: the alula or BASTARD WING (see WING).

ALAUDIDAE: a family of the PASSERIFORMES, suborder Oscines; see LARK.

ALAUWAHIO: *Loxops maculata* also called Hawaiian Creeper (for family see HAWAIIAN HONEYCREEPER).

ALBATROSS: see PETREL. See photos AGE; DISPLAY; FLIGHT.

ALBINO; ALBINISM: see PLUMAGE, ABNORMAL.

ALBUMEN: see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA; EGG.

ALCAE: see under CHARADRIIFORMES; AUK.

ALCEDINES; ALCEDINIDAE: see CORACIIFORMES; KINGFISHER.

ALCEDINOIDEA: see under CORACIIFORMES; KINGFISHER.

ALCIDAE: see under CHARADRIIFORMES; AUK.

ALETHE: generic name used as substantive common name for species of chats (see THRUSH).

ALIMENTARY SYSTEM: consists essentially of (1) the buccal apparatus (bill, mouth, tongue, salivary glands and sensory receptors), (2) the oesophagus (and crop if present), (3) stomach (proventriculus and ventriculus), (4) the small intestine (duodenum and ileum), (5) the large intestine (caeca, colon and cloaca) and (6) various glands and organs including the liver, biliary system and gall-bladder, the pancreas and the bursa of Fabricius. Most of the these components are derived from the endoderm during the development of the bird in the egg.

During the course of evolution, modern birds have acquired mechanisms for the regulation of body temperature, a high metabolic rate, powered flight and a world-wide distribution. Consequently birds feed on relatively large quantities of a great variety of substances including fish, flesh, carrion, fruit, roots, leaves, seeds, pollen, nectar and all kinds of invertebrates (see FEEDING HABITS). Their diets may change as they mature, as the seasons change or as a result of migration. Nevertheless, unless wild birds are markedly different from their domesticated relatives, we may assume that the food of any bird must supply about forty chemical compounds to provide the energy and nutrients for growth, activity, reproduction and general maintenance (see NUTRITION). The alimentary system has become adapted to obtain and process the food and extract the nutrients. Several features of the avian alimentary system are probably related to the fact that most birds are supremely modified for powered flight. For example, the relatively heavy cephalic apparatus of many mammals is not present in modern birds. Instead, trituration occurs, when necessary, in the ventriculus or gizzard, which is located deep in the body where equilibrium will not be disturbed during flight. Other features of the tract are assumed to be functional adaptations for the digestion of a particular diet (see below).

Morphology and structure. Some general information about the form of the alimentary tract is given in Figs 1 to 20. Details of the bill are given elsewhere (see BILL). The mouth accommodates the tongue, which is as varied in form as the bill (see TONGUE), and the salivary glands. The oesophagus leads out of the mouth and enters the proventriculus (Fig. 1). In some birds, a thin-walled pouch, called the crop or ingluvies (Figs 4, 6 and 8), extends from the ventral wall of the oesophagus. The oesophageal lining consists of longitudinally-folded stratified squamous epithelium which is capable of considerable distension (Fig. 5). The stomach comprises the secretory or glandular proventriculus and the muscular ventriculus or gizzard (Fig. 1). The degree of development of the secretory and muscular tissue can often be correlated with the nature of the diet (Figs 9 and 11). Much of the thickness of the proventricular wall is due to the proventricular glands consisting of secretory cells some of which produce mucus while others (oxyntico-peptic cells) secrete both hydrochloric acid and pepsinogen (pepsin precursor). The ventriculus, in birds which ingest hard or fibrous food, is generally very muscular and may contain grit or other abrasive material so that it functions not unlike a ball mill. The ventricular lumen is lined by a polysaccharide-protein substance known as koilin which protects the tissues from acidic and abrasive damage.

The pylorus connects the stomach with the small intestine which consists of the duodenum and ileum (Fig. 1). The pancreas is usually located between the descending and ascending limbs of the duodenum and its digestive secretions usually enter the small intestine at the caudal end of the ascending limb near the entry of the bile ducts. This point may be taken as the end of the duodenum and the start of the ileum. Most birds possess a gall-bladder, which is usually embedded to some extent in the right lobe of the liver. There are usually two bile ducts which carry bile either directly from the liver or in a more concentrated form from the gall-bladder into the small intestine (Fig. 2).

The length of the ileum, which is often smaller in diameter than the duodenum, appears to be related to the nature of the diet. Carnivorous birds tend to possess relatively short intestines and herbivorous birds usually have long ones. The large intestine, consisting of the paired caeca, colon and cloaca, extends from the ileo-caeco-colic junction to the vent (Fig. 1). The caeca are variable in size and shape; some birds (herons) possess one caecum and not two (Figs. 12–18) while others (kingfishers) do not seem to have any obvious caeca. The complex cloaca receives and discharges intestinal and caecal faeces and urine from the bird (Fig. 3) (see DROPPINGS). In young birds, a small diverticulum called the bursa of Fabricius extends from the mid-dorsal wall of the cloaca. The bursa has an important immunological function similar in some respects to that of the thymus.

Throughout its length, the alimentary tract is made up of concentric layers known, in the small intestine, as the mucosa, submucosa, muscularis and serosa (Fig. 19). The mucosa consists mainly of villi which are formed from a layer of epithelial cells enclosing the lamina propria (Fig. 20). The lamina contains blood vessels, connective tissue and many white corpuscles which contribute to the immune responses of the bird. Numerous white corpuscles are to be found in the caecal tissues and the caecal tonsil, which is located near the ileo-caeco-colic junction and is reminiscent of a lymph node. The surfaces of many of the epithelial cells are composed of numerous microvilli. The effect of this enormous elaboration of intestinal surface membrane, together with the increase in surface area due to the villi, is to provide a very large surface area for the absorption of nutrients from the contents of the intestinal lumen. Goblet cells, which produce mucus, are also located in the epithelium. There are usually more goblet cells in the posterior small intestine and the caeca than in the duodenum. The submucosa is similar in appearance to the lamina propria although the white corpuscles may be found in discrete colonies and more connective tissue is present in addition to nerve fibres and larger blood vessels. The muscularis consists of a relatively thick coat of circular muscle and a thinner layer of longitudinal muscle (Fig. 19). The outer serosal layer is formed from connective tissue.

The principal blood vessels of the post-pyloric part of the tract of the domestic fowl are illustrated in Fig. 1. Most blood is supplied to this part of the tract by the coeliac, anterior and posterior mesenteric arteries which originate from the dorsal aorta. The blood leaves the small intestine along the veins of the hepatic portal system which transports recently absorbed nutrients directly to the liver (see METABOLISM). The tract receives an extensive autonomic or sympathetic innervation which is partially responsible for regulation of the variable motility of the tract.

Physiology of digestion. Digestion involves the sequential mechanical and chemical breakdown of food into components which are in a suitable condition for absorption. The alimentary tract provides not only the agents for this process but also the physico-chemical conditions for their efficient action. The intestinal motility serves to move the food along the tract, to mix the food and agents of digestion for the optimum time and to present the products of digestion to the absorptive surface of the small intestine.

Fig. 1. Stomach and intestine of a domestic fowl *Gallus gallus*.

Fig. 2. Gall-bladder and bile ducts of a domestic fowl.

Fig. 3. Cloaca of a domestic fowl.

Fig. 4. Crop of Hooded Vulture *Necrosyrtes monachus*.

Fig. 5. Extensible oesophagus of Red-tailed Hawk *Buteo jamaicensis*.

Fig. 6. Crop of Bobwhite Quail *Colinus virginianus*.

Fig. 7. Oesophagus of Ruby-throated Hummingbird *Archilochus colubris*.

Fig. 8. Crop of Rock Dove *Columba livia*.

Fig. 9. Stomach region of Double-crested Cormorant *Phalacrocorax auritus*.

Fig. 10. Stomach region of American Woodcock *Scolopax minor*.

Fig. 11. Stomach region of Pink-footed Goose *Anser brachyrhynchos*.

Fig. 12. Caeca of Yellow-billed Cuckoo *Coccyzus americanus*.

Fig. 13. Caeca of Coot *Fulica atra*.

Fig. 14. Caeca of Great Horned Owl *Bubo virginianus*.

Fig. 15. Rudimentary caeca of Chestnut-sided Warbler *Dendroica pensylvanica*.

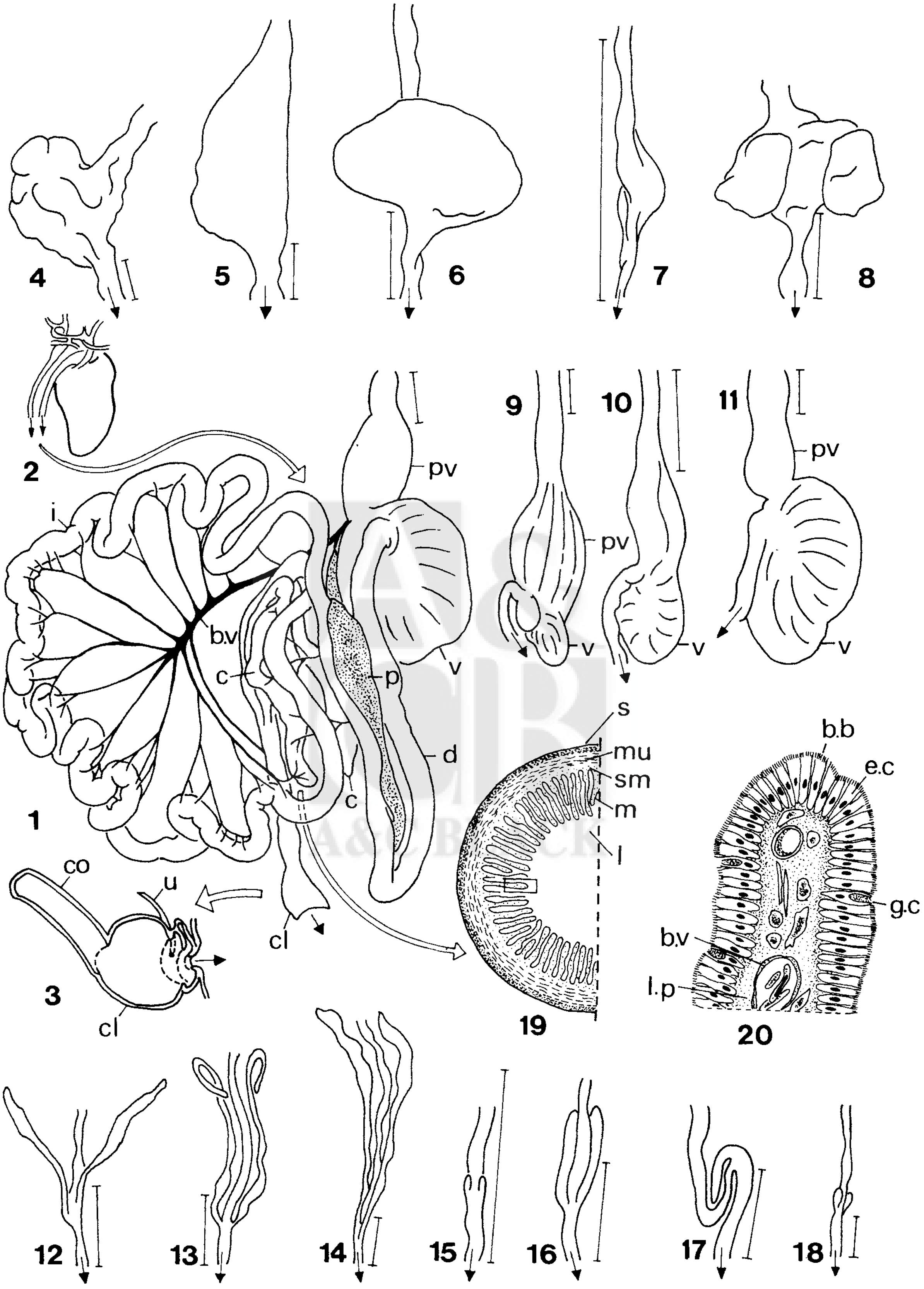
Fig. 16. Caeca of Snipe *Gallinago gallinago*.

Fig. 17. Caecum of Heron *Ardea cinerea*.

Fig. 18. Caeca of Great Black-backed Gull *Larus marinus*.

Fig. 19. Transverse section of part of the ileum.

Fig. 20. Detail of the structure of a villus from the ileum (see inset on Fig. 19).



Figs 1–20. Diagrammatic representations of aspects of the morphology of the avian alimentary tract. In all figures, the scale bar represents about 20 mm and the solid arrows show the usual direction of intestinal flow.

Abbreviations: **b.b.** brush border; **b.v.** blood vessel; **c.** caecum; **cl.** cloaca; **co.** colon; **d.** duodenum; **e.c.** epithelial cell; **g.c.** gland cell; **i.** ileum; **l.** lumen; **l.p.** lamina propria; **m.** mucosa; **sm.** submucosa; **mu.** muscularis; **p.** pancreas; **pv.** proventriculus; **s.** serosa; **u.** ureter; **v.** ventriculus.

In birds, food is moistened and swallowed quickly. The salivary glands undoubtedly produce mucus, but evidence suggests that the secretion of salivary amylase varies from species to species. The lining of the oesophagus also produces a lubricant and the food may pass straight into the proventriculus or be diverted and stored in the crop or in the extensible oesophagus. The period for which food is retained in the crop is very variable, but microbial fermentation processes may occur when it is delayed for several hours. The crop of the HOATZIN *Opisthocomus hoatzin* is muscular and is capable of squeezing the sap out of the leaves on which the bird feeds. The control of motility in the anterior part of the tract allows the direction to be reversed and regurgitation is an important process in many birds (see PARENTAL CARE; PELLET). On entering the proventriculus, the food is soon mixed with more mucus, hydrochloric acid and pepsin which begins the digestion of protein. This phase of digestion continues in the ventriculus where the muscular contractions break up the food and ensure a thorough mixing of pepsin with its substrate. The activity of pepsin depends on a low hydrogen ion concentration (*c.* < pH 3.5); the hydrogen ion concentration in the oesophagus and post-pyloric portion of the tract is usually maintained at about pH 6.5 to 7.5 which favours the activity of the other enzymes involved in digestion.

The partially digested food or chyme is forced out of the ventriculus through the pylorus into the duodenum where the main phase of chemical digestion begins. Under hormonal control, pancreatic juice and bile enter the intestinal lumen. Pancreatic juice contains a large amount of bicarbonate, which neutralizes the proventricular acid, and several enzymes including (in the domestic fowl) amylase, cholesterol esterase, esterase, lipase, phospholipase, trypsin and chymotrypsin. Bile contains the sodium salts of cholic, chenodeoxycholic and lithocholic acids. These salts are detergents which emulsify fats prior to enzymic hydrolysis by esterases, lipases and phospholipases, and also facilitate the absorption of the end products of fat digestion. Pancreatic amylase together with various disaccharidases synthesized by the mucosa hydrolyse certain carbohydrates to their constituent sugars which are then absorbed. Simultaneously, the hydrolysis of the polypeptides, which were liberated by the action of pepsin, to amino acids is completed by the trypsin, chymotrypsin and peptidases.

The chyme continues to be propelled rather more slowly along the tract and gradually indigestible materials accumulate posteriorly. Cellulose and other complex carbohydrates often form the major proportion of the contents of the large intestine together with many micro-organisms. Some of the indigestible material together with urine from the cloaca (Fig. 3) are forced by retroperistalsis into the caeca where as many as 10^{11} microbial cells per g of caecal contents may be found. The caecal bacteria of some birds, particularly galliforms, degrade plant products to volatile fatty acids which may contribute significantly to the energy budget of the bird. In other respects, the evidence for the contribution of the intestinal flora to the nutrition of the bird is equivocal; birds given an adequate diet can be reared in isolators in a germ-free state. Similarly, the functions of the caeca are not fully understood. Caecal tissue may be involved in water reabsorption, which also occurs in the colon, and in the immune responses. However, domestic birds continue to grow and develop normally in the laboratory after surgical removal of the caeca.

Certain parts of the anterior alimentary tract have acquired secondary functions during the evolution of some birds. The cells of the crop lining in both sexes of pigeons liberate a nutrititive substance which is regurgitated and fed to the squabs (see CROP MILK). The cells of the proventriculus in some species of PETREL probably produce the oily secretion which is vomited and considered to have a defensive function. Secretions from the salivary glands are used to build the nests of various species of cave swiftlet (see EDIBLE NESTS).

Generalizations about the form and function of the avian alimentary tract are difficult to make. First, the ecological relationships and diets of birds are very diverse. Secondly, most knowledge of digestive physiology in birds has been obtained from studies on the domestic fowl. Thirdly, for any given species we may expect that the amount of food and water consumed, the motility of the tract and the digestive and absorptive processes will depend on (1) the bird's age, sex and metabolic rate, (2) its nutritional, physiological and reproductive status, (3) the availability of food, (4) the physical and chemical properties of the food and (5) various environmental factors. (A.N.W.) D.W.T.C.

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ALLANTOIS: see DEVELOPMENT, EMBRYONIC.

ALLELE: see GENETICS.

ALLELOMIMETIC: term sometimes applied to similar behaviour on the part of two or more individuals when some element of mutual stimulation is involved.

ALLELOMORPH: sometimes abbreviated to 'allele' (see GENETICS).

ALLEN'S RULE: that among the forms of a polytypic species, extensions of the body (in birds, chiefly bill) tend to be longer in the warmer parts of the total range and shorter in the cooler parts. It is generally accepted that the adaptive basis for this rule is reduction of heat loss in cold climates (see ADAPTATIONS, ENVIRONMENTAL; ENERGETICS).

ALLOCHRONIC: existing at different levels of geological time (applied to two or more forms)—contrasted with SYNCHRONIC.

ALLOCRYPTIC: adventitious concealing coloration, as distinct from 'cryptic' coloration adapted to the purpose.

ALLOMETRY: the differential growth of one part of the body in relation to the whole or to other parts (see SIZE).

ALLOPATRIC: mutually exclusive geographically (usually applied to taxonomically related populations)—contrasted with SYMPATRIC; also used in the substantive form, ALLOPATRY. Species whose geographical ranges are closely contiguous but do not overlap are generally referred to as PARAPATRIC.

ALLOPREENING: term that has been introduced (with 'autopreening' as antonym) for preening of one bird by another bird, usually of the same species and commonly a mate—often mutual (see COMFORT BEHAVIOUR).

Allopreening of white-eyes *Zosterops*. (*N. Kikkawa*).

ALLOSEMATIC: see under SEMATIC.

ALLOSPECIES: one of the constituent species of a SUPERSPECIES.

ALLOTYPE: term sometimes applied to a paratype of the opposite sex from the holotype (see TYPE SPECIMEN).

ALPHA-CHLORALOSE: see PESTS, BIRDS AS; TOXIC CHEMICALS.

ALTERNATE PLUMAGE: in species which have two different plumages a year, the alternate plumage is usually that worn during the breeding season. The term is modern American usage, its equivalent in classical terminology is nuptial plumage (see PLUMAGE).

ALTITUDINAL DISTRIBUTION: distribution in accordance with height above sea-level in a particular area. See also MONTANE.

ALTITUDINAL MIGRATION: a local movement in which the displacement is principally a matter of altitude.

ALTRICIAL: helpless when hatched (see YOUNG BIRD).

ALTRUISM: in its biological usage defined as an act that has the effect of increasing the chance of survival (or more precisely, FITNESS) of another individual, but decreases the chance of survival of the altruist. Avian examples of altruism include any form of care of the young, whether the 'parent' in question is the young bird's genetic parent, a foster parent (see BROOD-PARASITISM) or some other bird (as occurs when there are helpers at the nest; see CO-OPERATIVE BREEDING). An altruistic act may be purely behavioural, such as feeding or protecting the young, or it may involve some physiological or anatomical trait. A bee's sting, for example, is an altruistic adaptation, for the bee dies after stinging, but benefits its colony.

In its everyday usage for describing human behaviour, altruism not only means that some benefit is transferred to the recipient at a cost to the altruist, but also that the altruist intended to be kind. The subjective motive of the altruist is ignored in biology, and there is no reason to suppose that an animal intends to produce a biologically altruistic effect when it does so. If a cuckoo's foster parent really knew the effects of its action, it would probably stop feeding the cuckoo.

Evolution. The existence of altruism is a paradox for the Darwinian theory of evolution, which claims that those individuals that reproduce most will come to prevail in the population. This theory predicts that altruism, in which by definition the recipient reproduces more than the altruist, should not exist. Four solutions to the paradox have been suggested, of which three are at present thought valid.

One solution is the theory of GROUP SELECTION. Although altruism is not beneficial to the individual altruist, it does benefit the group of altruists and recipients as a whole; therefore a group containing altruists would produce more offspring in all than a group that lacked altruists. So by inter-group selection, altruism could come to prevail. Group selection is thought not to have much effect in nature because, when modelled precisely, it is found to require conditions that are unlikely to exist very often, and it is very open to 'cheating'.

The three mechanisms that can account for altruism are named kin selection, reciprocal altruism and manipulation. KIN SELECTION, an idea mainly developed by W.D. Hamilton, can explain altruism between genetically related individuals. Parents are selected to feed their young because by doing so they are helping an individual that is genetically similar. Altruism between other kinds of genetic relatives can be selected for exactly the same reason. So kin selection has probably been important in the evolution of some species with helpers at the nest. In some of these it has been confirmed that the helpers are close relatives.

Reciprocal altruism can explain altruism between genetically unrelated as well as related individuals. If an individual can expect to be repaid in the future for acting altruistically now, then it would be selected to be altruistic. Reciprocal altruism will only be favoured by natural selection in species which are sufficiently intelligent to recognize particular individuals. In other species, cheaters (who receive altruism but do not repay) will not be discriminated against, and the system will break down. This theory cannot account for the initial spread of an altruistic trait, since the mechanism relies on an altruist encountering a reciprocator.

The altruism of some birds to brood parasites is presumably explained by manipulation. The parasite is in some way able to deceive, or manipulate, its foster-parent into feeding it.

Although these mechanisms by which altruism might evolve have been identified, few cases of altruism have been studied in sufficient detail for it to be known which mechanism was responsible for its evolution. M.R.

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ALULA: see WING.

AMADINI: see ESTRILDID FINCH.

AMAKIHI: *Loxops virens* (for family see HAWAIIAN HONEYCREEPER).

AMAZON: substantive name of Neotropical *Amazona* spp. (see PARROT).

AMBIENS: a muscle of the leg (see MUSCULATURE). The presence or absence of this has been used as a taxonomic character. Garrod (1874) even proposed to divide birds into two subclasses, Homalogonatae ('typically-kneed', i.e. ambiens present) and Anomalogonatae (ambiens absent), but his classification produced too many inconsistencies in relation to other characters and was soon abandoned. The ambiens is a reptilian feature and, broadly speaking, is present in what we regard as the more primitive groups of birds and absent from the more highly developed, including the Apodiformes and the Passeriformes. It may be noted that the ambiens is present in the Falconiformes but not in the Strigiformes; and also that differences in this respect occur within certain groups, notably the Psittacidae and the Columbidae.

AMBIVALENCE: term applied to behaviour that is the outcome of two (or more) conflicting tendencies, such as approach and avoidance, or attacking and copulating with the partner. Ambivalent motivation is present in many social interactions. For instance, among Gannets *Sula bassana*, in which the male is exceptionally aggressive towards the female even in well established pairs, the male bites the female's nape during copulation, revealing the presence of aggressive as well as sexual tendencies during this act.

During phylogeny, ambivalent behaviour has given rise to social displays used in communication. Some displays are a mosaic of elements of the conflicting tendencies. The 'upright posture' of the Herring Gull *Larus argentatus*, used in threat, includes a downward pointing bill and upward stretched neck (preparations for a pecking attack) and raised carpal joints (preparation to deliver a wing blow) combined with signs of fear, a withdrawn neck and flattened plumage. Since the posture combines elements of both tendencies, it is termed formally ambivalent. Where the elements of the conflicting tendencies are shown in rapid alternation (for instance in 'pendulum fights' of songbirds at a territorial boundary) the term successive ambivalence may be used. Where behaviour involves only the elements which are common to both conflicting tendencies, the term compromise activity is used. For example, in a conflict between flying towards and sidling towards an object, buntings (*Emberiza* spp.) show tail flicks, a component of both flying and sidling.

The motivation of an ambivalent movement may be inferred firstly by scoring the overt behaviour shown in rapid alternation with it ('time score method'). For instance, agonistic postures tend to alternate with attack and escape rather than with feeding or preening; but where displays alternate with other displays, this method is not helpful. Secondly, the context in which the behaviour is shown can be examined. If stimuli for two incompatible types of behaviour are known to be present, it is likely that the behaviour seen is ambivalent, and both 'natural experiments' and laboratory experiments can provide evidence of this sort. Thirdly, the orientation adopted during the act may also provide an indication of subtle variations in motivation. Finally, where a movement is formally ambivalent, the form itself may provide clues to its motivation, although the possibility that the movement has become divorced from its original motivation during the course of evolution must be considered. (Comparisons between species using this type of evidence provided the first indications of the importance of ambivalence in social behaviour.) Physiological work, in which areas of the brain were stimulated electrically, had been expected to provide a further line of evidence, but has proved difficult to interpret; it has not provided unequivocal support in any instance for analyses based on the behaviour alone.

The generality of the actual behavioural tendencies involved may vary considerably. Some agonistic postures depend specifically on the arousal of attack and escape tendencies, others on the arousal of the tendency to attack together with any incompatible tendency. 'Beak hiding' in the Kittiwake *Rissa tridactyla* occurs when fear interacts with any tendency towards approach or staying. In the buntings described above, the conflict was between tendencies to move towards the object in alternative ways.

The presence of ambivalence in some social interactions (for instance, during a fight) is easy to understand, but the reasons for its presence in others (such as mating) are less obvious. One possibility is that it is a consequence of the evolutionary origin of the signal postures used, which constrains future evolution much as the pentadactyl limb constrains the evolution of wings or flippers. Alternatively, it may represent a compromise between conflicting selection pressures on the individual. For example, aggressive courtship by the male dove *Streptopelia roseogrisea* (='*risoria*') delays ovulation, but may confer advantages in preventing cuckoldry. (N.T.) P.G.C.

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AMERICA: see NEARCTIC REGION; NEOTROPICAL REGION. Note that the term 'Middle America' is now much used to designate the area comprising Mexico, Central America, and Panama (the last being by political history part of South America), and sometimes including the West Indies. This usage has the consequence that 'North America' is often used in ornithological literature as excluding Mexico.

AMERICAN USAGE: as regards vernacular names, see under NAME, ENGLISH.

AMETHYST: *Philodice mitchellii* (for family see HUMMINGBIRD).

AMINO-ACIDS: see ENERGETICS.

AMNION: see DEVELOPMENT, EMBRYONIC.

AMNIOTA: term embracing reptiles, birds, and mammals.

AMNIOTIC CLOSURE: term for the protective sealing of the eyes and ears during the first few days of life in some birds, the function being analogous to that earlier performed for the embryo by the amnion (see GROWTH; YOUNG BIRD).

AMPHIRHINAL: see NARIS.

AMPULLA: term for a vesicle, among other things the dilated end of a semicircular canal in the labyrinth of the ear (see HEARING AND BALANCE).

ANABOLISM: see ENERGETICS.

ANALOGUE: a structure adaptively similar to another but of basically different nature—compare HOMOLOGUE.

ANATIDAE: see under ANSERIFORMES; DUCK. The family comprises birds variously designated as 'ducks', 'geese', and 'swans'; but the application of these primary English names cuts across the taxonomic arrangement. For all, see under DUCK.

ANATOMY: bodily structure; also the science of this. By derivation, the term relates to internal structure as revealed by dissection, as contrasted with external form (see MORPHOLOGY); but the two terms have come to be used almost synonymously. Special branches of anatomy, such as osteology, deal with particular systems of the body; 'histology' refers to the microscopic structure of the tissues; 'morbid anatomy' is diseased structure, or the branch of pathology dealing with this. The structure of birds is dealt with in this work under the names of the systems, organs, and tissues of the body, and under other special heads.

ANCONEAL: pertaining to the elbow; sometime used with reference to the whole dorsal surface of the wing.

ANGEL: see RADAR.

ANGULAR: a paired bone of the lower jaw (see SKULL).

ANHIMAE; ANHIMIDAE: see under ANSERIFORMES; SCREAMER.

ANHINGA: used (America) as vernacular name of *Anhinga anhinga* (see DARTER).

ANHINGIDAE: see under PELECANIFORMES; DARTER.

ANI: substantive name of *Crotophaga* spp. (see CUCKOO).

ANIANIAU: *Loxops parva* (see HAWAIIAN HONEYCREEPER).

ANIMAL KINGDOM: in the perspective of the Animal Kingdom as a whole, the taxonomic position of birds may be defined as: Sub-kingdom Metazoa, Phylum Chordata, Subphylum Vertebrata, Class Aves (see AVES).

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ANISODACTYL: having three toes directed forwards and one (hallux) backwards (see LEG).

ANKLE: the intertarsal joint—sometimes popularly mistaken, in birds, for the knee (see LEG; SKELETON, POST-CRANIAL).

ANKYLOSIS: a stiffening or fixed union of a joint, a natural feature of development in some joints, but also occurring as a pathological condition of joints that are normally movable (see SKELETON, POST-CRANIAL).

ANOMALOGONATAE: see AMBIENS.

ANOMALOPTERYGIDAE: see STRUTHIONIFORMES; MOA.

ANOSMATIC: without olfactory sense (see SMELL).

ANSERANATINAE: see DUCK.

ANSERES: see below.

ANSERIFORMES: an order, alternatively 'Anseres', comprising 2 suborders: Anhimae, Anseres; 2 families: Anhimidae (SCREAMER), Anatidae (DUCK). Although these groups show affinities in their anatomy, they are very different in external appearance and mode of life. Among the most obvious characters common to both are the unspotted eggs and the nidifugous young clad in thick down. In the Anseres (in the subordinal sense) the front 3 toes are connected by a web and the small hind-toe is placed high; in the Anhimae there is only a slight web, and the hind-toe is long and on the same level as the others. In the Anseres the bill and tongue have special characteristics.

ANTAGONISTIC DISPLAY: see DISPLAY.

ANTARCTIC: usually defined as the continent of Antarctica (including the Antarctic Peninsula), its offlying islands, sea ice and surrounding ocean and islands northwards to the Antarctic Convergence, the circumpolar boundary where north-flowing Antarctic surface water sinks beneath warmer, south-flowing sub-Antarctic water.

At the water surface this shows as a zone in which temperature changes by 3°C in half a degree of latitude and whose mean position is usually constant to within 100 km, roughly following the 50°S parallel in the Atlantic and Indian Oceans but lying between 55°S and 62°S in the Pacific Ocean.

Biologically the Antarctic can be divided into several regions. The continental Antarctic region comprises the central high plateau and coastal fringe zones, the latter including Peter I Øya, Scott and Balleny Islands and the east coast of the Antarctic Peninsula south of *c*. 64°S. The maritime Antarctic region includes the west coast of the Antarctic Peninsula and its offshore islands to *c*. 70°S, Bouvetøya and the South Shetland, South Orkney and South Sandwich Islands.

The sub-Antarctic region includes South Georgia and Heard Islands, lying just south and Kerguelen and Macquarie Islands lying just north, of the Convergence. Iles Crozet and the Prince Edward Islands, although further north, are close enough to the Convergence for the sinking cold Antarctic water to upwell against them. Still further north (and not far south of the sub-tropical Convergence, the northern limit of sub-Antarctic surface water) are the temperate oceanic islands of the Tristan da Cunha group (including Gough Island) and St. Paul and Amsterdam Islands; these have much in common with the New Zealand shelf islands (e.g. Auckland, Campbell and Chatham Islands) and the Falkland Islands.

Land climate and vegetation. Of the 14.3 million km^2 surface of the Antarctic Continent most is covered with a thick sheet of glacial ice at a mean elevation of about 2,000 m with peaks rising to 5,140 m. Only about 8,000 km^2 of rock and soil are exposed, mainly on the Antarctic Peninsula and around the edge of the continent. Of this much is either too inhospitable or too far from the sea to be suitable for birds, which principally use rock ledges, rock debris, shingle beaches and fast sea ice for breeding. The continental climate is cold, dry and windy. Temperatures on the continental plateau rarely exceed $-20°C$ in summer and the world's lowest temperature record of $-89.2°C$ was made at an inland site. However, mean annual temperatures at coastal sites range from $-10°C$ to $-12°C$ (summer means $-1°C$ to $-3°C$; winter means $-16°C$ to $-17°C$). Precipitation is virtually all as snow and rarely more than 40 $cm\,yr^{-1}$ on the coast, less inland where some areas are complete deserts. Winds are strong and reach a mean velocity of 72 $km\,hr^{-1}$ on the Adélie Coast with gusts of over 240 $km\,hr^{-1}$.

In the maritime Antarctic region the climate is milder, being cold, wet and windy. Mean temperatures from December to March may be at or just above freezing, precipitation reaches 100 $cm\,yr^{-1}$ and mean wind velocity rarely exceeds 30 $km\,hr^{-1}$. In protected areas at low altitudes a modified feldmark vegetation exists, dominated by mosses and lichens, the former developing, under favourable conditions, into moss peat banks over 1 m deep. Numerous crevices and ledges are available for birds but the ground is unsuitable for burrowing although storm petrels are often abundant in scree and debris slopes. Rocky promontories and beaches provide many breeding sites, especially for penguins.

At the sub-Antarctic islands mean monthly air temperature remains above freezing for at least half the year (annual range $-2°C$ to 8°C). Precipitation is usually between 100–150 cm, mostly as rain in summer, and often as snow in winter, and cloudy, windy weather with frequent mist and low cloud is typical. The Atlantic and Indian Ocean sectors are generally colder than the Pacific at the same latitude, partly due to the eccentric position of the Antarctic Continent. At these islands moss and lichen communities are abundant on higher ground (which rises to 2,900 m at South Georgia) but at lower elevations thick vegetation and often deep, peaty soils provide shelter, nest sites and nest material for both surface and burrow-dwelling birds. The most important vegetation type is tussock grassland, usually dominated by species of *Poa*, which may form a continuous cover to 2 m high. Short grass and rush tundra meadows are frequent on flat land and carpets of large-leaved perennial herbs may occur in sheltered places. Peat bogs, usually with small lakes and ponds, are present. In contrast to more southerly areas where ice abrasion and other factors result in a biologically impoverished intertidal zone, sub-Antarctic islands have a rich intertidal fauna, and luxuriant coastal kelp beds also contribute to tideline debris.

Oceanography. One important feature is the Antarctic Convergence where Antarctic surface and sub-Antarctic intermediate water meet. Below the latter is a southward flowing layer of warm circumpolar deep water. This rises close to the surface not far from the edge of the Antarctic Continent, in the area of the Antarctic Divergence, the boundary between the east flowing currents near the continent and the west flowing currents of the main Antarctic Ocean. This divergence is a major upwelling area and the abundant nutrients brought to the surface there facilitate vast phytoplankton blooms in the austral summer. Although the waters to the south of the Antarctic Convergence are generally considerably richer than temperate waters, and coastal waters exceptionally so, there are areas of the open ocean, especially in the Pacific, that are of low productivity. The key organism nourished in the highly productive regions is krill, a collective term for crustaceans of the genus *Euphausia*, particularly *E. superba*. As the food either directly, or indirectly through many fish and squid, of most Antarctic whales, seals and birds, it is the hub of the Antarctic food web and a vital factor in sustaining the vast animal biomass of the Antarctic Ocean in summer.

Avifauna. The birds are dominated by representatives of those two most marine of all orders, the PENGUINS and PETRELS.

Within the Antarctic zone and at the islands near the Antarctic Convergence the breeding species comprise 7 penguins (Spheniscidae), 6 albatrosses (Diomedeidae), 18 petrels (Procellariidae), 3 storm-petrels (Hydrobatidae), 2 diving petrels (Pelecanoididae), 2 shags *Phalacrocorax*, 2 skuas *Stercorarius*, 2 terns *Sterna*, 1 gull *Larus* and 2 sheathbills *Chionis* plus 4 ducks *Anas* (2 at South Georgia, one each at Kerguelen and Macquarie), a pipit *Anthus antarcticus* (South Georgia only), Starling *Sturnus vulgaris* (self-introduced), Redpoll *Carduelis flammea* and an introduced rail *Gallirallus australis* at Macquarie Island (where another rail *Hypotaenidia macquariensis* and a parakeet *Cyanorhamphus novaezelandiae erythrotis* became extinct by 1894 and 1911 respectively). Farther north at the temperate sub-Antarctic islands a number of other birds occur, principally shearwaters *Puffinus*, other gadfly petrels *Pterodroma* and additional land birds, particularly at the Tristan da Cunha group and the Chatham Islands.

The most important boundaries affecting seabird distribution are the Antarctic Convergence and the northern limit of pack ice. However, as there are relatively few suitable breeding sites for seabirds in Antarctic areas, few species are confined, even in the breeding season, to only one of the resulting circumpolar zones. Thus as a breeding species only the Antarctic Petrel *Thalassoica antarctica* is restricted to the cold Antarctic sub-zone although the Adélie Penguin *Pygoscelis adeliae*, Snow Petrel *Pagodroma nivea*, and particularly the Antarctic Skua *Catharacta maccormicki* and Emperor Penguin *Aptenodytes forsteri* have by far their greatest concentrations here. Only 11 species have been recorded breeding in this zone; the 5 mentioned above, plus Chinstrap Penguin *Pygoscelis antarctica*, Southern Giant Petrel *Macronectes giganteus*, Antarctic Fulmar *Fulmarus glacialoides*, Cape Pigeon *Daption capense*, Antarctic Prion *Pachyptila desolata* and Wilson's Storm Petrel *Oceanites oceanicus*. The maritime Antarctic sub-zone (Antarctic Peninsula and adjacent islands) provides a bridge along which Antarctic and sub-Antarctic species have been able to move on a north-south axis. Chinstrap Penguin and probably Black-bellied Storm Petrel *Fregetta tropica* are at their most abundant here and at some sites 4 penguins, 5 petrels, 2 storm petrels and 2 skuas occur (together with a sheathbill, shag, gull and tern). At the sub-Antarctic islands, in addition to abundant King *Aptenodytes patagonicus*, Gentoo *Pygoscelis papua* and Crested *Eudyptes* spp. Penguins, the well vegetated areas are extensively colonized by large surface-nesting species (albatrosses and giant petrels *Macronectes* spp.) and by many species of burrowing petrels. Iles Crozet has the richest avifauna (34 breeding

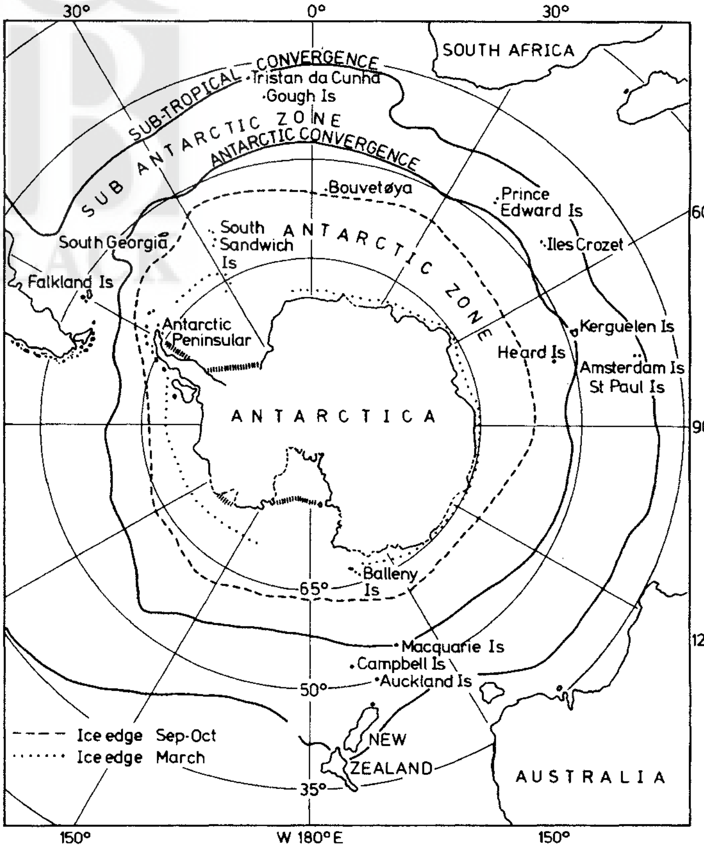

Fig. 1. The Antarctic and Sub-tropical Convergences, and apparent mean position of the ice edge in summer and winter.

species, including 16 burrowing species), followed by Kerguelen (30 species) and South Georgia and the Prince Edward Islands (26 species).

Zonal (i.e. latitude-based) speciation is much more marked than longitudinal (i.e. island-based) differentiation. Thus, except for the large and small forms of Snow Petrel, none of the species of the Antarctic zone shows regional differentiation within this zone. In the sub-Antarctic zone the only clear example is the existence of the Royal Penguin *Eudyptes chrysolophus schlegeli* at Macquarie Island and Macaroni Penguin *E.c. chrysolophus* at the other cold sub-Antarctic islands. However, part of the taxonomic complexity of the prions *Pachyptila* is due to the occurrence of morphometrically distinguishable populations at most breeding sites. In contrast there are distinct races of Rockhopper Penguin *Eudyptes chrysocome moseleyi*, Wandering Albatross *Diomedea exulans dabbenena*, Cape Pigeon *Daption capense australe*, White-chinned Petrel *Procellaria aequinoctialis conspicillata* and Black-bellied Storm Petrel *Fregetta tropica melanoleuca* at the temperate sub-Antarctic sub-zone islands and well-marked (but probably essentially clinal) disjunctions in Gentoo Penguin and Wilson's Storm Petrel farther south. There are also several examples of species which doubtless evolved in adjacent zones and which show largely non-overlapping circumpolar distributions but with varying degrees of coexistence. Thus Sooty *Phoebetria fusca* and Light-mantled Sooty *P. palpebrata* Albatrosses, Yellow-nosed *Diomedea chlororhynchos* and Grey-headed *D. chrysostoma* Albatrosses, Northern *Macronectes halli* and Southern Giant Petrels, Rockhopper and Macaroni Penguins, Thin-billed *Pachyptila belcheri* and Antarctic Prions are all respectively northerly and southerly replacement species, although the penguins and giant petrels co-exist fairly extensively at the cold sub-Antarctic islands. Antarctic and Brown *Stercorarius lonnbergi* Skuas are another 'species pair', with a zone of hybridization in the central Antarctic Peninsula and King *Phalacrocorax albiventer* and Blue-eyed *P. atriceps* Shags are basically zonal taxa which hybridize in southern South America; the status of the Kerguelen Shag *P. verrucosus* is uncertain. The New Zealand sub-Antarctic islands are an important centre of speciation for small albatrosses and crested penguins.

Breeding habitat. Most of the seabirds in the region are basically colonial, except for Light-mantled Sooty Albatross and the skuas, gull, terns and sheathbills, which defend isolated nest territories and, in the case of sheathbills and skuas, often feeding territories in penguin colonies. On the Antarctic Continent and Peninsula the smaller petrels are crevice nesters, larger ones using sheltered ledges, while the penguins often choose very exposed sites (including flat sea-ice by Emperor Penguin) as these are frequently associated with wind-assisted early break-out of pack-ice in summer, thus improving access to breeding sites. At the sub-Antarctic islands the tussock grasslands are used by nearly all species: large albatrosses, giant petrels, and Gentoo Penguins in flatter areas, smaller albatrosses usually on steep slopes and burrowing petrels underground in a wide range of conditions of slope, aspect and general topography. Storm petrels mainly nest in cliff crevices, boulder scree and moss banks and the South Georgia Diving Petrel *Pelecanoides georgicus* only in fine consolidated scree. King Penguins favour flat land usually near glacier moraines, the other penguins utilizing a wide variety of rock and boulder slopes or beaches.

General biology. The breeding biology of most Antarctic birds (see especially PENGUIN, PETREL, SHEATHBILL, SKUA) is basically very similar to that of their more temperate relatives. With the short duration of summer in high latitudes most species show high synchrony of breeding events within populations although this is least true of some inshore feeding species (e.g. Gentoo Penguin, Blue-eyed Shag, Antarctic Tern *Sterna vittata*, some storm petrels). Even so, most larger species, with correspondingly long incubation and fledging periods, commence breeding in early spring and only finish at the end of April, when food stocks are first starting to diminish. Smaller species can be more flexible in their timing and there are several cases of similar species having mutually exclusive chick-raising periods (e.g. Common *Pelecanoides urinatrix* and South Georgia *P. georgicus* Diving Petrels, Blue Petrel *Halobaena caerulea* and Fulmar Prion *Pachyptila crassirostris* as opposed to all other prions, Antarctic and Kerguelen *Sterna virgata* Terns). The fulmarine petrels (e.g. Snow, Antarctic and Cape Petrels, Antarctic Fulmar *Fulmarus glacialoides* and giant petrels) have especially short incubation and fledging periods and this may have been an important factor in determining why most members of this group and not other Procellariidae became successful colonists of the Antarctic Continent. A small number of Antarctic species consistently breed in winter. These are two burrowing petrels of more northerly sites, Great-winged Petrel *Pterodroma macroptera* and Grey Petrel *Procellaria cinerea*, which thus avoid times when their congeners are active, Wandering Albatross, with Royal Albatross *Diomedea epomophora* the only albatrosses with this strategy, and Emperor Penguin. King Penguin chicks, although remaining in the colony over winter, are only fed very occasionally and this species is essentially a summer breeder. The Emperor Penguin, however, raises its chick through the high Antarctic winter, under the most extreme conditions of any bird, and a number of ecological, physiological and behavioural adaptations combine to make this possible. Most other Antarctic seabirds show fewer special adaptations to cope with the rigorous environmental conditions of the region. Like seabirds elsewhere they have thick layers of subdermal fat and these are especially well developed in penguins, which also have a particularly dense covering of overlapping feathers and a highly developed vascular heat exchange system in the flippers and legs. Selection of nest sites that are sheltered but not prone to blockage with snow is often critical.

Climatic factors also strongly influence breeding success, either causing chick loss directly through chilling in very cold weather or indirectly by causing poor feeding conditions for adults or delaying the onset of breeding so that adults feed and chicks fledge at less favourable times. Native predators are of much less importance although locally sheathbills and skuas may be responsible for appreciable losses of eggs and small chicks. Burrowing petrels, however, have been drastically affected on many sub-Antarctic islands by introduced rats (taking eggs and chicks) and on some islands by cats (taking chicks and adults). In many areas, particularly on Macquarie Island (where erosion induced by rabbits is also a problem) and parts of Iles Crozet and Marion Island, burrowing petrels are virtually restricted to offshore predator-free islands. On South Georgia the pipit and South Georgia Pintail *Anas georgica* have been similarly affected by rats in many areas.

For many species the full rigours of the Antarctic climate are avoided by moving north in winter, whether to the pack-ice edge (Adélie Penguin, Snow and Antarctic Petrel) or, like most species, to between the Antarctic and Sub-tropical Convergences, with several species (e.g. giant petrels, Wandering Albatross, Black-browed Albatross *Diomedea melanophris*) reaching at least 35°S, particularly off coastal South America and South Africa and in the Tasman Sea. Juvenile dispersal is wide, and best documented for albatrosses and giant petrels where birds reach low latitudes in all Southern Hemisphere oceans. In many species both immatures and adults probably not infrequently encircle the globe in the zone of the West Wind Drift. A few species are transequatorial migrants: Sooty Shearwater *Puffinus griseus*, Great Shearwater *Puffinus gravis* and Mottled Petrel *Pterodroma inexpectata* all from mainly temperate sub-Antarctic sites, and Wilson's Storm Petrel and also, in the reverse direction, Arctic Tern *Sterna paradisaea* which is a widespread austral summer visitor to the Antarctic Ocean.

Population dynamics. Antarctic seabirds, like those elsewhere, are generally long-lived and delay breeding until several years old. Mean annual survival of breeding adults of Antarctic seabirds so far studied is around 90–95%, the main exceptions so far being diving petrels (70%), and most penguins (70–85%). Young birds clearly sustain high losses in the first year or so of life, but even so 45% of an age group of Wandering Albatrosses survive to 5 years of age. Mean life expectancy is correspondingly high and may reach 10–15 years for smaller petrels and 25 years for albatrosses and giant petrels. Maximum values are uncertain but there are proven field records of 16 year old Adélie Penguins, Wandering Albatrosses over 30 and Snow Petrels over 35 years of age. Most petrels commence to breed from age 4–6 but diving petrels do so from age 2 and Wilson's Storm Petrel from age 3, whereas albatrosses may commence at age 4–9, depending on species and location. Adélie and Emperor Penguins breed from age 3, King Penguins from age 4 but Royal Penguins not until 5.

One interesting feature of some Antarctic seabirds is their inability to breed in a season following that in which they raised a chick. This is not unexpected in King Penguins, Wandering and Royal Albatrosses which take nearly a year (or more) to raise a chick, but also occurs in Grey-headed (but not Black-browed), and both *Phoebetria* albatrosses. In these latter cases it is believed also to relate to the very long chick fledging period, itself probably a result of dietary restrictions.

Diet and feeding ecology. Terrestrial (and/or tideline—especially in winter) invertebrates are important to ducks, sheathbills (particularly Lesser Sheathbills *Chionis minor*), passerines (especially South Georgia Pipit), Southern Black-backed Gull *Larus dominicanus* and Kerguelen

Tern. Giant petrels, sheathbills and skuas scavenge extensively, particularly in penguin colonies; some Antarctic Skuas, however, take fish or krill at sea. The remaining species are exclusively marine and 4 main types of prey are taken; fish (especially Nototheniidae and Myctophidae), squid, krill and other, smaller crustaceans (amphipods, copepods). Fish are eaten extensively by inshore feeders like Gentoo Penguin and shags, the latter frequenting coastal kelp beds where many fish mature, but more pelagic species, like some albatrosses and Blue Petrel, also take much fish. King and Emperor Penguins, many albatrosses, *Procellaria* and *Pterodroma* petrels chiefly eat squid although some Antarctic species are considerably less nutritious than fish or krill. Krill predominates in the diet of most remaining species, especially penguins, and is also taken by many fish- and squid-eating seabirds. Small crustaceans are taken mainly by smaller seabirds e.g. diving petrels, storm petrels and particularly Antarctic Prion which (like the Broad-billed Prions *Pachyptila vittata*) has a broad, deep bill with a comb-like lamella fringing the upper mandible through which water is expelled to filter out small organisms. Apart from such specialized feeding adaptations, most Antarctic seabirds are either pursuit divers (penguins, shags and, near the surface, diving petrels) or surface feeders. This is done either by pattering along the surface like storm petrels, swooping down like gadfly petrels, plunging (chiefly terns) or, like most species, seizing prey while sitting on the surface. Most of the last type of feeding is probably done at night when krill and its associated predators reach the surface. Even for the rich and diverse seabird concentrations at sub-Antarctic islands, differences in diet, feeding technique and foraging range appear to act to reduce direct competition for food in summer, especially between related species. In winter, those that remain in high latitudes are chiefly fish and squid eaters as crustacean prey is greatly reduced in availability.

In terms of biomass and consumption penguins are the dominant Antarctic group with vast Adélie Penguin colonies around the coast of Antarctica, huge Chinstrap Penguin concentrations on the Antarctic Peninsula and adjacent islands and great numbers of crested penguins at the sub-Antarctic islands (there may be 10 million Macaroni Penguins in the South Georgia population alone). As most eat krill, it is not surprising that penguins may account for 75% of food consumed by Antarctic seabirds and in total this may approximate to krill consumption by present day Antarctic whale stocks and be not too far short of that by Antarctic seals; seabirds are thus important predators of the marine resources of Antarctic seas. (B.B.R.) J.P.C.

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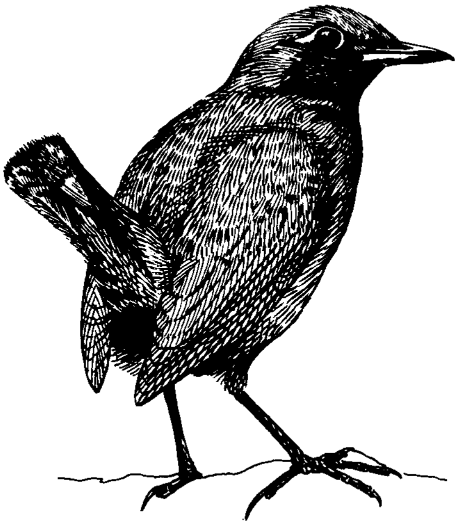
ANTBIRD: substantive name, referring to the habit of following army ants, of some of the 236 species of 53 genera in the large Neotropical family Formicariidae (Passeriformes, suborder Tyranni); in the plural, general name for the family. Species of this family have radiated so as to fill many forest niches, occupied by many different families on other continents. 'Gnateaters' (9 species, 1 genus, sometimes placed in the family Conopophagidae—see GNATEATER) are rotund and short-tailed little birds that hop or cling on or near the forest floor much like small 'antpittas' (38 species, 5 genera). 'Ant-thrushes' (9 species, 2 genera) walk rail-like on or near the forest floor, pounding their lifted tails as they go. Other formicariids, from warbler-like tiny 'antwrens' and small 'antvireos' to hook-beaked large 'antshrikes,' occur from the forest floor to the canopy.

Characteristics. Antbirds vary in size from 8 to 36 cm, the longest and perhaps largest being the 154 g Giant Antshrike *Batara cinerea*. Most have dark red eyes, becoming bright vermilion in 'fire-eyes' (*Pyriglena*). A few have pale or yellow eyes. Bare green, blue or red areas (the last in *Phlegopsis*, the 'bare-eyes') sometimes surround the eye and form giant 'eye-spots', which glow like eyes of huge mammals in the forest undergrowth. One species (*Gymnocichla nudiceps*) has a bare blue crown and forehead as well as face. Colour patterns are frequently striking, being varied combinations of black, brown, rufous, white, or greenish to yellowish. Females are often duller than males, with white or brown replacing black areas; but sexes are usually alike in bare-eyes, ant-thrushes, and antpittas. Nestling fire-eye males are black, females brown; but most small young look like adult females or have a dull plumage. Some young males take on the female plumage for nearly a year.



Black-faced Ant-thrush *Formicarius analis*. (*C.E.T.K.*).

The body plumage is usually loose and sparse, becoming long and silky on the lower back and rump; the forecrown is plush and dense in fire-eyes, while several antbirds have erectile crests and one, the White-plumed Antbird *Pithys albifrons*, a white crest and beard. Many species have concealed white back or shoulder patches, exposed mainly during disputes. The wings are rounded, with 10 primaries, and functional for short flights in dense vegetation rather than for long-distance travel in the open. Tails are short to medium in length, square or rounded, with 12 feathers (8 or 10 in some species). The slender to thick dark bill is often hooked, and is swollen slightly rather than pointed. One 'bushbird' (*Clytoctantes alixi*) has a laterally flattened bill with semicircular lower mandible, used for slitting stems of banana-like plants; another (*Neoctantes niger*) has a similar bill that tears into rotten logs in swamps. Legs and feet are slender or strong, pale or dark, while claws are very sharp and curved in forms that cling crosswise on vertical saplings near the forest floor.

Habitat. Antbirds live mostly in lowland tropical forests, and 30–50 species can be found in many equatorial forests of the Amazon valley. Numbers of species decline greatly as one goes to more open tropical or subtropical environments, or into swamps or up mountains. Antpittas, however, are more diverse in the Andes than in the lowlands. Except when sunning in a ray of sunlight, antbirds almost never leave the shade even when they live in the forest canopy; at midday few will cross a wide road through the forest, and different species or subspecies occur on the opposite banks of some wide rivers in the Amazon Valley. A few (such as *Myrmochanes hemileucus*) occur primarily on species-poor islands in the middle of the Amazon and other large rivers, and fly from one island to another without staying on the nearby shores. Others live only in swampy forest or scrub of the seasonally flooded *varzeas* of the Amazon, and apparently cross rivers readily.

Distribution. Neotropical; antbirds range from north-eastern Mexico to Argentina, but are absent from Chile and from the Antilles other than Trinidad and Tobago. Only two species are restricted to Central America; other species that occur there also occur in South America.

Populations. Some antbirds, such as the Slaty Antshrike *Thamnophilus punctatus* in Panama, occupy a hectare or less per pair. Others are less common, for instance the White-plumed Antbird at 1–2 pairs per km^2 near Manaus in central Brazil. All disappear rapidly when forest or other vegetation is cut, so that certain antbirds of south-eastern Brazil (the Slender Antbird *Rhopornis ardesiaca*, for instance) are threatened with extinction. Probably many other species of antbird will disappear as forests are cut and isolated; some antbird species have already disappeared from one forest reserve, Barro Colorado Island in central Panama.

Movements. Hudson reported that the Rufous-capped Antshrike *Thamnophilus ruficapillus* leaves Argentina in winter, but most species are nonmigratory. Young birds of most species wander locally, while adult birds tend to stay on territories. Young females and females that have lost their mates sometimes wander widely. In many species that follow army ant colonies, pairs have large and overlapping home ranges; White-plumed Antbirds wander 2–3 km or more through forests at Manaus. Often the pair or individual is dominant over neighbours only in the central area of its home range, an area that corresponds to the territory in less vagile related antbirds (ones that need not follow nomadic ants so widely).

Food. Antbirds for the most part capture small insects, spiders, lizards, frogs, and similar animals. Gleaning and short-distance sallies to the lower sides of foliage are common, less often rummaging in dense dead leaves or tossing fallen leaves with swipes of the side of the bill or by picking them up with the bill. Scratching with the feet is not recorded. Giant Antshrikes have been seen attacking small birds in mist nets. Gnateaters occasionally eat small fruit, but fruit-eating is rare in the family. Ants are rarely eaten, except larvae taken when ants flee a nest at the approach of army ants; in this case the adult ants are thrown away and the larvae they carry are retained. Only a few antbirds (notably Cinereous Antshrike *Thamnomanes caesius*) are good flycatchers, but sometimes individuals capture winged ants flying from a nest. Some 28 species regularly follow army ants for prey flushed by them. Many other antbirds, as well as many species in other bird families, occasionally follow army ants. Sometimes an ant-following bird follows domestic pigs or herds of white-lipped peccaries; and one Bicoloured Antbird *Gymnopithys bicolor* came to follow the Costa Rican naturalist Alexander Skutch when he stirred the leaf litter with a stick. The two ant species followed regularly are both 'swarm raiders,' which form wide phalanxes on the forest floor or up tree trunks in lowland Neotropical forest: *Eciton burchelli* and *Labidus praedator*. Swarm raiders flush large numbers of cockroaches, spiders, and other small animals that are snapped up by waiting birds. Typically the ant-following antbirds cling crosswise on slender vertical saplings just above the ants and dart briefly to the ground for prey. Some antbirds, such as hopping Black-crowned Antpittas *Pittasoma michleri* and walking ant-thrushes *Formicarius* spp., wander on the ground on the outskirts of an advancing swarm. The Scale-backed Antbird *Hylophylax poecilinota* of equatorial South America can cling horizontally to vertical thick trunks, a type of perch usually occupied only by ant-following woodcreepers, and hence finds places over ants despite the aggression of larger antbird species.

Behaviour. Most antbirds form pairs that last for life, with rarely a divorce. White-plumed Antbird females, however, rapidly leave mates to care for single young, and find another male so as to start a new nest. Young birds occasionally stay with their parents for some months or years, although none are known to help with later nestings. Clan formation in Ocellated Antbirds *Phaenostictus mcleannani* involves the occasional association of sons and grandsons with a pair, the male offspring bringing back mates from other clans. At times the members of a clan cooperate briefly in attacking intruders from another clan. Antbirds form the centres of many of the mixed-species flocks of insectivorous birds that wander through Neotropical forests. These flocks, unlike the flocks around army ants, do not feed at concentrated food sources. Fifty species or more may be present, including 20–30 species of antbirds. Each species forages differently, some peering in dead curled-up leaves and others in green foliage. Some stay in the canopy, others in the subcanopy, midlevels, lower midlevels, lower levels, or on the ground. Others occupy only dense foliage, such as around vine tangles; and the whole flock is likely to slow down and search intensively in the dense foliage around a light gap where a forest tree has fallen. If a hawk appears, alarm calls from the most alert flycatchers warn even the species that forage inside dense foliage or in dead leaves. Certain flycatching antshrikes (*Thamnomanes* spp.), centres of Amazonian flocks, are extremely alert and noisy and hence are followed by other species, which then flush food for the antshrikes. Regular flock members often have the same territories (but defend only against their own species when meeting a neighbouring flock), roost together, and preen together. Other species join the flocks less readily or wander between one flock and another. Ground and low-level antbirds tend to ignore flocks, apparently depending on protective coloration because they forage too slowly to keep up with birds gleaning through sparser foliage high above the ground.

Antbirds usually scratch the head over the wing. Alarm behaviour often produces upward 'flicking' of the tail or downward 'pounding' of the tail, depending on the species.

Voice. Antbirds have simple songs, mostly resonant series of whistles or chattering notes. Both sexes sing; the female sometimes has a song unlike that of the male. Some, such as the Ferruginous Antbird *Myrmeciza ferruginea*, have pleasant short warbles. The strangest vocalization is that of the White-plumed Antbird, a series of several hundred buzzy *zee* notes given for up to 3 min while performing a wing-waving display. Call notes of antbird species tend to be very varied. There is often a sharp chipping note of alarm, a buzzy rattle or churr at a nuisance (like a human), and a thin whistle at distant hawks. Faint songs and chirps go to mates and young. Snarling and bugling notes, as well as songs and bill-snapping and growls, may accompany aggressive fluffing to show concealed white back, crown, or wing patches at intruders. Whimpering peeps signify subordinate status, commonly associated with hangdog fluffing or wing-quivering submissive display. Young birds peep song-like phrases and squeak when fed.

Breeding. Courtship feeding by the male often precedes copulation; mutual grooming and pair association are regular. (Aggressive displays have at times been incorrectly interpreted as courtship.) Antbird pairs work together at building simple nest cups or oven-shaped nests, the last on the ground by fire-eyes and above the ground by Brown-bellied Antwrens *Myrmotherula gutturalis*. Some nests resemble piles of debris, others are sunk in tree cavities or in the ground at the base of a tree. Ant-thrushes of the genus *Formicarius* lay white eggs deep in cavities of saplings, but most antbird eggs are speckled with brown, purple, or other colours. Blue eggs occur in some antpittas of the genus *Grallaria*, perhaps because such eggs look like the scattered foliage of the montane understorey where most live. Buff ground colour is known in some gnateaters, resembling the brown leaf litter just below their cup nests. Two eggs are the normal clutch, rarely 3; eggs are laid 2 days apart. Incubation, about 14–20 days, is by both sexes during the day and by the female at night. She fluffs out and, with her beak in her back, looks like a tuft of feathers. Eggs are covered most of the day, but White-flanked Antwrens *Myrmotherula axillaris* are off the nest 25–50% of the day despite pair cooperation. Young are brooded and fed by both parents for 9–18 days, and can hop and flutter actively on leaving the nest. Long incubation or brooding spells are the rule, as is infrequent feeding with large insects. Rufous Gnateaters *Conopophaga lineata*, however, feed small insects rapidly. Droppings are eaten or carried off by parents. Long incubation and nestling periods are found mainly in cavity-nesting species, notably the Black-faced Ant-thrush *Formicarius analis* with 20 days incubation and 18 days nestling period. Young Black-faced Ant-thrushes are covered with down at hatching, unlike the naked young of most other antbirds. Injury feigning has been recorded for some species nesting on or near the ground, and for canopy species (*Terenura spodioptila*) when young have fluttered to the ground. If 2 young survive, the male often cares for one and the female for the other. Young depend on their parents for food 1–2 months, then forage with them or wander away. Rufous Gnateater pairs leave corners of their territories for independent young, but young are driven away when they gain adult colour in Bicoloured Antbirds. Several broods may be reared in a season, and because of repeated nest destruction some pairs may nest 6 or more times per year. Breeding seasons of pairs may be short, 3–6 months, in equatorial regions as well as far from the equator; other species in the same areas nest 10 months or so per year. Some species apparently have two breeding seasons per year, while others nest all year or only during rainy seasons. (S.M.) E.O.W.

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ANTCATCHER: obsolete (and misleading—see ANTBIRD) formerly applied to some medium-sized antbirds.

ANT-CHAT: substantive name of *Myrmecocichla* spp. (see THRUSH).

ANTCREEPER: substantive name of some species of Formicariidae, e.g. *Myrmoborus* spp. (see ANTBIRD).

ANTEPISEMATIC: see under EPISEMATIC.

ANTHROPOMORPHISM: denotes, in the biological context, the fallacy of describing or interpreting the actions of animals, other than Man, in terms of human actions and mental processes.

ANTIBODIES: see BLOOD; DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA.

ANTICOELOUS: see ALIMENTARY SYSTEM.

ANTICRYPTIC: see under CRYPTIC.

ANTIGEN: see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA; SEROLOGICAL CHARACTERS.

ANTING: highly specialized, stereotyped behaviour of passerine birds, whereby certain areas of plumage are treated with the defence and other body fluids of worker ants, chiefly of two non-stinging subfamilies, the Formicinae, which squirt formic acid from the tip of the gaster, and the Dolichoderinae, which exude sticky droplets of a repugnatory nature from the anal glands.

Between 200 and 250 species of passerine birds, representing some 40 families or subfamilies, have been recorded using ants, though other insects and invertebrates producing similar fluids may be used occasionally. In addition, and especially in captivity, 'anting' has been observed with a variety of substances, mainly pungent, and in the presence of smoke (see SMOKE-BATHING). True anting has been claimed for a few non-passerines, but such records remain to be substantiated; some may be due to misapprehension of other behaviour (see also COMFORT BEHAVIOUR).

Birds ant mainly in two ways: (1) directly by applying ants in the bill to the feathers ('active anting'); (2) indirectly by permitting ants to invade the plumage ('passive anting'). The direct manner, by far the commoner, is typical of babblers, starlings, tanagers, and weavers (Ploceidae). They apply ants with quivering or stroking movements, characteristically with the wing partly open and lifted out at the side and the spread tail thrust sideways. The ant fluids, often mixed with copious saliva, mainly reach the ventral tips of the primaries and to a lesser extent the head (via the wing) and the undersurface of the tail near the vent. A small minority of species, including certain crows, drongos and New World orioles, practise a more extended form of direct anting, by applying ants to other areas, sometimes with preening actions. The ants are generally used singly but, notably by many starlings and some corvids, may be collected up progressively into a wad; then eaten or discarded afterwards. Birds anting in the indirect manner are mainly larger species of thrushes and crows (Corvidae), but the tiny waxbills and allies (Estrildidae) also do so. While some crows (*Corvus* spp.) will lie spread-eagled among the ants, most indirect anters squat in a special posture with both wings thrust forward in front of the body, allowing the ants to ascend the plumage while discharging their defence fluids. The birds may stir up the insects by repositioning themselves, by shuddering their wings among the ants, e.g. the Jay *Garrulus glandarius*, or even by quivering the tail, e.g. the Red-billed Magpie *Cissa erythrorhyncha*. Many species only use one or other of the two main methods but some also apply ants directly in the bill while anting 'passively', or as in the case of the Jay, the estrildine finches and the Grey Thrush *Turdus cardis*, just go through the motions without actually picking up ants. A few, notably *Turdus* thrushes, e.g. the Blackbird *T. merula*, ant in one way or the other on different occasions. All members of the same family or subfamily may use the same method but some taxa, notably the crows, show great variation even among closely related species.

There is still controversy over the function of anting, but evidence points to it being a form of COMFORT BEHAVIOUR. It may help with feather maintenance, especially of the wings, perhaps to combat feather ectoparasites or remove stale or excess lipids (see DUSTING). Formic acid and anal fluids are insecticidal, and certain organic fluids from ants are essential oils, perhaps supplementing the bird's own preen oil. Preening often follows anting, and some birds also bathe and oil.

Most anting is reported during the period when the post-breeding and juvenile moult occurs, at least in the Northern Hemisphere, but speculation that birds ant to soothe the skin during feather replacement seems ill-founded. The correlation is more likely to be with the weather and seasonal factors that produce the maximum activity of the ants, most records being at swarms of ants, especially those related to the nuptial flights of the royal castes. Theories on the auto-erotic or self-stimulating effects of anting appear to be misguided; nor is anting a means of removing distasteful liquids from the ants before eating them.

Jay *Garrulus glandarius* in 'passive' anting position. (*Photo: Jane Burton*).

See also COMFORT BEHAVIOUR; DUSTING; SUNNING. K.E.L.S.

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ANTIPHONAL SONG: 'duetting' (see VOCALIZATION).

ANTI-PREDATOR REACTIONS: see PARENTAL CARE.

ANTPECKER: substantive name of estrildid *Parmoptila jamesoni* (see ESTRILDID FINCH).

ANTPIPIT: substantive name of the 2 species of *Corythopis*, small and superficially pipit-like birds that forage close to the ground in the Amazonian and other forests east of the Andes in South America. They were formerly placed with the GNATEATERS in a small family, Conopophagidae, but it has recently been shown that gnateaters are specialized members of the ANTBIRD family, while the antpipits are probably aberrant members of the tyrant-flycatcher family (see FLYCATCHER (2)).

ANTPITTA: substantive names of species of *Pittasoma*, *Grallaria*, *Hylopezus*, *Myrmothera* and *Grallaricula* (see ANTBIRD).

ANTRORSE: directed forwards; applied, e.g., to rictal bristles that do not conform with the usual backward direction of plumage elements.

ANTSHRIKE: substantive name of *Taraba major*, *Thamnophilus* spp., *Sakesphorus* spp., and other large antbirds (see ANTBIRD).

ANT-TANAGER: substantive name of *Habia* spp. (see TANAGER).

ANT-THRUSH: substantive name of *Formicarius* and *Chamaeza* spp. (see ANTBIRD); and of *Neocossyphus* spp. (for subfamily see THRUSH); sometimes used also for species of Pittidae (see PITTA).

ANTVIREO: substantive name of *Dysithamnus* spp. and allies (see ANTBIRD).

ANTWREN: substantive name of *Myrmotherula* spp., *Terenura* spp., *Microrhopias quixensis*, and other small antbirds (see ANTBIRD).

ANVIL: stone or hard object used for smashing snail shells.

ANVIL-HEAD: name sometimes used for *Scopus umbretta* (see HAMERKOP).

AORTIC ARCH: see DEVELOPMENT, EMBRYONIC; VASCULAR SYSTEM.

APALIS: generic name used as substantive name of *Apalis* spp. of Africa (for subfamily see WARBLER (1)).

APAPANE: *Himatione sanguinea* (see HAWAIIAN HONEYCREEPER).

APODI; APODIDAE: see below.

APODIFORMES: an order comprising 2 suborders: Apodi, Trochili; 3 families: Hemiprocnidae (CRESTED SWIFT), Apodidae (SWIFT; SWIFTLET), Trochilidae (HUMMINGBIRD). The suborders Apodi and Trochili do not at first sight seem very similar, but in the structure of the wings and the extreme shortness of the legs they are much alike, in both the number of rectrices is 10 (not 12, as in most other birds), and they show similarities of cranial structure which are unlikely to be the result of convergence. Wing movements are very rapid in both groups. Swifts are cosmopolitan, while hummingbirds are exclusively American, with remarkable specific radiation in all altitudinal zones of northern South America.

APONEUROSIS: a flattened tendon for the insertion of a muscle (see MUSCULATURE).

APOSEMATIC: having a protective role—applied particularly to coloration. 'Proaposematic' means that the protection is in the form of a warning (e.g. of unpalatability); 'pseudaposematic' means that the warning is a bluff (protective mimicry); 'synaposematic' means that the warning signal is shared in common with other species. Compare EPISEMATIC; and, in general, see COLORATION, ADAPTIVE; MIMICRY.

APOSTLEBIRD: *Struthidea cinerea* (see under CHOUGH (2)).

APPENDICULAR SKELETON: the part of the skeleton consisting of the pectoral and pelvic girdles and the limbs; contrasted with the AXIAL SKELETON (see SKELETON, POST-CRANIAL).

APPETITIVE BEHAVIOUR: 'the variable introductory phase of an instinctive behaviour pattern or sequence' (Thorpe 1951)—compare CONSUMMATORY ACT (see BEHAVIOUR, HISTORY OF).

APPLIED ORNITHOLOGY: the application of ornithological knowledge to human activities concerned with birds (see especially AVICULTURE; CONSERVATION; DOMESTICATION; FALCONRY; GAMEBIRDS; GUANO; UTILIZATION BY MAN, with cross-references thereunder).

APTERIUM (plural APTERIA): an area of skin bare of contour feathers, lying between pterylae. Apteria may be feathered with semiplumes, down or powderdown (see PTERYLOSIS).

APTERYGES; APTERYGIDAE: see STRUTHIONIFORMES; KIWI.

AQUATIC HABIT: for adaptations to this see SWIMMING AND DIVING; SKULL; VISION.

AQUINTOCUBITALISM: or 'diastataxis' (see WING).

ARAÇARI: substantive name of *Pteroglossus* spp. (see TOUCAN).

ARAMIDAE: see under GRUIFORMES; LIMPKIN.

ARCHAEOPTERYX: *Archaeopteryx lithographica* von Meyer—the earliest known fossil bird. It is represented by five partial skeletons with feather impressions and one isolated feather:

1. Described by von Meyer in 1861, the feather is presently housed in two museums. The main specimen or slab which may include some mineralized tissues is at the Munich Museum while the counterslab is in the Museum fur Naturkunde in Berlin. According to Brodkorb (1963) this feather is the holotype for the species, but most later workers accept the London specimen as the holotype (Ostrom, 1976). The feather was found in the communal quarry at Solnhofen, Bavaria, West Germany.

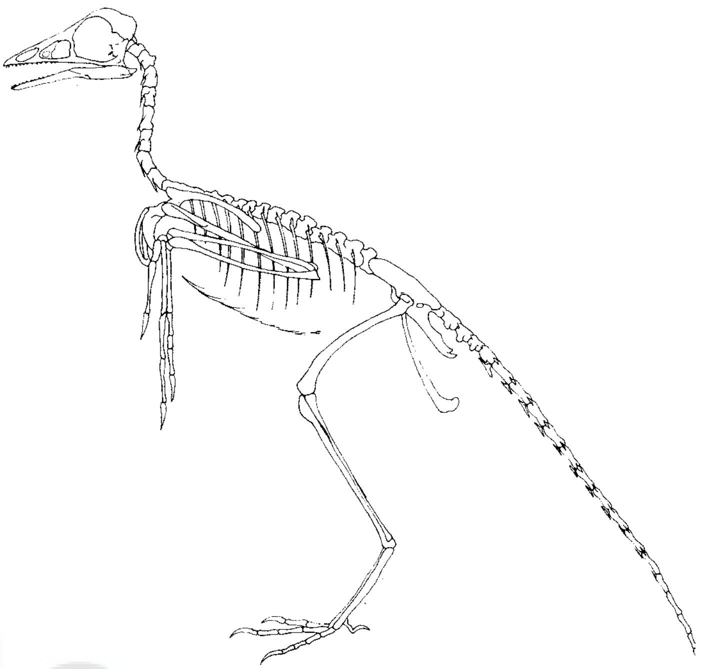

Fig. 1. Restoration of the skeleton of *Archaeopteryx* (approximately 1/3 size).

2. The London specimen was found in 1861 in the Ottmann quarry near Solnhofen. This was the first skeleton to be described in detail and its discovery lent considerable support to the then recently proposed theory of evolution. It is presently housed in the British Museum (Natural History).

3. The Berlin specimen was discovered in 1877 in the Durr quarry at Wegscheidt near Eichstatt. This is the specimen upon which Heilmann made most of his observations for his famous book on the origin of birds. It is in the Museum für Naturkunde in Berlin.

4. The Maxburg specimen was found in 1956 in the Opitsch quarry near Solnhofen. This specimen is presently in private hands although there are casts of it in the Senckenberg Museum in Frankfurt and the Solnhofen Museum in Maxburg near Solnhofen.

5. The Haarlem specimen was first recognized as an *Archaeopteryx* by Ostrom in 1970. It had been described by von Meyer in 1857 as a pterosaur, *Pterodactylus crassipes*. Ostrom (1972) proposed that *Archaeopteryx crassipes* be suppressed by the International Committee on Zoological Nomenclature. It is housed in the Tyler Museum in the Netherlands.

6. The Eichstatt specimen was found in 1951 in a small quarry near Workersaell a few miles north of Eichstatt. It was originally thought to be a small dinosaur, *Compsognathus*, but in 1973 F.X. Mayr announced that it was an *Archaeopteryx*. It was later monographed by Wellnhofer (1974) and has the distinction of being the most thoroughly described of any *Archaeopteryx* specimen.

The assignment of an isolated feather from an upper Jurassic lithographic limestone near Santa Maria de Meya, Sierra de Montsech, Lerida, Spain, to *Archaeopteryx* is extremely tentative. In reality it only demonstrates the presence in Spain of Jurassic birds, and of course the potential that a skeleton will one day be found in these same beds. The only other reasonable case that has been made for a Jurassic bird other than the German *Archaeopteryx* specimens is *Laopteryx* from the Late Jurassic Morrison Formation of the United States. Recent study of the only known specimen (a partial cranium) of *Laopteryx* demonstrates that it is a pterosaur.

Plumage. *Archaeopteryx* is the oldest and most primitive known bird, and provides us with our best evidence concerning the origin of birds and the evolution of avian structures. Perhaps the most interesting features preserved are the feather impressions. These show that *Archaeopteryx* had feathers of an essentially modern type composed of a quill supporting a system of vanes, rachi and barbs. Barbules and hamuli also seem to be present although the best evidence for the latter is the even arrangement of the barbs on the specimens. The next oldest fossil feathers were described by Schlee from Lower Cretaceous (Neocomian) amber of the Lebanon Mountains. These feathers clearly show the presence of barbules and hamuli. Taken as a whole the fossil record shows that the microstructure of the feathers was one of the earliest avian features to evolve fully. The feathers of *Archaeopteryx* are also divided into rectrices and remiges as in modern birds and the remiges have the anterior vanes narrower than the posterior vanes. This relationship is characteristic of modern flying birds where it helps to form the airfoil. Feduccia and Tordoff (1979) have argued persuasively that these asymmetrical feathers indicate that *Archaeopteryx* had some aerodynamic capabilities. The flight feathers are divided into primaries and secondaries. Coverts are also present and the whole plumage has a very modern aspect. Contour feathers are present on the legs of the Berlin specimen, but there is no evidence of horny structures or scales. This is especially surprising as well preserved metatarsal scutes have been found with at least two specimens of Mesozoic marine hesperornithiforms.

Skeleton. Our knowledge of the skull was greatly enhanced by the discovery of the Eichstatt specimen. Both it and the Berlin skull share a pointed snout with the external nares bordered primarily by the premaxillary bones. Just behind the nares is a large triangular antorbital fenestra containing a nasal septum perforated by large holes. According to Wellnhofer (1974) a separate lacrimal and prefrontal are present. The orbits are very large and contain well-developed sclerotic rings. The quadratojugal and the jugal have dorsal extensions bracing against the quadrate. The postorbital does not appear to be present. The squamosal is either very small or lost altogether. Its reduction is a derived character for *Archaeopteryx*. The skull does not seem to be mesokinetic as suggested by Bock (1964), nor was it prokinetic or rhynchokinetic. The snout was probably not covered by a horny bill, as teeth are found on the premaxillary (4 teeth), maxilla (9) and dentary (11). These counts are based on the Eichstatt skull which has the clearest preservation. The teeth have sharp-pointed, posteriorly directed, flattened crowns separated from the expanded root by a constricted neck. Similar teeth have been described from other Mesozoic toothed birds by Martin, Stewart and Whetstone (1980) who also point out that this type of tooth is found in crocodilians.

The palate is best observed in the Eichstatt specimen, but even in that specimen it is impossible to determine its detailed structure. Previous statements that it was schizognathous (neognathous) are based on the Berlin specimen and are unfounded. Although it appears to have had a very open palate with long narrow palatines like *Hesperornis*, the identity of the palatal bones must remain in doubt until a new specimen is recovered or the Eichstatt specimen is further prepared.

The London specimen preserves a relatively undistorted braincase with an endocranial cast and this, along with the shape of the braincase of the Eichstatt specimen, gives a good approximation of the shape and relative size of the lobes of the brain. The brain was small, but bird-like in its general shape and proportions.

The lower jaw is slender and has an anterior, downward bend. It does not appear to have had a mandibular fenestra and resembles *Ichthyornis* and the Hesperornithiformes in that respect. It also does not appear to have had an intramandibular joint, a feature found in *Ichthyornis* and the Hesperornithiformes.

Archaeopteryx does have a large retroarticular process which in lateral aspect resembles the type found in *Hesperonis* and crocodilians.

The Eichstatt specimen provides the clearest vertebral count and in this specimen Wellnhofer counted 9 cervical vertebrae, 14 dorsal vertebrae, 5 sacral vertebrae and 22 caudal vertebrae. The dorsal and caudal vertebrae are amphicoelous or platycoelous. The cervical vertebrae bear long cervical ribs and some of the dorsal vertebrae have slight pleurocoels. The caudal vertebrae are elongate and no pygostyle is present. Instead each caudal vertebra bears a pair of large feathers similar to the remiges on the wing. The caudal vertebrae have long pre- and post-zygapophyses and are tied together ventrally by broad intercentra. The tail itself was not flexible and tended to move as a unit.

The 7 cervical vertebrae posterior to the axis all bear cervical ribs. There are 13 thoracic ribs. They are double headed and do not attach to ossified sternal ribs nor do they bear ossified uncinate processes. According to de Beer about 12 pairs of abdominal ribs (gastralia) are present. The gastralia continue anteriorly almost to the coracoids, leaving little space for a sternum. This, coupled with the fact that no sternum is preserved in any of the specimens (radiographs recently made by Whetstone indicate that the supposed sternum of the London specimen is really some 3 vertebral centra), demonstrates that *Archaeopteryx* differs from any other known bird in lacking an ossified sternum.

The shoulder girdle of *Archaeopteryx* is also unique in having large, broad coracoids which must have almost met on the midline of the chest, forming with the huge furcula a sort of surrogate sternum. The role of the furcula in providing a site for the origin of flight muscles has been discussed by Olson and Feduccia (1979) who show that the absence of an ossified sternum does not preclude the possibility of flight for *Archaeopteryx*.

The scapulae are narrow and lie almost flat above the ribs and near the transverse processes of the vertebrae, unlike the scapulae of the coelurosaurian dinosaurs which lie more on the side of the chest. The scapulae are fused to the coracoids and tie the shoulder girdle tightly to the axial skeleton.

The furcula is relatively larger and more massive than in any other known bird. It appears to have attached to the coracoids at the site of the 'biceps tubercle.'

The humerus has a large, elongate deltoid crest and 2 distal condyles. It is slightly longer than the ulna. The ulna is slightly longer than the radius because of its low, blunt olecranon process.

The carpus shows at least 3 carpal bones. The most important of these is a large lunate carpal thought to be composed of the fused distal carpals 1 and 2. In modern birds this carpal bone forms the trochlea carpalis. The 3 metacarpal bones which form the rest of the carpometacarpus in modern birds are unfused in *Archaeopteryx*. The digits contain a full complement of unreduced phalanges. Ostrom counts the digits present as I (2 phalanges), II (3 phalanges) and III (4 phalanges). This would suggest that the digits present in modern birds are I–III (contrary to most embryological interpretations). The penultimate phalanges of the digits are elongate as they are in theropod dinosaurs. The terminal phalanges form large claws with long, sharp horny sheaths.

The pelvic girdle is best studied on the London and Berlin specimens. The ilium is fairly large and elongate anterior to the acetabulum but is short and pointed posterior to it. The ischium is recurved posteriorly and much shorter than the pubis. It curves ventrally and may have met the ischium on the other side to form an ischial symphysis similar to the long pubic symphysis. The acetabulum is partially closed and resembles *Hesperornis* and *Ichthyornis* in this respect rather than modern birds, which have the acetabulum completely open.

Although Ostrom (1976) has published a new restoration of the pelvis of *Archaeopteryx* showing the pubis directed downwards, the London and Berlin specimens leave little doubt that it was directed posteriorly as in all other known birds (opisthopubic).

The femur is relatively long and slender. It has a shallow anterior curve and resembles galliforms in this respect. It has a small lesser trochanter separated from the greater trochanter by a groove. The tibia is a long, straight bone with only a very slight cnemial crest. It is bounded laterally by a long and very slender fibula which terminates distally in an expansion flattened against the lateral border of the tibia. The fibula does not contact the tarsal joint as it does in reptiles. The distal end of the tibia bears two condyles composed, as in modern birds, of the proximal tarsal bones which fuse on to the tibia. The medial condyle and most of the intercondylar articulation is composed of the astragalus and the lateral condyle is made up of the calcaneum. There is a long triangular bone (pretibial bone) above the calcaneum which fuses with the calcaneum and the astragalus. The pretibial bone is found in all other birds but not in reptiles.

The metatarsals are fused proximally but it is difficult to determine whether the distal tarsals are fused to form a real tarsometatarsus. A short, slender metatarsal V is described for the Eichstatt specimen but it did not bear any phalanges. The trochleae are somewhat arched on the distal end and the hallux is directed posteriorly. The digits resemble those of modern birds and the claws are long, sharp, and recurved.

The invasion of the skeleton by the air sac system seems to have occurred relatively late in avian evolution. The postcranial skeletons of *Archaeopteryx*, *Hesperornis*, and *Ichthyornis* are all nonpneumatic.

Mode of life. *Archaeopteryx* was a small predator which probably caught insects and small vertebrates like lizards. Whether it was terrestrial or arboreal has recently become the subject of controversy. The presence of an opposable hallux which would enable the foot to grasp small branches and the relatively sharp claws on the hind toes suggest arboreality, while the curved femur and bipedal stance might suggest a terrestrial mode of life. The presence of a fused tarsometatarsus could be used to support either argument. The clawed digits on the wings might have been used for prey capture or they might have been used to climb trees and manipulate food. In some respects they resemble pterosaurian claws, which are generally accepted as being for climbing.

Ostrom (1979) has argued that *Archaeopteryx* was a terrestrial, cursorial predator which may have had limited powers of flight, but was derived from a flightless ancestor that used its remiges as an insect net. He proposes that the forelimbs were clapped together in advance of the running bird in order to catch flying insects. This is an extension of the cursorial origin of bird flight expounded by Nopsca, and has some serious flaws. Even if one ignores the wear and tear to which such a prey capture mechanism would subject the feathers, it is difficult to see how such a predator could capture prey without creating a gust of air which would drive the prey from its grasp. It also seems unlikely that enough ground speed could be attained to provide the impetus for the early, poorly adapted, phases of powered flight.

Most workers accept some real flight capacity for *Archaeopteryx*, although all would agree that it must have been a relatively weak flyer. The small size of the brain suggests a relatively poor quality of sensory-motor coordination for flight, but probably adequate for a weak flyer traversing short distances. The brain of *Ichthyornis* is also comparatively primitive, but no one doubts that *Ichthyornis* was a good flyer. The long tail contains many free vertebrae but these are locked together so that they function as a unit. The tail itself is so designed that it must have provided some lift. In this case, the absence of a pygostyle would not preclude active, powered flight although some lack of manoeuvrability would be expected.

Origin of birds. Ostrom has argued that *Archaeopteryx* provides the best evidence concerning the origin of birds and he is correct as far as the evidence goes. However, some aspects of the anatomy of *Archaeopteryx* are not available for comparison (for instance the basicranial and otic regions of the skull) and in those areas we must rely on other Mesozoic birds or modern birds.

Archaeopteryx shows a mosaic of reptilian and avian features. Among the avian features are:

1. The presence and structure of the feathers.
2. The differentiation of the remiges into primaries and secondaries.
3. The angle between the scapula and the coracoid.
4. The fusion of the clavicles into a furcula.
5. The opisthopubic pubes.
6. The presence of a pretibial bone on the tibiotarsus.
7. The fusion of the metatarsals and probably the distal tarsals to form a tarsometatarsus.
8. The opposable hallux in the foot.

The reptilian features include:

1. Teeth on the premaxillary, maxillary and dentary. These teeth are unserrated, have a flattened triangular crown, and are separated from the expanded bony base by a distinct waist. In all of these features they resemble the teeth of crocodilians.
2. The amphicoelous or opisthocoelous articulations between the vertebral centra. All living birds have heterocoelous vertebrae at least in the anterior thoracic and cervical region.
3. The short sacral region.
4. The long tail with 20–23 free vertebrae and no pygostyle.
5. Simple unjointed ribs lacking ossified uncinate processes.
6. The presence of gastralia.
7. The absence of an ossified sternum.
8. The absence of a fused carpometacarpus.
9. The presence of clawed digits on the hand. The front foot has a lunate carpal bone and elongated penultimate digits much like the condition in theropod dinosaurs.
10. Relatively simple brain with large olfactory lobes.

Relationship of *Archaeopteryx* to modern birds. *Archaeopteryx* is maintained in a separate subclass, the Sauriurae, by Brodkorb (1963). This subclass seems to be supported by a wide variety of derived characters which include: (1) the reduction or loss of the squamosal; (2) the fusion of the proximal but not the distal ends of the metatarsals, and the fusion of the proximal metatarsals in a row rather than having the proximal end of metatarsal III posterior to the proximal ends of metatarsals II and IV, as in modern birds. These features suggest that *Archaeopteryx* was not the direct ancestor of modern birds but was on a side branch of avian evolution. There must be undiscovered birds contemporary with *Archaeopteryx* that more closely resemble modern birds, and *Archaeopteryx* cannot be utilized as the sole model for avian origins.

See also EARLY EVOLUTION OF BIRDS; FOSSIL BIRDS.

(G. de B.) L.D.M.

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ARCHAEORNITHES: a subclass (see under CLASS; also ARCHAEOPTERYX; FOSSIL BIRDS).

ARCTIC: unlike the Antarctic, does not represent a separate zoogeographical area but rather the northern extremities of the Palearctic and Nearctic Regions (together Holarctic). See DISTRIBUTION, GEOGRAPHICAL; NEARCTIC REGION; OCEANIC BIRDS; PALEARCTIC REGION.

ARCTOGAEA: a grouping by T.H. Huxley (1868) of the classical zoogeographical regions that excludes only the Neotropical and Australasian Regions, which he called 'Neogaea' and 'Notogaea' respectively; Arctogaea has more recently been termed 'Megagea' (see DISTRIBUTION, GEOGRAPHICAL).

ARDEAE; ARDEIDAE: see under CICONIIFORMES. For the purposes of this work, *Cochlearius* is included in the Ardeidae, although by some regarded as constituting a separate monotypic family. There are 2 subfamilies, Ardeinae (see HERON), and Botaurinae (see BITTERN).

ARENA DISPLAY: see LEK.

ARGUS: substantive name, alternatively 'argus pheasant', of the Great Argus *Argusianus argus* and the Crested Argus *Rheinardia ocellata* (see PHEASANT).

ARRANGEMENT: in taxonomy, the process (and its result) of placing the items of a category, i.e. the taxa of next lower rank, in some sequence or pattern. In any work in which birds have to be systematically listed, there arises not only the matter of assigning them to their appropriate taxa but also the question of arranging the items within a taxon—it may be species within a genus (or subgenus, if any), or genera within a family (or subfamily or tribe), or the like. Subspecies are commonly arranged, within the species, on some geographical basis; this is reasonable, as subspecies are in fact geographical forms and by definition allopatric. At other levels there is a convention that the items are arranged in a 'natural' sequence, which is supposed to keep together those that are most closely related; and the more 'primitive' (according to belief) are placed first. The objection to this, strongly voiced by some taxonomists, is that the information necessary for confidently making such an arrangement seldom exists; and that, if it did, the facts could often not be adequately expressed in any linear sequence. On this view, the so-called 'natural' arrangement is apt to be misleading; and unless the reasons are fully stated, which often is not the case, the basis cannot be critically examined and the practice is therefore devoid of scientific value. The alternative course—frankly admitting ignorance—is to arrange the items within each taxon alphabetically; this is already followed by taxonomists dealing with certain other classes of animals and has obvious convenience for the reader where the number of items is considerable. Those who advocate this procedure suggest that it remains possible to indicate views about relationships by the use of symbols. Alphabetical arrangements have not, however, been widely used by ornithologists, who generally prefer to attempt an arrangement which reflects evolutionary relationships; but they have been used to advantage in world lists of species where quick and easy reference is the primary aim.

ARRESTED MOULT: interruption of moult within a tract of feathers, usually the primaries or other flight feathers. At the time of interruption, growing feathers continue to grow to their normal length, but the next in sequence to be moulted is (are) retained until a later date. When moult recommences, it usually does so from the first retained feathers (a phenomenon sometimes separately termed 'suspended' moult) but occasionally from the original moult focus or even from a new focus in that feather tract. Moult may be arrested to allow migration or breeding at an appropriate date.

ARROWSNAKE: see BIBLE, BIRDS OF THE.

ARTAMIDAE: a family of PASSERIFORMES, suborder Oscines; WOODSWALLOW.

ART, BIRDS IN: bird subjects that have from the very earliest times featured in man's artistic efforts. Amongst the pictures which have survived through the ages not the least interesting are those painted by the ancient Egyptians; birds were thought to be 'winged souls' and some species were assigned to particular gods, a hawk being the emblem of Horus, and Thoth (god of learning) being represented by the Sacred Ibis, to quote two examples. The discovery at Hermopolis of a great number of mummified ibises, with their likenesses painted on their wrappings, seems to denote that this species was the object of a cult. The belief that a soul should not go unattended to the next life is accountable for the interesting pictures found on the walls and sarcophagi of excavated tombs. Originally food, chattels, and slaves were buried with the deceased, but later this practice gave way to pictorial records of the dead man's life and everything connected therewith. Some fascinating examples of these early Egyptian bird paintings are to be seen in the British Museum; ducks swimming in a pond, geese feeding, and—of greater interest still—a study of fowlers surrounded by a variety of birds in flight. Birds were also popular with the artists of ancient Greece, who introduced them into their still-life paintings of fruit and flowers in much the same way as did the Dutch painters many centuries later. Examples of bird studies by Greek artists were brought to light in the excavations of Pompeii and Herculaneum.

Passing from ancient times to the Middle Ages, those who have looked closely at illuminated manuscripts will have noticed how often brilliant tiny bird forms were used in decorating the elaborate borders of psalters and breviaries. At first these were inclined to be somewhat linear and frequently fabulous representations; but in the 13th century nature came to be studied more closely, with the result that the pictures gained realism and animation. In the middle of the century the Emperor Frederick II wrote his treatise on falconry, *De Arte Venandi cum Avibus* (now in the Vatican), with very carefully executed marginal illustrations of hawking scenes and bird life. Another example of this type of illustration is in the British Museum (Add. MSS. 27695, 28 841); it consists of fragments of a Latin 'Treatise of the Vices' written by one of the Cocharelli family of Genoa towards the end of the 14th century, and the characteristics of the birds which appear in this manuscript, their postures, movements, and flight denote a remarkably keen study of avian life. Another document of great interest is the sketchbook of a 14th century monk in the Pepys Library at Magdalene College, Cambridge; this contains several pages devoted to coloured studies of birds, the majority of which are identifiable.

With the Renaissance came a break with tradition, and art ceased to be controlled by the Church. Painters expressed themselves more freely and with greater imagination, and all forms of nature received their closer attention. Giotto was one of the first to adopt naturalism in art, and at Assisi is still preserved amongst his frescoes the touching scene of a group of small birds listening attentively to St Francis preaching, whilst a late-comer flutters down to join the congregation. From the 14th century onwards, birds appeared frequently in the works of the great masters, sometimes in a symbolic role or in some mythological composition, sometimes as pets in portrait studies or as colourful details in landscapes. Since many birds appear in pictures in the National Gallery in London, it is proposed to refer to a few of these pictures with an explanation of their particular significance in each instance.

Those well acquainted with religious paintings may have noticed how often the Goldfinch is depicted. On account of its preference for thistles it was adopted by the Church to symbolize the Passion of Christ, and in the National Gallery it is several times represented. Baroccio in his 'Holy Family' (No. 29) places the bird in the hand of St John, who holds it high out of reach of an interested cat; whilst in Benozzo's altarpiece (No. 283) a Goldfinch has settled at the Madonna's feet in company with a Great Tit, the latter having no particular significance so far as is known. In Cima's 'Madonna and Child' (No. 634) a Goldfinch flutters in the hand of the Christ Child. Crivelli made two very different studies of this bird (Nos. 668, 788); in both pictures the usually gay little creature sits dejectedly on a leafless branch with its back turned on the spectator. A whole 'charm' of Goldfinches captured by the brush of Rubens is to be seen fluttering in a thicket in his famous landscape 'Chateau de Steen' (No. 66).

The Peacock graces many a Nativity and Annunciation, and in his wonderful painting of the latter scene (No. 739) Crivelli has shown to the full the grace and dignity of this bird, the symbol of Immortality owing to the legend that its flesh does not decay. Botticelli introduces it into his 'Adoration of the Magi' (No. 1033). The Peacock is perhaps best known as representing Pride and Vanity; and in classical mythology it is assigned to the goddess Juno, whom it accompanies in Rubens's 'Judgment of Paris' (No. 194) and is shown having an altercation with Paris's dog. In the same picture figures Minerva's owl, here symbolizing the wisdom of its mistress, although in the Christian Church it was sometimes adopted as a Satanic symbol due to its preference for darkness and horror of the light. As a symbol of wisdom, an owl is sometimes shown with St Jerome, as in the picture by Tura (No. 773).

That such a pleasant creature and charming songster as the Blackbird should be connected with the Prince of Darkness seems hard indeed but, in the eyes of the early Church, apparently the bird's very charms were sufficient to merit such an association. The dove, besides representing the Holy Ghost, also stood for Purity and Peace and is often shown with the Blessed Virgin, especially in scenes of the Purification, it being customary on such an occasion to make an offering of a pair of Turtle Doves in the Temple. A Turtle Dove can be seen in Crivelli's 'Annunciation' to which reference has already been made. In mythology the dove is attributed to Venus. The Partridge, chosen to signify Truth, was also curiously enough sometimes symbolic of the Devil. Two of Catena's pictures include it (Nos. 234, 694), and in Antonello's 'St Jerome' (No. 1418) a Partridge and a Peacock are in the foreground with their backs turned to each other, which possibly indicates that here they represent Truth and Vanity respectively. In Crivelli's 'Madonna and Child' (No. 724), perched high on the ornate throne is a Swallow, placed there as the symbol of the Incarnation. Scenes of the Annunciation also show this bird, which was connected too with the Resurrection owing to a belief that in winter it hibernated in the mud to emerge again at springtime to herald the reblossoming of nature.

The domestic cock, associated with St Peter, denotes watchfulness and vigilance because of its early rising. It was also the emblem of St Vitus of Bohemia, under whose patronage come actors, dancers, and those who find difficulty in rising in the morning. Another bird denoting vigilance is the Crane. According to a legend the King of the Cranes was guarded each night by sentries standing on one foot with a stone in the other. If sleep overcame them the stone was supposed to drop on the other foot and awaken them.

The Eagle symbolized the Resurrection and also became the emblem of St John the Evangelist, and thus formed an appropriate support for the base of lecterns in churches, a fine contemporary example by Elizabeth Frink being in Coventry Cathedral, England. In Mantegna's 'Agony in the Garden' (No. 1417) a Golden Eagle, which has been referred to as the 'Bird of Fate', occupies a prominent place in the picture. It is also to be seen in greater detail in the painting ascribed to Damiano Mazza (No. 32) showing the bird carrying off Ganymede to Olympus. A very much finer eagle painting is contained in the picture by Rubens of 'Prometheus

Bound'. In this, as in others where birds or other animals were concerned, Rubens collaborated with Frans Snyders. The painting is now in Philadelphia, but Snyders's remarkable sketch for it can be seen in the British Museum. The story of Jupiter's attentions to Leda, in the guise of a swan, captured the imagination of more than one painter. The National Gallery picture after Michelangelo (No. 1868) shows the most intimate phase of the liaison between the god and his mortal mistress, whilst Leonardo da Vinci in his treatment of the subject (Galleria Borghese, Rome, and other versions elsewhere) depicts the couple standing happily side by side whilst their offspring hatch out of egg-shells in the background.

So far, reference has been made to the birds which appear in the paintings of the Italian school and chiefly those of a religious nature; but mention must be made of one of the great masters of the Early Netherlandish school, Hieronymus Bosch. His painting 'The Garden of Delights' in the Prado is remarkable for the extent to which the artist relied on avian symbols to convey a sense of the paranormal. Birds abound in the painting, ranging from an evil and foreboding owl to the myriads of swallows which fly in serpentine curves through the skull-like rocks. Later Dutch artists of the 17th century treated birds in a more straightforward manner, not a few of them specializing in this branch of painting. Whilst their still-life pictures very often contained a profusion of dead game-birds of every kind, the studies of live birds are very much more interesting; there are some very fine examples in the Wallace Collection (London). One painting there, by d'Hondecoeter, shows a domestic rooster and a Peacock stepping out side by side through a farm-yard with all the dash and swagger of Regency dandies. A coloured drawing by the same artist, in the British Museum, portrays the same two species engaged in a fight, with smaller fowls fluttering round them.

The Wallace Collection also has paintings of Peacocks, and of macaws and other birds of the parrot family, by Jan Weenix, a cousin of d'Hondecoeter; and there are studies of hawks by Joannes van Noord, and of Pheasants and other game-birds by Desportes. The French painter Oudry is well represented in this collection by some very fine action pictures such as 'A Fox in a Farmyard', 'Hawk attacking Partridges', 'Hawk attacking Wild Duck', and 'Wild Duck aroused'. Another 17th century bird painter of note was Jakob Bogdany, of Hungarian origin, who was employed by William III to decorate the royal palaces. He specialized in exotic fowls, which are to be seen in the large collection of his works at Kew Palace and Hampton Court.

While John White (fl. 1577–1590), who recorded the birds of Virginia and Florida on a voyage made with Sir Walter Raleigh, can claim to be the first British bird artist, his drawings in the British Museum are not widely known. Far more famous was Francis Barlow, a native of Lincolnshire, who specialized in sporting pictures and painted birds with great spirit and accuracy. The owners of large country houses were so taken with his work that they employed him to decorate their ceilings. His pictures are mostly in private collections, but his 'Owl being Mocked by Small Birds' may be seen at Ham House (London). At the British Museum, besides a drawing of an eagle carrying off a duckling, there is a large collection of his illustrations for Aesop's Fables (published 1666), quite a number of which are bird pictures. There are also water-colours by Barlow at the Victoria and Albert Museum, and the Marquess of Bath's collection at Longleat contains striking portraits of a Cassowary and an Ostrich.

The 18th century, the age of rococo, saw the great flowering of the decorative arts in Europe, which entailed much use of avian forms. Among the first productions of the Meissen porcelain manufactury, by the great modellers Johann Gottlob Kirchner and Johann Joachim Kaendler, were the large white figures of birds—vultures, swans, cocks, peacocks and pelicans, modelled from living specimens in the private menagerie of Augustus the Strong. The Meissen example was to be followed by virtually all the later porcelain factories, and the use of George Edwards' illustrations of birds by the painters and modellers of the Chelsea porcelain factory is but one example. Another important decorative innovation in the 18th century was the importation of wallpapers from China, which featured prominently the gay plumage of peacocks, Mallards and other wildfowl. These were the first Oriental pictorial depictions of birds to arrive in Europe.

The productions of sporting painting, that peculiarly English genre of the 18th and early 19th century, have perhaps few appeals for the contemporary bird-lover, for they consist of depictions of snipe and game shooting by George Morland, Samuel Howitt and James Pollard, and cock fighting scenes by Thomas Rowlandson and George Morland. One of the finest paintings of the latter sport was executed in India by Johann Zoffany, his 'Captain Mordaunt's Cock Fight' (private collection). The great anatomist George Stubbs never completed his detailed comparative studies of 'The Tiger, the Human Female and the Common Fowl', (Worcester Public Library, Massachusetts).

Although romantic poetry is suffused with avian imagery as the appropriate symbol of freedom, romantic painting provides us with surprisingly few pictures depicting birds, with the exception of some magical evocations by J.M.W. Turner in the Tate Gallery and at Petworth House, Sussex, of ducks landing and taking flight, and a powerful painting by James Ward of 'The Ascent of the Swan' in a private collection, a beautiful drawing for which is also in the Tate. The Victorian master of animal painting, Sir Edwin Landseer, also portrayed birds extremely well, notably the 'Golden Eagle and its Nest' in the Victoria and Albert Museum, and the maternal affection of the hen for its chicks which can be seen in 'The Drover's Departure' in the same collection. The great champion of the Pre-Raphaelite School's doctrines of fidelity to nature, John Ruskin, himself produced a number of studies of birds of the utmost virtuosity, notably an exquisite Kingfisher in the Ashmolean Museum, Oxford. In more humorous vein, the Royal Academician Henry Stacy Marks specialized in anthropomorphic portrayals of birds in human situations. A fine example, of parrots in conclave like politicans, is in the Russell Cotes Art Gallery, Bournemouth, England. Both Stacy Marks and Sir John Everett Millais painted genre studies of ornithologists revelling in their collections of stuffed specimens, Millais's work 'The Ruling Passion' at Glasgow Art Gallery being particularly interesting, since it was inspired by a visit to John Gould in old age.

The arrival in the 1860s of the first Japanese prints in this country, which included bird studies by Hokusai and Hiroshige, was to have a marked influence on British art. In the aesthetic 1870s it led to a remarkable concentration on two very dissimilar birds, the sparrow and the peacock. Sir Edward Burne-Jones produced several lively studies of sparrows, in Birmingham Art Gallery, England, inspired by Hokusai's depiction of the bird in the Mangwa, and the sparrow was also widely depicted on ceramics, fans and painted furniture. The peacock, which flaunted its beauties both on Chinese decorative wallpapers and on the robes of Japanese geisha in prints, inspired both J.A.M. Whistler and Albert Moore to decorate rooms with peacock motifs, Whistler's room being preserved in the Freer Gallery in Washington. Peacock feathers indeed became the virtual banner of the aesthetic movement, finding a later echo in America in the striking posters of Will Bradley and the art nouveau glass of Louis Comfort Tiffany. But the British artist most influenced by oriental art was Joseph Crawhall, whose memorable paintings of cockerels and pheasants, rendered in a fluid watercolour technique which recalls the Zen masters, can be seen at Glasgow Art Gallery.

If the peacock, symbol of vanity and luxury, was the bird most identified with the aesthetic movement, the goose was to be especially favoured by the Barbizon School in France, and their spiritual followers in the New English Art Club. Jean François Millet was particularly fond of the theme of the goose girl, with the opportunities it afforded for conveying the simple calm of rural life, and this enthusiasm was shared by followers as diverse as Camille Pissarro, and the English artists George Clausen and Edward Stott. While the Impressionists rarely painted birds, Manet's lithographs for Edgar Allen Poe's poem 'The Raven', and Monet's swaggering 'Turkeys' in the Jeu de Paume, Paris, should be mentioned. A few hours before he shot himself, Van Gogh painted a flight of black Rooks, traditionally birds of ill omen, flying low over a corn field against a stormy sky (Van Gogh Museum, Amsterdam).

In the 20th century, when man himself took flight, the bird continued to occupy its central position as a symbol in the realm of art, not only in pictorial but, surprisingly, even more in sculptural form. The smooth contours of birds provided an ideal point of departure for the highly stylized yet naturalistic technique of the French sculptor François Pompon (1855–1933) who can claim to be the finest sculptor of avian subjects since Egyptian times. His work, which includes examples of owls, pheasants, doves, turkeys, ducks, crows, marabou storks and geese can be studied in the Muséum d'Histoire Naturelle in Paris. In contrast to Pompon's classical style, the bronzes of Rembrandt Bugatti (1885–1916) are characterized by an exuberant Romantic force. They crystalize a strikingly observed moment, as, for example, a pair of courting pelicans with outstretched wings, in freely modelled studies which were produced very quickly, after long observation, in Antwerp Zoo, where examples of his work can be seen in a collection of great artistic interest. But the most important sculptor to be inspired by birds in the present century was Brancusi, whose 'Bird in Space' (Beaubourg, Paris; Peggy Guggenheim Collection, Venice) demonstrates that the inspiration of avian flight can be transposed into a strikingly beautiful abstract form.

Picasso's eclectic genius was also to find inspiration in birds. His monumental etchings for Buffon's 'Natural History' are among the most memorable of his graphic work, while later he also produced sculptural birds and ceramic owls at Vallauris, although his most famous avian image is undoubtedly the Dove of Peace. His contemporary Georges Braque also depicted the dove and the pigeon, and during what was virtually a lifetime's obsession with this subject matter produced synthesized, highly stylized abstract shapes which always retained an implicit life force.

A notable German Expressionist who depicted birds was Emil Nolde in a powerful series of watercolours of storks and cranes painted at Berlin Zoo, which can be seen at the Nolde Foundation in Seebull. Chagall and Max Ernst, the Surrealists, produced respectively blue birds symbolic of hope, and images of avian menace of nightmarish proportions. See also ILLUSTRATION, BIRD.

(R.T.) L.L.

ARTENKREIS: see under SUPERSPECIES; RASSENKREIS.

ARTERY: see HEART; VASCULAR SYSTEM.

ARTICULAR: when used as a noun, a paired bone of the lower jaw (see SKULL).

ARTICULATION: jointing (see SKELETON, POST-CRANIAL).

ARTIFICIAL NEST SITES: see NEST SITES, MAN-MADE.

ASCENDENT MOULT: see DESCENDENT MOULT.

ASITY: the name used for the 2 *Philepitta* species in the family Philepittidae (Passeriformes, suborder Deutero-Oscines); Sunbird-Asity is used for the 2 members of the genus *Neodrepanis*.

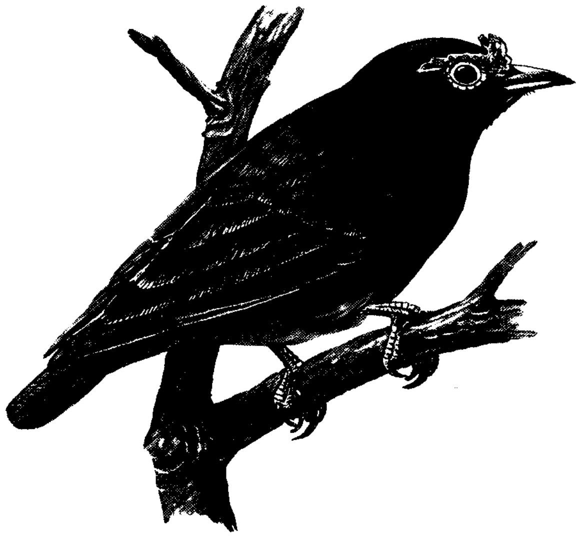
The family, confined to Madagascar, belongs to the assemblage of primitive perching birds related by the simple musculature of the syrinx, and the morphology of the bony stapes, to the tyrant-flycatcher group (Tyrannidae etc), with so many species in the New World, but represented in the Old World only by the broadbills Eurylaimidae, pittas Pittidae and New Zealand wrens Xenicidae. This relict type of distribution, and the great difference between the 2 genera, indicate that the Philepittidae are of considerable antiquity.

Characteristics. The 2 *Philepitta* spp. are *c.* 15 cm long, stoutly built, the bill not as long as the head and broad at the base, wings and feet of moderate length, tail short. The male of the Velvet Asity *P. castanea* when freshly moulted is black, most of the feathers fringed with yellow. These fringes wear off, and in the breeding season the plumage is velvety black, with a wattle of bright blue and emerald developed above the eye. The female and young male are olive above, greenish white scaled with olive below. Those of Schlegel's Asity *P. schlegeli* are very similar, but the adult male is mainly olive and yellow, with black confined to the top of the head and to the breeding wattle surrounding the eye.

The Sunbird-Asity *Neodrepanis coruscans* is *c.* 10 cm long, with a short tail and long, decurved bill. In the breeding season the male is iridescent blue above, dull yellow below, with a bright blue wattle around the eye. Unlike *Philepitta*, with apparently only one moult annually, *Neodrepanis* has two. In the off-season the male of *coruscans* is mainly olive above, and lacks the wattle. The female at all seasons is similar to the off-season male. Salomonsen's (1965) Sunbird-Asity *N. hypoxantha* differs from *coruscans* by its shorter bill, differently shaped outermost primary and much brighter yellow underparts. For many years *Neodrepanis* was associated with the sunbirds Nectariniidae, until it was shown that the throat musculature was similar to that of *Philepitta*. The external resemblance to sunbirds is due to convergence.

Habitat. All 4 species frequent dense evergreen forest, *Philepitta* for the most part the undergrowth, *Neodrepanis* probably at all levels.

Distribution. The family is confined to the forests of the humid east of Madagascar, except that *P. schlegeli* may replace *castanea* completely in the north-west.



Velvet Asity *Philepitta castanea*. (*M.W.*).

Populations. The *Philepitta* species and *Neodrepanis coruscans* are common in suitable habitat, but numbers must be continually diminishing due to replacement of forest by cultivation. Records of *N. hypoxantha* are few, but it is probably not extinct, as sometimes suggested.

Movements. All 4 species appear to be strictly sedentary.

Food. *Philepitta* is predominantly frugivorous, plucking small fruits from forest shrubs. *Neodrepanis coruscans* (and presumably *hypoxantha*) is primarily insectivorous, but also probes the corollas of certain flowers, probably for nectar.

Behaviour. *Philepitta* is sluggish and confiding, usually solitary. *Neodrepanis coruscans* is usually solitary. Despite its superficial resemblance to sunbirds, it is less active.

Voice. The male of *P. castanea* is said to have a thrust-like song, questionable in view of the primitive syrinx. A 'soft, hissing *Shee-shee* . . .' has been recorded for *N. coruscans*.

Breeding. Only the nest of *P. castanea* is known—a pear-shaped pensile structure, the top woven about the supporting branches, a projecting roof over the side entrance near the top. A clutch of 3 eggs was elongate ovate, and pure white.

(A.L.R.) C.W.B.

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ASPECT RATIO: see FLIGHT, SPEEDS OF.

ASPERGILLOSIS: see DISEASE.

ASSEMBLY, NOUN OF: a collective noun for a number of birds (or other animals) of one kind together; some of these words are of general application, while others have restricted meanings. The usual term for an assemblage of birds is 'flock'; sometimes 'flight' if they are on the wing; sometimes 'party' if the number is quite small. Other ordinary English words can of course be used for descriptive purposes in appropriate circumstances, e.g. 'assemblage', 'congregation', 'multitude', 'horde', 'host', and (on the water) 'raft'. The word 'brood' is used for the chicks or nestlings hatched from a 'clutch' or 'set' of eggs laid by one hen bird for simultaneous incubation. Birds breeding gregariously are referred to as a 'colony'. 'Pair' means a male and a female, presumably united. 'Brace' means two birds, usually dead—a measure used in counting the sportsman's 'bag'.

Then there are the special nouns of assembly which it is correct, or supposedly correct, to apply to particular kinds of birds in preference to the more general term, and only to such kinds. Some of these are genuine items from the vocabulary of medieval venery, whether now obsolete or still to some extent current (mainly among sportsmen). Others are mere inventions of later pedantry. Others again are erroneous, having found their way into the category by misconception. No attempt at an exhaustive list need be made here.

The word 'covey' is used for a family party or similarly sized flock of partridge or grouse, and is perhaps the only one of these special words that has any wide currency in English as spoken in Great Britain at the present day. There are some people, however who would always be careful to speak of a 'gaggle' or (if flying) 'skein' of geese, a 'pack' (bigger than a covey) of grouse, a 'wisp' of snipe, or a 'spring' of teal. On the other hand, one would be only half serious in speaking of a 'murder' of crows, a 'charm' of goldfinches, a 'watch' of nightingales, a 'nye' (various spellings) of pheasants, a 'clattering' of choughs, a 'covert' of coots, a 'siege' of herons or bitterns, a 'fall' of woodcock, a 'herd' of cranes, curlew, or swans, a 'trip' of dotterel, a 'bevy' of quail, a 'chattering' or 'murmuration' of starlings, or a 'dissimulation' of small birds.

There are a few specific terms for colonies, according to the kind of bird concerned. 'Rookery' and 'heronry' are of the best usage, and the former has been adopted also for penguins (Spheniscidae) by ornithologists in the Antarctic. Others are easily invented, where euphony permits, and some have wide currency—'gullery', 'ternery', 'swannery'; but 'loomery' (guillemots) is a more sophisticated usage. These inventions are not free from affectation, however, and the general term 'colony' is usually to be preferred.

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ASSOCIATION, INTERSPECIFIC: either between different species of birds or between birds and other than avian species—see under BROOD-PARASITISM; CROCODILE-BIRD; FEEDING HABITS; FLOCKING; HONEYGUIDE; MAMMALS, ASSOCIATION WITH; NESTING ASSOCIATION; OXPECKER; PARASITISM; TAMENESS.

ASTRAPIA: substantive name sometimes used for the BIRDS-OF-PARADISE of the genus *Astrapia*.

ASYMMETRY: a condition not usually present in any marked degree in the external characters of birds, apart from individual abnormalities. A striking exception is that of the Wrybill Plover *Anarhynchus frontalis*, in which the bill is deflected to the right (see BILL; PLOVER). Not ordinarily visible is the often great disparity between the ear openings on the two sides in owls (Strigiformes) (see HEARING AND BALANCE; OWL). As in mammals, there is some asymmetry in the internal organs; thus, only the right aortic arch develops (in mammals it is the left)—see VASCULAR SYSTEM; and only the left ovary of birds is functional as a rule (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM). See also FOOTEDNESS.

ASYNCHRONOUS HATCHING: see HATCHING.

ATAVISM: see PLUMAGE.

ATLAS (1): in ornithology, understood to mean a collection of maps showing bird distributions within a defined region. It is based on dot-distributions within a defined, regular grid, during a defined, limited time period in which fieldwork for the maps was carried out. Thus, a 'breeding bird atlas project' or a 'winter atlas scheme' would involve the gathering of information for the production of maps of the breeding or wintering distributions of birds within the defined area. Atlas projects involve every bird species present (and not just a selection of those present) in the defined area at the relevant season.

The first national breeding bird atlas project covered Britain and Ireland during 1968–1972, but others have followed in many European countries and also in various states in the USA, in parts of southern Africa, and in Australia and New Zealand. In countries where some species are breeding in all seasons, where knowledge of the avifauna is meagre or where manpower for fieldwork is in short supply, atlas projects have covered all 12 months of the year. Elsewhere, breeding or winter atlas surveys have usually been restricted to 4 or 5 months of the year (with special exceptions for species which nest earlier or later than others). Surveys usually extend over several years, to ensure complete cover and to avoid bias due to one freak year, but the time span is kept short to 'freeze' distributions, so far as possible, even for those species expanding or contracting their ranges.

Fieldwork is carried out within units of a defined grid, which may vary from 1 km × 1 km squares to much larger units, depending upon the total area of the region being surveyed and, often, on the dimensions of the most easily obtained maps. For instance, the continent-wide mapping of Europe is being carried out using the 50 km × 50 km Universal Transverse Mercator grid; mapping in Britain and Ireland uses the 10 km × 10 km squares of the National Grid; mapping in English counties often uses 2 km × 2 km squares (tetrads); mapping in France in 1970–74 used 20 km × 27 km rectangles corresponding to available maps.

Atlas surveys are often based on presence/absence, but with other information added (such as proof of breeding, see below). Some projects, however, attempt quantitative assessments within the grid units, usually based on mathematical progressions (1–10, 11–100, 101–1000, and so on).

The internationally agreed criteria for breeding evidence are as follows:

Grade A		**Present**
O	0	Species OBSERVED in breeding season.
Grade B		**Possibly breeding**
H	1	Species observed in breeding season in possible nesting HABITAT.
S	2	SINGING male(s) present (or breeding calls heard) in the breeding season.
Grade C		**Probably breeding**
P	3	PAIR observed in suitable nesting habitat in breeding season.
T	4	Permanent TERRITORY presumed through registration of territorial behaviour (song, etc.) on at least two different days a week or more apart at the same place.
D	5	DISPLAY and courtship.
N	6	Visiting probable NEST-SITE.
A	7	AGITATED behaviour, or ANXIETY calls from adults.
I	8	Brood patch on adult examined in the hand, indicating probably INCUBATING.
B	9	BUILDING nest or excavating nest-hole.
Grade D		**Confirmed breeding**
DD	10	DISTRACTION DISPLAY or injury feigning.
UN	11	USED NEST or egg shells found (occupied or laid within period of survey).
FL	12	Recently FLEDGED young (nidicolous species) or downy young (nidifugous species).
ON	13	Adults entering or leaving nest-site in circumstances indicating OCCUPIED NEST (including high nests or nest-holes, the contents of which cannot be seen) or adults seen sitting on the nest.
FY	14	Adults carrying FOOD for YOUNG or faecal sac.
NE	15	NEST containing EGGS.
NY	16	NEST with YOUNG seen or heard.

Two supranational co-ordinating bodies exist: the European Ornithological Atlas Committee (EOAC) and the North American Ornithological Atlas Committee (NAOAC). J.T.R.S.

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Yeatman, L. (ed.). 1976. Atlas des Oiseaux Nicheurs de France. Paris.

ATLAS (2): the first vertebra, articulating with the skull (see SKELETON, POST-CRANIAL).

ATRICHORNITHIDAE: see under PASSERIFORMES, suborder Oscines; SCRUB-BIRD.

ATRIUM: a chamber, especially one or other of the anterior chambers of the heart ('atria', formerly more often called 'auricles'—see HEART).

ATTACK: see AGGRESSION.

ATTILA: generic name used as substantive name of *Attila* spp. (see FLYCATCHER (2)).

AUDITORY MEATUS: see TOPOGRAPHY.

AUGURY: see OMENS, BIRDS AS; ORNITHOMANCY.

AUK: substantive name of 3 species of Alcidae (Charadriiformes, suborder Alcae); in the plural it is the general term for the family. Auks are medium sized birds, ranging in size or weight from 14 cm and 90 g (Least Auklet *Aethia pusilla*) to 36 cm and 1,000 g (guillemots or murres *Uria* spp.): the extinct and flightless Great Auk *Alca* (*Pinguinus*) *impennis* was much larger (*c*. 5,000 g). The family is thought to have evolved from a gull-like ancestor some time during the Upper Cretaceous or Paleocene, 100–70 million years ago. Different authorities recognize between 10 and 14 living genera in 7 tribes containing 22 species. Sixteen of these are found in the Bering Sea region, 12 of which are endemic, and this is probably the auks' area of origin. Several species show geographical variation in size and colour and have been divided into subspecies (especially the Common Guillemot *Uria aalge* and Black Guillemot *Cepphus grylle*). The validity of these subspecies needs to be reassessed in the light of new material, new techniques and new ideas in avian taxonomy. The auks are unique among bird families in the diversity of developmental patterns they display. Three groups have been recognized; one (truly precocial) in which the chicks leave the nest, accompanied by their parents, 2–4 days after hatching, another (semi-precocial) in which the chicks remain at the nest-site until they have attained adult weight, and the third (intermediate) in which the chicks fledge when only part grown. Detailed studies using biochemical techniques are still needed to elucidate relationships.

Characteristics. Auks are monogamous and sexually monomorphic; males are, in general, slightly larger than females. The bill varies in form from nearly cylindrical and pointed (guillemots) to rather broad bills (auklets *Aethia* spp.) which develop during the breeding season a sublingual diverticulum (or gular pouch) which is used to transport liquid food to the nestlings. In puffins (*Fratercula* spp.) and some auklets, the bill is laterally compressed and very high in the vertical plane. Both the tail and the legs are short. The first toe is lacking or vestigial, the other three are fully webbed. The claw of the second toe in puffins is modified and used to dig out nesting burrows.

All have relatively small wings, more or less pointed, which represent a compromise between aerial and submarine flight. In the larger species (guillemots and Razorbill *Alca torda*) remiges are moulted simultaneously, so adults remain flightless for several weeks. This occurs probably because in these species wing-loading is high and, if sequential moult occurred, it would result in energetically inefficient flight. By contrast, the remiges of the smaller species (Least Auklet, Whiskered Auklet *Aethia pygmaea*) are moulted sequentially, as were those of the Great Auk.

Like many other pursuit-diving birds most auks have white ventral and dark dorsal plumage, although a few are predominantly dark (e.g. Tufted Puffin *Fratercula cirrhata*, Rhinoceros Auklet *Cerorhinca monocerata*, Black Guillemot, Pigeon Guillemot *Cepphus columba* and Spectacled Guillemot *C. carbo*). The true auks (*Uria* and *Alca* spp.) are all dark above and white below. In winter the throat is white, and black or brown in summer. A ringed or bridled mutant of the Common Guillemot occurs in the Atlantic and this has a white eye ring and auricular groove. The proportion of bridled individuals is small in southern parts of its range, and rises as high as 50% in the northern parts. Studies of hand-reared birds, of known parentage, suggest that bridling is controlled by a single gene on one of the autosomes. Its selective advantage, if any, is unknown.

In winter the Black Guillemot has varying amounts of white in the upperparts and white underparts, but apart from a white wing patch the breeding plumage is black. The winter plumage of the murrelets (*Synthliboramphus*, *Brachyramphus*) of the North Pacific is grey and white and the majority have no distinctive breeding plumage, any seasonal difference being confined to the colour of the plumage on the head. Two murrelets have very distinctive breeding dress which provides excellent camouflage for the adults while incubating. The plumage of the Marbled Murrelet *Brachyramphus marmoratus* is barred and coloured rufous and brown, and that of Kittlitz's Murrelet *B. brevirostris* is mottled blue-grey and buff.

Atlantic Puffin *Fratercula arctica*. (*B.P.*).

Bright colours, if present, are confined to bill, feet and lining of mouth. Most species of small auklets (*Aethia* spp.) and puffins develop elongated plumes on the head and brightly coloured plates on the bill just before the breeding season. In addition, the Atlantic Puffin *Fratercula arctica* and Horned Puffin *Fratercula corniculata* have these plate-like structures above and below the eye and fleshy rosettes at the gape. In the Crested Auklet *Aethia cristatella* the plates give out an odour like that of tangerine oranges.

High wing loadings result in a fast flapping flight which provides an excellent field character. Gliding over short distances may occur in very strong winds. The neck is retracted in flight and the feet may be covered by the plumage of the underparts, particularly during long flights.

On the ground the posture may be upright (true auks), duck-like (*Cepphus* spp.) or intermediate (puffins), the position and relative size of the legs differing from group to group.

Habitat, distribution and populations. Auks are predominantly pelagic, remaining at sea except during the breeding season. The family is confined mainly to the cooler parts of the Pacific and Atlantic oceans, but some inhabit fresh water in the Baltic and warm water in the Gulf of California. Eighteen species occur in the North Pacific, and 3 (Common Guillemot or Common Murre, Brünnich's Guillemot or Thick-billed Murre *Uria lomvia*, Black Guillemot or Tystie) occur in both oceans. The 2 murres are partially sympatric; the Thick-billed nests further north and the other further south reaching northern Portugal and southern California. The Black Guillemot, unlike the 2 murres, does not nest south of the Bering Strait, being replaced in the North Pacific by the closely related Pigeon Guillemot. The Atlantic Puffin of the North Atlantic is replaced by the Horned Puffin, a close relative, in the North Pacific. The 2 murrelets, Xantus' Murrelet *Synthliboramphus hypoleucus* and Craveri's Murrelet *S. craveri*, which may be conspecific, have restricted ranges off southern California and Baja California. The Great Auk occurred in the North Atlantic.

Some auks are extremely abundant and rank among the most numerous seabirds in the northern hemisphere. Puffins and guillemots are thought to number millions of pairs, as do the Little Auk or Dovekie *Alle alle*, Least Auklet, and Crested Auklet. However, auks are notoriously difficult to census, and until the 1970s few systematic attempts had been made to count them. Nevertheless, it is clear that many species have declined during the present century. Several factors are considered to be responsible: an increase in adult mortality through oiling, drowning in fishing nets, disturbance and shooting (for human consumption) at breeding colonies, changes in distribution and abundance of prey species due to changes in the marine environment or to commercial fisheries. Much of the recent research in alcid biology is a result of industry's efforts to locate oil in off-shore waters and the concomitant threat to these species.

Movements. Little detail of movements is known for most species. Guillemots are thought not to move far from their breeding grounds but ringed individuals from Britain have been located in Denmark and Norway and south to the Bay of Biscay and one (a juvenile) off Gibraltar. Some Razorbills migrate from Britain to the central Mediterranean as do some Puffins from southern populations in Britain, but those from northern populations remain in the North Sea, reaching Newfoundland. Other Puffins have turned up in the Azores. Little Auks regularly move southwards from their northern breeding grounds some reaching the Azores, and are regular winter visitors on passage in Britain.

Food. The diet of adult auks is poorly known, but most species feed on small fish or planktonic crustaceans. The diets of adult and chicks often differ, as do the diets of sympatric species. Even when the same prey are utilized, different alcid species take different size classes of prey. The prey is usually obtained by underwater pursuit, using wings for propulsion and feet for steering, but a few forms are bottom feeders. In the North Pacific there are 5 plankton feeding species (auklets) but only one (Little Auk) in the North Atlantic.

Voice. Most auks are silent at sea. Vocalizations during pair formation and social interactions at the breeding site are relatively simple, and have been described as grunts, growls and *Arrrrs* in the larger species, and as twitters, peeps and whistles in the smaller species.

Behaviour. Auks use a variety of postures and calls during pair formation and other social interactions at the breeding site. In those species with brightly coloured linings to their mouths (red or yellow) the displays often involve the simultaneous use of a body posture, open bill and vocalization. Postural displays involve components such as head turning, raised wings, and in some species a slow 'butterfly flight'. Postural displays used by auks appear to be less ritualized than they are in some other seabirds e.g. gulls Laridae and gannets Sulidae.

Breeding. Most species breed colonially near the sea, on mainland cliffs or on off-shore islands, either on ledges, vegetated seaward slopes or in boulder screes. Within colonies, some of which have as many as 8 alcid species breeding together, the spacing of breeding pairs varies between species. Coexistence is achieved through the use of different nest sites and food types. In addition, for those species which breed in the open, spacing is controlled by social behaviour, but in crevice or burrow nesting species physical features may also determine spacing. In some auks habitat selection and spacing patterns have been shown to be important in breeding success. In all species, both parents take part in incubation and in care of the young. The 4 small precocial species (Xantus' Murrelet, Craveri's Murrelet, Ancient Murrelet *Synthliboramphus antiquus* and Japanese Murrelet *S. wumizusume*) produce a clutch of 2 relatively large eggs (each weighing 22–24% of adult body weight) which give rise to well developed chicks with feet of nearly adult size. They nest in burrows or crevices from which the fledging chicks scramble down to the sea. The Ancient Murrelet is the only one of the group which has been studied in detail; it is unusual among auks in having long (72 h) incubation shifts. The young of this group are led directly to feeding areas 2–4 days after hatching. As the parents do not spend time and energy transporting food to the nest site (as in other auks), this energy saving may explain why members of this group are able to rear a brood of two.

The semi-precocial species consist of 4 groups; the puffins, *Cepphus* species, auklets and the Little Auk, and 2 species of murrelets (*Brachyramphus*). The 4 species of puffins (Atlantic, Horned, Tufted Puffin, and the misnamed Rhinoceros Auklet, which is not an auklet but a puffin) are diurnal at the breeding colonies. They breed in burrows (dug by themselves) or in rock crevices. The single immaculate or obscurely marked egg hatches after about 40 days and the chick fledges after 40–50 days at about 70–80% adult weight. Parents carry fish in the bill for feeding to the chick. The *Cepphus* species (Black Guillemot, Pigeon Guillemot and Spectacled Guillemot) are diurnal, and form loose colonies. They feed close inshore, and this minimizes travelling time and energy and allows adults normally to rear 2 chicks. Incubation shifts and intervals between chick feeds are shorter than in most other auks. Nest sites are located in rock crevices, and incubation of the 2 eggs takes about 30 days. The chicks fledge after 30–40 days at about 90% adult weight. Chicks are fed on fish and crustacea.

All the auklets, except Cassin's Auklet *Ptychoramphus aleuticus*, and the Little Auk, are diurnal and all 6 breed colonially in talus or earth burrows and lay one egg. The incubation period and nestling period of all species are in the range 30–40 days, and chicks fledge at 70–90% of adult weight. The young are fed on a plankton 'soup'. Cassin's Auklet is unique among auks and unusual among seabirds in being double brooded on the Farallon Islands, California.

The 2 members of the fourth group (Marbled Murrelet and Kittlitz's Murrelet) are unusual as they are nocturnal and breed solitarily several km inland. The Marbled Murrelet nests high up on the branches of large coniferous trees, and Kittlitz's Murrelet nests on the ground in the open above the timber line in Alaska and neighbouring islands. The breeding plumage of both species provides excellent camouflage for the adults while incubating. Each lays only a single egg, but few nests have been found, so little else is known of their breeding.

Four species (Common Guillemot, Brünnich's Guillemot, Razorbill, and extinct Great Auk) make up the intermediate group. These breed mainly in the open on cliff ledges. The eggs of *Uria* spp. are pyriform in shape which reduces their chances of rolling off the ledge. The rolling radius changes from 17 cm (fresh eggs) to 11 cm (fully incubated eggs). This is not an adaptation but rather the fortuitous outcome of a change in the eggs' centre of gravity as the embryo develops. *Uria* spp. breed in dense colonies and lay one egg (12% of adult body weight) which is rested across the tarsi when incubated. The remarkable variation in colour and pattern of the eggs enables adults to recognize their own eggs. In addition, they recognize their own chicks through their voice which is of major importance in a crowded colony. The incubation period is in the range 28–35 days and chicks fledge at 18–21 days old, are then well feathered but flightless, and they free-fall on open wings to the sea at dusk in order to avoid predators. In Brünnich's Guillemot fledging occurs synchronously in a colony and early hatched chicks are older at fledging than the later hatched chicks. Guillemot chicks are cared for by their male parent for several weeks after fledging. Males moult their primaries while they undertake a swimming migration/dispersal away from the colony with their flightless chicks. The female returns to the nest site for up to 2 weeks after the young leave and moults later. The intermediate pattern of chick development has evolved either to minimize the period of time (and hence predation) at the nest-site, or because adults are unable to provision chicks at a fast enough rate to permit them to attain near adult weight at the nest-site. Because these species nest in the open, one adult must always be present to protect and brood the chick, so reducing their feeding rate. In all other groups chicks are provisioned by both parents after about one week, once the chick is able to maintain a stable body temperature.

Studies of colour-ringed birds show that auks share the following life-history features with other seabirds; high adult survival (at least 90% per annum), deferred maturity and low reproductive output (age of first breeding is 4 or 5 years in *Alca*, *Uria* and *Fratercula*), marked nest-site tenacity and mate fidelity from year to year. See photo FLIGHT.

(R.W.S.) T.R.B.

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AUKLET: substantive name of *Aethia* spp. and *Ptychoramphus aleuticus* (see AUK).

AURICLE: in general, an ear-shaped lobe; formerly the common term (in the plural) for what are now more usually called the 'atria' of the heart (see ATRIUM; HEART).

AURICULARS: the ear coverts (see PLUMAGE; TOPOGRAPHY).

AUSTRAL: term applied in North America to a climatic life-zone, or series of zones, lying south of the 'boreal' (see BOREAL; LIFE-ZONE).

AUSTRALASIAN REGION: comprising the Australian and New Zealand Regions of some zoogeographers, but in respect of avifauna more appropriately treated as a unit with subdivisions (see DISTRIBUTION, GEOGRAPHICAL). The heart of the Australasian Region is the island continent of Australia, with an area of about 7,682,000 km^2 (including Tasmania). New Guinea (the south-eastern part of which is called Papua) covers an area of 890,000 km^2, and New Zealand and its Dependencies 271,000 km^2. The total land area of the Region, including the smaller island groups, is about 8,930,000 km^2.

Australia extends between 11° and 43° S, and nearly 40% of its total area is within the tropics. It is a land of low, subdued relief with large expanses of plain, and with a notable absence of mountains of alpine type, conditions that impart a certain uniformity of landscape and vegetation. The climate is predominantly warm and dry, the continent having an arid centre with concentric zones of more favoured country, culminating in restricted humid areas in interrupted coastal strips, particularly in the north-east, east, south-east and south-west. Both New Guinea and New Zealand, with their high mountain cordilleras and lush vegetation—the one tropical, the other temperate—present marked physiographic and vegetational contrasts to their larger neighbour.

For its area Australia has a low number of bird species; recent RAOU checklists give 734 species, of which 578 are native breeders. New Guinea has a similar number, with 910 breeding species for the two together. The list is over 300 for New Zealand but only about 45 are native land-birds (cf. 110 in the British Isles, which have a smaller area). Four of these land birds have become extinct, but several others have colonized naturally from Australia and over 30 have been introduced, chiefly from Europe.

Origin of the avifauna. Until recently it was believed that Australia had always been close to south-east Asia. Hence the most likely explanation for the origin of its avifauna was that it had developed by island-hopping from the Oriental Region (Mayr 1944). Most people now accept the theory of Continental Drift. Australia parted company with the great southern continent Gondwanaland at the beginning of the Tertiary, some 50 million years ago (Keast 1981). New Zealand probably separated somewhat earlier, as might have New Caledonia. Australia moved slowly towards south-east Asia and may not have been in a position to receive many immigrants until at most 10 million years ago. The dramatic discovery of fossil bird feathers from Lower Cretaceous deposits in Victoria showed that some birds existed in Australia early in avian evolution. Thus some birds entered Australia by the southern route, from South America, and possibly Africa, via Antarctica, which was at that time milder than it is today. The possibility of southern origins has been raised by both D.L. Serventy and Cracraft (1972). The ratites and penguins are clear candidates for a southern origin as they are now almost restricted to the Southern Hemisphere. Perhaps parrots, bronze cuckoos (*Chrysococcyx*), pigeons and caprimulgids were also ancient colonizers (Cracraft 1972, Marchant 1972). Many marine or freshwater forms could also have been present, though they could have colonized Australia later when it was isolated.

The origin of the passerines is complex. The lyrebirds *Menura* and scrub-birds *Atrichornis* appear to be related to each other and to be an ancient group. J.A. Feduccia and S.L. Olson have shown that the osteology of both is remarkably similar to that of the tapaculos (Rhinocryptidae) of South America. They raise the exciting possibility that the passerines originated in the Southern Hemisphere.

Electrophoresis of proteins and hybridization of DNA has recently indicated that most Australian passerines fall into one of a few assemblages that are not closely related to the major Asian groups. One such group includes the honeyeaters, the fairy-wrens (see WREN (2)) and the Australian warblers. Another comprises the whistlers (thickheads) Pachycephalidae, with the Australian flycatchers, wood-swallows and cuckoo-shrikes as relatives. Crows and orioles may be close to this group. When the ancestors of these groups arrived and where they came from is a matter of conjecture at this stage.

These groups include some remarkable cases of convergence in form and habit towards unrelated birds in the northern hemisphere. The *Gerygone* warblers look and behave very like Sylviid and Parulid warblers of Eurasia and America, the sittellas (*Daphoenositta*) climb trees and have dagger-shaped beaks very like nuthatches (Sittidae), and the small *Myzomela* honeyeaters closely resemble sunbirds. The evidence strongly indicates that there has been an adaptive radiation of a few early colonizers, which parallels that of the Australian marsupials.

Despite the domination of the avifauna by these few early assemblages there are several species that clearly belong to Palearctic families and which have arrived recently. There are several Sylviids (e.g. *Megalurus*, *Cincloramphus*), a few crows, thrushes (*Turdus*, *Zoothera*), silvereyes (*Zosterops*) and orioles (*Oriolus*). Australia has single species of sunbirds (*Nectarinia*), flower-peckers (*Dicaeum*) and starlings (*Aplonis*) though New Guinea has several of each of these. Among non-passerines, bee-eaters (*Merops*) and rollers (*Eurystomus*) have colonized. However, several groups have failed to colonize, including Old World vultures (Aegypiinae), sandgrouse, trogons, barbets, woodpeckers, broadbills, true finches (Fringillidae) and buntings (Emberizidae). Interestingly, flamingos are absent from the region, but were present in the Tertiary, and the Australian Banded Stilt *Cladorhynchus leucocephalus* is apparently this family's closest living relative. A few groups, e.g. the bulbuls, hornbills and shrikes, have reached the Australasian Region but not Australia itself.

New Guinea has at times been connected to Australia, most recently about 10,000 years ago. It shares many taxa with Australia, though it has many more rain-forest specialists and generally a higher proportion of birds of Asian origin. It has also acted as a source of re-invasion for Australia, notably of honeyeaters (*Meliphaga*) and fruit-doves (*Ptilinopus*).

New Zealand also probably had birds when it broke off from Gondwanaland. The extinct moas (Dinornithidae) and the kiwis (Apterygidae) are ratites. The New Zealand wrens (Acanthisittidae) are also apparently very ancient. Their closest relatives are probably the lyrebirds and scrub-birds in Australia and the primitive South American sub-oscines. The wattlebirds (Callaeidae), comprising the Saddleback *Philesturnus carunculatus*, the extinct Huia *Heteralocha acutirostris* and the Kokako *Callaeas cinerea*, are perhaps equally ancient.

Many other New Zealand birds are more obviously derived from Australian families, including the 3 honeyeaters, the warblers *Gerygone*, robins *Petroica* and fantails *Rhipidura*. This colonization is continuing, several Australian species having become established in New Zealand in the last century. In Pleistocene and early Recent times, according to Falla, a vigorous waterfowl and open-country fauna allied to Australian types flourished in New Zealand and then died out, possibly because of the onset of arid conditions. These included a swan allied to the Australian Black Swan *Cygnus atratus*, a large eagle *Harpagornis moorei*, a coot *Palaeolimnas*, a corvid, and representatives of 2 Australian monotypic ducks (*Biziura*, *Malacorhynchos*).

The other Pacific islands have received birds from Australia and the Oriental Region, with a very few from the Palearctic or the Americas. Thrushes of the genus *Turdus* reached many islands but not Australia or New Zealand. New Caledonia has the unique Kagu *Rhynochetos jubatus*, belonging to a family found nowhere else.

The Australasian Region is usually separated from the Oriental Region at Wallace's line between Bali and Lombok, though the avifaunas of the two regions have intermingled (but see DISTRIBUTION, GEOGRAPHICAL). Immigrants from the north have been discussed earlier but several groups have colonized the Oriental Region from Australia. Thickheads, monarch flycatchers and *Gerygone* occur on the Malay Peninsula, wood-swallows reached India and China. Two species of honeyeaters have also crossed Wallace's line, if *Apalopteron* on the Bonin Islands is a honeyeater.

Speciation. Most birds, and virtually all of the land-birds in the Australasian Region are endemic. Many have originated from the adaptive radiation of a few ancient groups. Some speciation has taken place on islands, especially those around New Guinea. Elsewhere there are apparent cases of double or even triple invasions (e.g. *Zosterops* on Norfolk Island). There has been some colonization of north-eastern Australia by New Guinea species, but most Australian species must have originated on that land-mass, which has few off-shore islands. Cycles of arid and mesic climates have contributed to much of this speciation. In arid times the central desert spread outwards to isolate humid refuges in the north-west, along the east coast and in the south-west. Populations in these areas would have diverged due to the different environments they offered. With the return to moister conditions these refuges expanded and were connected again (Keast 1961). In some cases the meeting populations would have diverged sufficiently to achieve reproductive isolation. There are many cases of pairs of species in south-western and south-eastern Australia (e.g. Western and Eastern Spinebill *Acanthorhynchus superciliosus* and *A. tenuirostris*) or where the south-western isolate has spread inland and eastwards (e.g. Western Whipbird *Psophodes nigrogularis*). The rosellas (*Platycercus eximius*, *P. adscitus*, *P. venustus*, *P.*

icterotis) presumably evolved in 4 separate refuges and the races of Sittella *Daphoenositta chrysoptera* in 5. In some cases refuges have been invaded twice, giving a pair of similar species (e.g. black cockatoos *Calyptorhynchus* and robins *Eopsaltria* in south-western Australia).

Migrants. With the striking exception of numerous waders (Scolopacidae, Charadriidae) which breed in the Palearctic, very few Old World migrants winter in the region. Two swifts (Apodidae) from eastern Asia are regular migrants to southern Australia as is the Oriental Cuckoo *Cuculus saturatus* to northern Australia. The eastern race of the Swallow *Hirundo rustica gutturalis* winters in New Guinea and north-western Australia, and 4 species of wagtails *Motacilla* and a reed warbler *Acrocephalus arundinaceus* occur in small numbers. The virtual absence of Palearctic migrants in Australia during the northern winter contrasts with their abundance in southern Africa and is probably a legacy of Australia's isolation from Asia in the past. Although several species move from Australia to New Guinea in the southern winter, none reaches Asia in any numbers. A wader and several seabirds migrate from New Zealand to Australia and a cuckoo from New Zealand to the Solomon Islands.

Within Australia many species show complex migratory patterns; indeed some appear nomadic in their movements.

Subregions. In Australia itself the existing fauna can be grouped into three major assemblages (Serventy and Whittell 1962): a northern tropical one (the Torresian Fauna), a south-eastern and south-western temperate one (the Bassian Fauna), and over most of the arid and semi-arid interior a widespread Eyrean Fauna. In the south-west of Australia there is an intermingling of Bassian and Eyrean elements. Kikkawa and Pearse (1969) have confirmed the validity of these divisions by numerical computer analysis, proposing an alteration of names and dividing the Torresian into two faunas by separating a western component which they term the Timorian. R. Schodde and J.H. Calaby have separated from the Torresian two faunas: the Tumbunan (montane unit) comprising the highlands of New Guinea and the sub-tropical rain-forests of eastern Australia, and the Papuasian unit in the lowlands of New Guinea and pockets of rain-forest on Cape York Peninsula.

Special characteristics. Australia and New Guinea have a whole range of ecological types as shown on other continents. But, compared with Europe and North America, temperate Australia has rather few small seed-eaters (finches are to some extent replaced by parrots) whereas nectar-feeding birds are diverse and abundant. Honeyeaters and other birds have co-evolved with the flora to become significant pollinators. Australian land-birds appear long-lived and are mostly resident, perhaps because most habitats are not strongly seasonal. Perhaps for this reason many species have complex breeding biologies. Many species breed co-operatively, sometimes as permanent groups as in babblers *Pomatostomus* and apostlebirds *Struthidea* or semicolonially as in the miners *Manorina*. The lyrebirds of Australia and the birds-of-paradise of New Guinea have spectacular displays and most are polygamous. The bowerbirds construct bowers of sticks which they decorate with colourful ornaments. Another curious breeding system is shown by the MEGAPODES, which incubate their eggs in mounds of sand or decaying vegetable matter or even volcanically heated soil.

New Zealand has a virtually flightless parrot which booms and another species which has become a meat-eater. The nocturnal kiwi has almost lost its wings and has its nostrils at the end of its beak. The extinct Huia was strikingly sexually dimorphic; the stout-beaked male broke apart dead wood while the scimitar-beaked female probed into holes.

D.L.S. and H.A.F.

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AUSTRINGER: see FALCONRY.

AUTECOLOGY: term for the ecology of individuals—contrasted with SYNECOLOGY (see also ECOLOGY).

AUTOCHTHONOUS: applied to species, etc., meaning aboriginally INDIGENOUS.

AUTOMOLUS: generic name used as substantive name, alternatively 'foliage-gleaner', of *Automolus* spp. (see OVENBIRD (1)).

AUTOSOME: any chromosome other than a sex chromosome.

AVADAVAT: substantive name of 2 Asian *Estrilda* spp. (see ESTRILDID FINCH).

AVAILABILITY: of scientific names, see NOMENCLATURE.

AVERAGE: see BIOSTATISTICS; MEAN, ARITHMETIC.

AVES: plural of the Latin 'avis' and used as the scientific name of the Class of animals known as birds (see ANIMAL KINGDOM). The common name is, in this instance, as precise as the scientific one (see BIRD). A primary definition may indeed be taken as self-evident; the category is perfectly distinct in the mind of anyone who has grasped the elementary fact that bats are, and pterosaurs were, animals of quite different sorts. This is because birds possess obvious characteristics that distinguish them easily from all other animals. Moreover, the main characteristics are present in all birds, producing a high degree of resemblance between one kind and another.

The distinctiveness and relative uniformity in the Class are due to its high degree of specialization. This has separated birds sharply from all other kinds of animal; and it has at the same time imposed strict limits, within the Class, on the possible extent of divergence from the general type. The specialization is for flight, and it follows lines of adaptation different from those of other flying animals (see FLIGHT; WINGS, COMPARATIVE ANATOMY OF). Apart from the flightlessness of nearly all very young birds, it is true that a few species lack the power completely; but this can be regarded as a secondary loss, incurred after the main line of evolution had been determined, seeing that the associated adaptations are to a great extent retained. Thus, just as flight is the outstanding characteristic of birds in general, so the immediately obvious thing about the exceptions is that they do not fly (see EARLY EVOLUTION OF BIRDS; FLIGHTLESSNESS).

The first essential character in the specialization of birds for flight is the modification of the forelimbs as wings (see WING). That the wings are in some birds used, also or instead, as swimming organs, and in others have become rudimentary, is merely incidental. The possession of wings, except in some instances where the function has been lost, is associated with a great development of breast muscles and with a keel on the sternum for their attachment (see MUSCULATURE; SKELETON, POSTCRANIAL). It is associated also with a fused rigidity of parts of the skeleton providing a fulcrum, with remarkable lightness in weight, and with a general 'stream-lining' of the body (see PNEUMATIZATION OF BONE; RESPIRATORY SYSTEM; SIZE).

Likewise associated with flight, although also (and perhaps originally) serving other purposes, is the plumage (see FEATHER; PLUMAGE). This character is unique, as feathers are not found in any other kind of animal and are present in all birds except the very young of some forms (see YOUNG BIRD). Feathers are thus conclusively diagnostic of the Class; they are present in the earliest known fossil (see ARCHAEOPTERYX).

The modification of the forelimbs for a special purpose has the consequence that birds are necessarily bipedal in their terrestrial stance and locomotion (see LOCOMOTION, TERRESTRIAL; SIZE). It likewise throws upon the head, armed with its bill (or beak), and sometimes on an elongated as well as flexible neck, most of the 'manual' functions performed by the forelimb in many other animals (see BILL); only in relatively few birds are the hindlimbs so used to any considerable extent (see FEEDING HABITS; LEG).

Birds share with mammals alone (at least at the present day) the character of being 'warm-blooded', which together with an intense metabolism enables the possessor to lead a highly active life in a widely variable environment (see HEAT REGULATION; METABOLISM). Also correlated with the mode of life of a flying animal are the facts that a bird lays only one egg at a time, thus causing the minimum of change of weight in the gravid female (see LAYING), and that development of the young is usually very rapid, thus reducing the period of vulnerability during which the advantages of being able to fly have not yet been attained (see DEVELOPMENT, EMBRYONIC; GROWTH).

The Aves share with some other classes such characters as being chordate, vertebrate, tetrapod (four-limbed), amniote, and oviparous. In various other respects of form and function, not too greatly involved in the specialization, they show some general conformity with other vertebrate animals, although the same ends may be achieved in different ways. In complexity of structure and in development of mental functions, the Aves may be said to stand parallel, if not quite level, with the Mammalia at the highest points of evolution. For their descent see ARCHAEOPTERYX; EARLY EVOLUTION OF BIRDS; FOSSIL BIRDS.

Despite the relatively high degree of structural uniformity among birds, as contrasted with other classes, they show great ecological diversity. Birds have indeed exploited every mode of life that is open to them. They are found in every part of the world except the polar wastes (see DISTRIBUTION, GEOGRAPHICAL), and they live in extremes of climate, although sometimes only seasonally (see MIGRATION). They inhabit environments ranging from the oceanic to the montane, from open plains to tropical forest, and from deserts to habitations of mankind (see ECOLOGY). They subsist on a wide variety of vegetable and animal foods, obtained in diverse ways (see FEEDING HABITS). They breed in all sorts of situation, from burrows in the earth to the highest treetops (see NEST). They fly and run, swim and dive (see FLIGHT; LOCOMOTION, TERRESTRIAL; SWIMMING AND DIVING). They may skulk in hiding, may keep largely to the water, may run boldly in the open, or may soar conspicuously in the sky. They may be solitary or gregarious (see FLOCKING), and they may be silent or noisy, uttering harsh cries, resonant notes, or musical song (see VOCALIZATION; also MECHANICAL SOUNDS). Their behaviour has many facets, sometimes including elaborate displays (see DISPLAY). Sometimes, quite small differences in adaptation enable closely related species—or unrelated species of similar mode of life—to inhabit the same area without extreme competition.

With all these variations on the main theme, it is not surprising that categories and kinds of birds have multiplied exceedingly. Apart from birds of the past, known only from the geological record or more recently lost, there are about 8,600 species of birds living in the world today. On the classification followed in this work, these are divisible among 29 orders, comprising 181 families (see CLASSIFICATION; and Table of Classification at the beginning of this book).

See also ORNITHOLOGY. A.L.T.

(The following is a list of some general works published in the present century, or in the last dozen years of its predecessor; some of them contain abundant references to earlier sources.)

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AVIAN: pertaining to birds. The alternative form 'avine', although said to be classically preferable, is little used.

AVIAN POX: see DISEASE.

AVIARY: see AVICULTURE.

AVICULTURE: the keeping and breeding of non-domesticated birds in captivity. The term does not include the breeding of domesticated species such as the Budgerigar, Canary and Zebra Finch (see CAGE BIRD). It embraces a very wide range of avian families of which the most popular are parrots (Psittaciformes), especially Australian parakeets, lovebirds and the larger parrots (Amazons, cockatoos and macaws), British finches, exotic finches such as grassfinches *Poephila* from Australia, waxbills *Estrilda* from Africa and mannikins (nuns) *Lonchura* from Asia and Indonesia, exotic pheasants and waterfowl and a wide variety of species known as softbills which are omnivorous or feed mainly on fruit and insects. The latter group includes such diverse kinds as hummingbirds, sunbirds, tanagers, white-eyes *Zosterops*, barbets, toucans and turacos.

Since the 1960s and 1970s the emphasis has changed gradually from imported to aviary-bred birds. There are two basic reasons: worldwide legislation which has reduced and, in many cases, strictly controlled trade in fauna, which had reached unacceptably high proportions, and the satisfaction which aviculturists have discovered in breeding birds. There is a more altruistic purpose for some: to conserve declining and endangered species in captivity. Habitat destruction, especially that of rain-forests, which harbour a richer and wider range of species than other habitats, has resulted in many bird species becoming endangered. Some of these adapt well to captivity and are being bred in numbers which ensure their future survival, even if they become extinct in their natural habitat. This is especially true of many species of pheasants and some waterfowl and parrots, but species in many other groups are destined, in the future, to be saved from extinction by captive breeding.

Private aviculturists, often known as 'bird-fanciers', are playing an increasingly significant role in this work and generally have done more to establish species in captivity than have zoos. Private aviculturists have also bred multiple generations of many species which are no longer available from their country of origin because export is prohibited. For example, since Australia ceased commercial export of its fauna in 1959, almost all the Australian parakeets and grassfinches have been established in captivity and all those available are aviary-bred—not imported—birds.

Formerly aviculturists tended to keep mixed collections of a wide variety of species. Today there is more specialization, thus resulting in better breeding results. Many specialist societies have arisen; in the UK they include the Australian Finch Society, the Parrot Society and the World Pheasant Association. Specialist societies produce journals, such as the monthly magazine of the Parrot Society, which reaches breeders all over the world. The longest established society worldwide, founded in 1894, is the Avicultural Society, whose journal, the *Avicultural Magazine* (published continuously since that date), widely acclaimed as the most scientific avicultural journal, publishes detailed accounts of breeding and behavioural studies of birds in aviculture. The Avicultural Society and Parrot Society also produce annual registers of birds bred by members, valuable documents in indicating the increase in captive breedings, and the World Pheasant Association carries out regular censuses to establish the status of all species of pheasants, a number of which have larger stocks in captivity than in the wild.

Since the 1970s veterinary and technological developments have resulted in aviculture being elevated from a hobby to the status of a science. Inauguration of sexing techniques, such as surgical and faecal analysis, and the careful formulation of commercial diets, have vastly increased its efficiency. See also AGE; BEHAVIOUR, HISTORY OF; CAGE BIRD; DOMESTICATION; VOCALIZATION. R.L.

AVIFAUNA: the bird-life of an area (see under Regional articles).

AVOCET: substantive name of species in one genus of Recurvirostridae (Charadriiformes, sub-order Charadrii), used without qualification for *Recurvirostra avosetta*; in the form 'stilts and avocets', general term for the family. This almost cosmopolitan group comprises 4 avocets *Recurvirostra* spp. and 2 species in monotypic genera: the Stilt *Himantopus*

himantopus (the several races having different adjectival English names) and the Banded or Red-breasted Stilt *Cladorhynchus leucocephalus*.

Characteristics. Avocets and stilts are long-legged, long-billed wading birds ranging from 29–48 cm in length, including the bill. Avocets have strongly recurved, slender awl-like bills; stilts have slender, slightly up-tilted bills. The legs of stilts are longer in proportion to the remainder of the body than in any other birds except flamingos. In general, the feet have slight or larger webs; the hind toe is rudimentary or absent. The head is small, the neck rather long; the wings are long and pointed; the tail is short and square.

The plumage of most species shows a pattern of black and white, but some have patches of tan to chestnut on some part of the head, neck or breast. The legs of avocets are slaty, those of the stilts some tone of pink. The Stilt's bright-red iris is noticeable under good conditions. Throughout the family the sexes are either alike or little different. Immature birds tend to have some brown in the plumage. The Banded Stilt has a chest-band of bright chestnut and yellowish legs.

Habitat. Avocets and stilts frequent shallow lakes, marshes and pools. Stilts, although found at the edges of large brackish or salty lakes, appear more commonly than avocets in freshwater areas and flooded marshlands. The Banded Stilt is a bird of salt marshes. The Avocet of the Palearctic breeds in saline areas near the coast, river deltas, muddy flats and lagoons, though in parts of the Netherlands breeding area the salinity is quite low. The American *Recurvirostra americana* breeds also on the shores of marshes and lakes; the Chilean *R. andina* frequents saline lagoons in the Andes. The Red-necked Avocet *R. novaehollandiae* is found along Australian estuaries, on mudflats, fresh and brackish swamps, inland waters, claypans and saltfields.

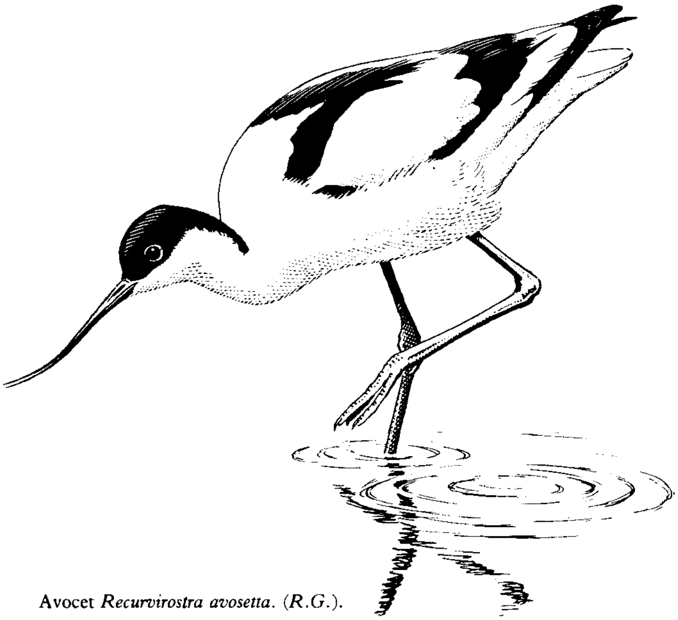
Distribution and populations. The Avocet *R. avosetta* is a Palearctic and Afrotropical species, breeding on the coasts of the North Sea and the Baltic, also around the Mediterranean and from the Caspian Sea eastwards to northern China and as far south as Iraq and Baluchistan. There is a population in south-west Africa. The Avocet ceased to nest in Britain for nearly a century after 1842; its return since the middle of the 20th century has been one of the triumphs of British wildlife conservation. Several hundred pairs now breed, out of a Baltic/North Sea population of some 10,000 pairs. The American Avocet breeds as far north as southern Canada and reaches Central America in winter; the Chilean Avocet is found from southern Peru and northern Chile to north-west Argentina. The Red-necked Avocet is patchily distributed over much of Australia and is a vagrant to New Zealand.

The Stilt is an almost cosmopolitan species with 5 recognized geographical races. The Black-winged *himantopus*, with white head and neck, breeds in the southern Palearctic from the Mediterranean east to China, also through much of southern Asia, Africa and Madagascar; it nests irregularly in central and western Europe. The Black-necked *mexicanus* breeds from southern North America to northern South America, including the West Indies and the Galapagos. The White-headed or Pied *leucocephalus* is the representative form in Australasia; melanistic birds are found in New Zealand and intermediates occur. Other races inhabit the middle latitudes of South America and Hawaii. The Banded Stilt is confined to Australia.

Movements. The winter range of the Palearctic Avocet extends from south of Brittany to Senegal and Gambia, from the Mediterranean to the Sahel south of the Sahara, in East Africa to Burundi and Tanzania, from the southern Caspian region to the Arabian peninsula. It further includes Pakistan, India and eastern China south of the Yangtze River. In mild winters many birds migrate no farther than western central Europe, e.g. in February 1975 at least 1,200 birds stayed in the Dollart (estuary of the Ems). A smaller number winter regularly in the west of England.

Food. In areas where there is little vegetation the Palearctic Avocet catches its food by a side-to-side sweep of the bill through shallow water or the surface slime exposed by the receding tide. In deeper water avocets put their heads beneath the surface and 'up-end'. In the British breeding places the main food has been found to be the larvae and imagines of Diptera (especially Chironomidae, Dolichopodidae and Ephydridae), of beetles (especially *Enochrus maritimus* and *Berosus spinosus*) and crustaceans (*Euryptemora velox*, *Mesochra lilljeborgi* and *Fabrina salina*). The other avocet species have similar feeding habits.

The Stilt also collects its food chiefly from the water surface or from floating vegetation. It consists mainly of insects and their larvae; also some freshwater molluscs and small worms and the spawn and tadpole stages of amphibia. The Banded Stilt feeds on the shrimps which multiply in the temporary sheets of water it frequents.



Avocet *Recurvirostra avosetta*. (*R.G.*).

Behaviour. Avocets when only a few hours old swim freely. Both they and stilts walk gracefully with long strides that quicken almost to a run. In water they wade to above the intertarsal joint, even belly deep in soft mud.

The sexes recognize each other by morphological and/or auditory signals, not only by individual behaviour during intraspecific contacts. The mating ceremonial begins with ritualized preening of the breast feathers, and the bill is dipped into the water. Pair formation is followed by 'false' nesting activities and grouping. The pair bond, which is particularly important to monogamous birds breeding in colonies, is strengthened by group display, which may take place either on land or in the water. It is performed by 3–12 (at first even up to 20) mainly paired birds, which endeavour to keep side by side and press close together. Occasionally copulation takes place before or after group display. Maturity is often reached at the age of 2 years, exceptionally when the bird is 1 year old. The display of the Stilt consists of dancing and jumping movements with wing-flapping and jerking of the head.

Voice. The characteristic call of the Avocet is a melodious *kluut* which gives the bird its Dutch name; repeated rapidly it becomes an alarm note. A number of others are used at the breeding colony and in display. The ordinary call of the Stilt is a rapid *kik kik kik*; that of the Banded Stilt is described as a 'wheezy puppy-like bark'.

Breeding. Avocets nest in colonies of 10–70, more rarely up to 200 or more pairs. The open nests, 2–60 m or farther apart, are made on grass, sand or mud, either bare hollows or lined with dead vegetation; in shallow water they may be built up to 25 cm. The clutch-size is usually 4, more rarely 3 or 2, exceptionally 5 eggs. Clutches of 8–12 eggs in large colonies must be due to more than one female. Laying in western Europe begins in the first third of April, but flightless young may still be seen in August. Both parents take part in incubation, which lasts 23–25 days. They also tend the young, which are able to fly in 32–42 days. There is only one brood.

The Stilt usually nests in colonies near or in shallow lagoons or on flooded areas near rivers. Some nests are substantial, built up of stalks and mud; others, in tussocks, are slight. The clutch is of 4 or 3 eggs. The relatively frequent occurrence of 5–9 eggs in one nest may be due to lack of nest-sites at some colonies. The breeding season in south-west Europe is from mid-April to June. The parents share incubation for 22–24 days and the young fledge in about 4 weeks, tended by both parents. Stilts are single-brooded. The Banded Stilt breeds in colonies, sometimes huge ones, on islands in large inland lakes. They tend to change their locations and for a long time no site was known. The clutch is of 3–4 chalky eggs.

(P.J.C. (1)) H.B.

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McGilp, J.N. & Morgan, A.M. 1931. The nesting of the Banded Stilt (*Cladorhynchus leucocephalus*). S. Australian Orn. 11: 37–52.
Makkink, G.F. 1936. An attempt at an ethogram of the European Avocet (*Recurvirostra avosetta* L.). Ardea 25: 1–62.
Olney, P.J.S. 1970. Studies of Avocet behaviour. Br. Birds 63: 206–209.
Tjallingii, S.T. 1969. Habitat-Keuze en-gebruik van de Kluut. Doktoraalonderzoek Zoöl. Labor. Rijksuniv. Groningen.

AVOCETBILL: substantive name of the HUMMINGBIRD *Opisthoprora euryptera*, except for the AWLBILL the only member of the family with an upturned bill.

AWLBILL: substantive name of the HUMMINGBIRD *Avocettula recurvirostris*, except for the AVOCETBILL the only member of the family with an upturned bill.

AXIAL SKELETON: the part of the skeleton consisting of the skull, vertebral column, ribs, and sternum; contrasted with the APPENDICULAR SKELETON (see also SKELETON, POST-CRANIAL; SKULL).

AXILLARIES: (plural) the feathers in the axilla ('armpit')—see TOPOGRAPHY.

AXIS: the second vertebra, immediately posterior to the atlas (see SKELETON, POST-CRANIAL).

AYTHYINI: see DUCK.

AZURECROWN: substantive name of some *Amazilia* spp. (for family see HUMMINGBIRD).

B

BABAX: substantive name sometimes used for 2 species of BABBLERS of the genus *Babax*.

BABBLER: substantive name of many species of the family Timaliidae (Passeriformes, suborder Oscines); in the plural, general term for the family. (The name has also been applied to some Rhinocryptidae—see TAPACULO). The genera of Old World insectivores combined under the general name of babblers include a considerable diversity of forms which defy precise physical characterization. Although here treated as a separate family, they are often regarded as a subfamily of the Muscicapidae, together with the Old World warblers (Sylviinae), flycatchers (Muscicapinae) and thrushes (Turdinae). Unlike these, however, the babblers do not occupy any well defined group of ecological niches, and include both thrush-like and warbler-like forms, as well as genera of mixed insect- and fruit-eaters comparable to the bulbuls (Pycnonotidae). Delacour (1946, 1950) considered the Timaliidae to be closest to the Sylviidae, some genera being difficult to assign between the two. He recognized 6 tribes; the jungle babblers (Pellorneini, 5 genera), scimitar-babblers and wren-babblers (Pomatorhinini, 11 genera), tit-babblers (Timaliini, 6 genera), wren-tit and reedlings (Chamaeini, 2 genera), song-babblers (Turdoidini, 17 genera) and the rockfowl (Picathartini, 1 genus). Voous, whose treatment is followed here, raises the wren-tits and rockfowl to the status of subfamilies (Chamaeinae, Picathartinae) and adds the parrotbills (Paradoxornithinae, see PARROTBILL), including the reedlings *Panurus*, as another subfamily. The rail-babblers, often regarded as a subfamily of the Muscicapidae, are also included in the Timaliidae but are treated separately (see RAIL-BABBLER).

Characteristics. Babblers, which range in length from 10–35 cm, differ from thrushes and flycatchers in having no distinctive juvenile plumage. Juvenile birds can usually be told from adults in the hand by their softer, less pointed flight feathers, particularly the first primary, and in some species by differences in the intensity of plumage coloration. There is normally a complete post-juvenile moult commencing one or two months after fledging. In most species the sexes are alike and sexual dimorphism in body measurements is small, so that sexing of individual birds, even in the hand, may be impossible. In the few genera where the sexes are dimorphic (*Pteruthius*, *Myzornis*, *Leiothrix*, *Cutia*) the post-juvenile moult involves only the body and covert feathers and the typical rounded shape of the juvenile flight feathers is absent. The colour of the adult plumage is very variable, with some genera showing bright colours while others are uniformly dull brown. In general the brightly coloured forms are found in moist habitats, particularly evergreen rain-forest.

As a rule, babblers tend to be heavy-bodied compared with warblers or flycatchers, with stronger legs and stouter bills. The largest babblers are similar in size to small corvids and the majority of these feed on the ground, although some small forms, resembling the robins *Erithacus*, are also ground-feeding. Species which forage in the forest canopy are mainly similar to warblers in size, while those inhabiting the shrub layer or occurring in scrub range from wren-like forms to birds the size of thrushes *Turdus*. The majority, however, are sparrow-sized or smaller. The sibias, *Heterophasia* spp., which inhabit the middle storey of the forest, are at the larger end of this scale. Non-arboreal babblers are characterized by short wings and moderately long tails, both probably associated with their infrequent bouts of sustained flight.

One of the most distinctive characteristics of the babblers is their gregariousness and this may be influenced by the completely sedentary nature of most species. Migration over long distances is not found in the group, in strong contrast to the thrushes, warblers and flycatchers.

Habitat and distribution. In keeping with the range of niches occupied, babblers occur in a wide variety of terrestrial habitats, from tropical evergreen rain-forest to full desert. In the Himalayas they occupy all altitude zones up to the alpine areas above the tree-line. Arboreal species are most numerous in rain-forest, particularly in the Oriental Region (a total of 139 species occur in south-eastern Asia), while shrub- and ground-living species occupy a wider range of ecosystems. None venture into completely open habitats, the desert-living species being found in bushes along wadis or in palm groves.

The song-babblers, the largest tribe, cover the whole Old World range of the family. The jungle babblers are restricted to the Old World tropics and the tit-babblers are found in Madagascar, where they are represented by the endemic genus *Neomixis*, and in the Oriental Region. The scimitar-babblers and wren-babblers are confined to the Oriental Region, Australia and New Guinea. The rockfowl are found locally in the upper and lower Guinea forests of Africa. The wren-tit *Chamaea* is found in coastal areas of western North America, from Oregon to Baja California. Only a few species penetrate the Palearctic Region; the desert-living members of *Turdoides* are found in North Africa, Arabia and Iran and representatives of a number of otherwise Oriental genera penetrate southern and western China, *Yuhina* reaching as far north as Japan. Throughout most of the Oriental Region babblers constitute 6—15% of all passerine species in forest or scrub ecosystems. In the middle-altitude forests of the Himalayas the proportion may rise as high as 20%, but in Africa the family generally constitutes a much smaller fraction of the avifauna.

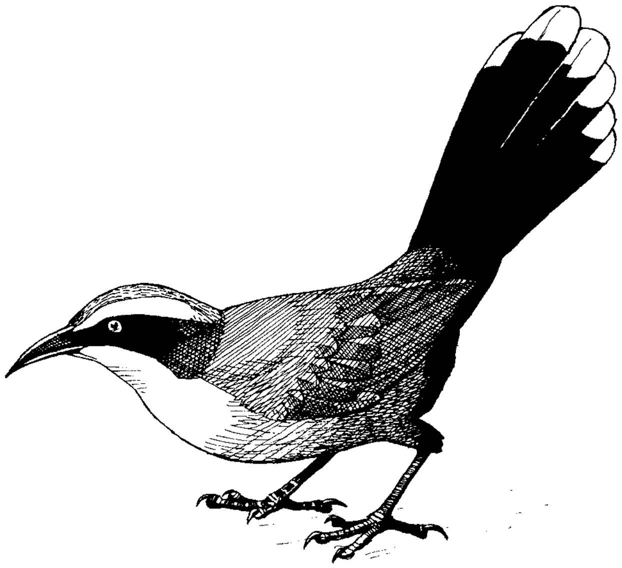
Food. Most species are insectivorous, but many augment their diet with fruit, seeds and nectar and some can be regarded as genuinely omnivorous, particularly outside the breeding season. Feeding strategies such as flycatching, hovering, or pouncing on ground-living invertebrates from a perch are rarely employed. Ground-feeding species usually rummage in leaf-litter, tossing it aside with their bills. Arboreal forms tend to feed by pedestrian searching, hopping from twig to twig, and gleaning food from the surface of leaves or bark.

Behaviour and voice. Practically all babblers occur during most of the year in small parties numbering 3–30 birds. Solitary babblers are rare, pairs are uncommon, and so are flocks of more than 30 birds of the same species. In several species which have been studied intensively, groups have been found to maintain a constant membership over weeks or months, defending a common territory against neighbouring groups. In some species of *Turdoides* only one or two pairs breed each year out of groups comprising up to 20 birds. Some non-breeders usually participate in incubation and post-juvenile group members bring food to the nestlings. Groups apparently originate through the deferred dispersal of young birds, which may remain for several years in their natal territory (Gaston 1977, 1978). Their vocalizations consist of a wide range of squawks and whistles. This pattern of behaviour and calls appears typical of all species of *Turdoides* except the Spiny Babbler *T. nipalensis*, which breeds in pairs and has a melodious, thrush-like song. It probably occurs also in many species of laughing thrushes or jay-thrushes *Garrulax*, several of which certainly defend group territories, advertising them by means of communal choruses. In the White-crested Laughing Thrush *G. leucolophus* the chorus is initiated by a single bird, others chiming in at intervals so that the noise rises to a crescendo. Similar choruses have been recorded in some species of *Turdoides* and in the Black-headed Babbler *Rhopocichla atriceps* and are delivered frequently just before groups go to roost.

Members of territorial groups usually roost in shrubs and trees but the Black-headed Babbler roosts in an old nest. Within the roost group members are in bodily contact with each other. In the Yellow-eyed Babbler *Chrysomma sinensis* roosting groups of 20–30 birds may split into several foraging parties during the day, reassembling in the evening. In the White-throated Laughing Thrush *Garrulax albogularis* the opposite occurs and large foraging groups of up to 40 birds split into sub-groups of 2–6 as they go to roost, each group occupying a different tree.

Group territorial babblers often perch in contact with one another during the day and this is frequently accompanied by ALLOPREENING. In the Jungle Babbler *Turdoides striatus* and the White-crested Laughing Thrush allopreening interactions are determined by a hierarchical structure within the group, with adults preening sub-adults more frequently than vice-versa. Groups feeding on the ground often maintain a sentinel in a nearby tree. This duty is changed at regular intervals but is assumed mainly by birds at the top of the social hierarchy, particularly the breeders. Observations of adult babblers feeding one another outside the breeding season may also relate to dominance within the group.

Although co-operative breeding is evidently widespread among babblers, the details of the social systems involved differ considerably. In the sparrow-sized Common Babbler *Turdoides caudatus* one male may breed



Grey-crowned Babbler *Pomatostomus temporalis.* (*N.W.C.*).

successively during the same season with two different females from within the same group. In the Yellow-eyed Babbler, a small species inhabiting scrub and grassland, groups fragment into pairs at the start of the breeding season, most nesting within the home range of their former group and some, but not all, having one or two non-breeding helpers. Helpers have also been recorded in the small arboreal genus *Yuhina* and the pattern seen in the Yellow-eyed Babbler may be typical of many of the smaller members of the family, although evidence is lacking for most species.

The sedentary behaviour of most babblers has undoubtedly contributed to the evolution of diverse patterns of social behaviour and to the prevalence of group territoriality and co-operative breeding. Genera such as *Turdoides* and *Garrulax* show a complexity of social relations within groups comparable with that observed in primates and other social mammals, suggesting that this behaviour has evolved over a long period. Among species which do not appear to hold group territories, the sibias form loose feeding aggregations outside the breeding season. The wren-like genera *Spelaeornis* and *Pnoepyga* occur in pairs during the breeding season and are otherwise solitary, giving regular loud vocalizations which apparently serve to advertise their presence and maintain spacing. Perhaps significantly, these genera include some of the most migratory species of babblers, breeding in the alpine zones of the Himalayas and moving down in winter to warm-temperate or subtropical altitudes. Scimitar-babblers of the genus *Pomatorhinus* are normally found in pairs which give regular antiphonal vocalizations as they move through dense undergrowth. Small parties of other babblers also keep up continuous low vocalizations while feeding, apparently to maintain contact.

Arboreal genera such as *Alcippe*, *Yuhina* and *Pteruthius*, which usually move in parties of 5–20 birds, often participate in mixed species flocks with other small insectivores such as tits *Parus* spp., warblers and flycatchers. In these associations the babbler groups sometimes appear to act as nuclei around which other species coalesce. Groups of ground-feeding *Garrulax* and *Turdoides* spp. also attract attendant birds, particularly drongos *Dicrurus* and woodpeckers in the genus *Dinopium*.

Breeding. Jungle babblers, scimitar-babblers, wren-babblers and tit-babblers normally build domed nests, either on the ground, or low down in dense vegetation. The song-babblers, on the other hand, mainly build open nests, rarely on the ground, more often in bushes or trees. The rockfowl build cups of mud on vertical or overhanging rock faces and usually nest in small loose colonies. The eggs of open-nesting song-babblers are frequently unmarked, either creamy white or blue, those of some jungle babblers and tit-babblers which build domed nests are speckled, and those of the rockfowl are heavily marked much like some corvids. The eggs of scimitar-babblers are white and those of the wren-babblers whitish with brown speckles. In the genus *Garrulax* there seems to be a relationship between egg-colour and social behaviour; species breeding in pairs usually lay speckled eggs, while those breeding in groups lay unmarked eggs.

Incubation periods, where known, are typical of insectivorous passerines, ranging from 13–16 days, and nestling periods are similar. However, the rockfowl of West Africa incubates for 24 days and young are in the nest for 26 days (Grimes and Darku 1968). Nestlings tend to leave the nest before fully capable of flight. Post-fledging dependence, by contrast, is usually prolonged, lasting for at least a month, although in group territorial species the period is hard to define because young birds remain with their natal group for at least a year and may occasionally receive food long after they have apparently achieved independence. (J.T.D.) A.J.G.

Delacour, J. 1946. Les timaliinés. Oiseau 16: 14–36.

Delacour, J. 1950. Les timaliinés. Additions et modifications. Oiseau 20: 186–191.

Gaston, A.J. 1977. Social behaviour within groups of Jungle Babblers *Turdoides striatus*. Anim. Behav. 25: 828–848.

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Grimes, L.G. & Darku, K. 1968. Some recent breeding records of *Picathartes gymnocephalus* in Ghana and notes on its distribution in West Africa. Ibis 110: 93–99.

Voous, K.H. 1977. List of recent Holarctic bird species (Passerines). Ibis 119: 223–250, 376–406.

BABBLER, RAIL-: see RAIL-BABBLER.

BACK: see TOPOGRAPHY.

BALAENICIPITES; BALAENICIPITIDAE: see under CICONIIFORMES; SHOEBILL.

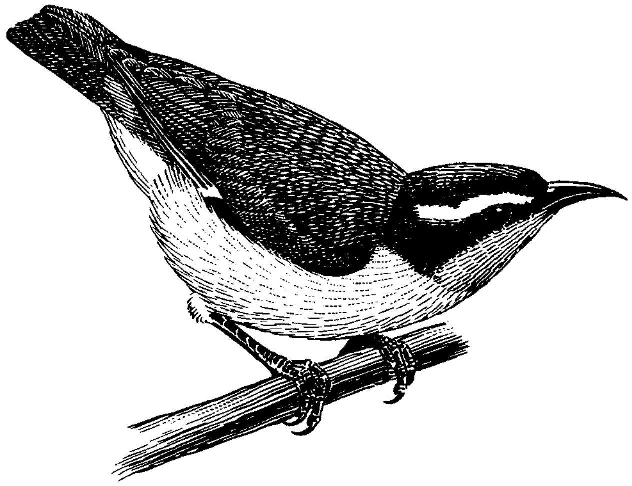
BALANCE: see HEARING AND BALANCE.

BALDPATE: a name for the American Wigeon *Anas americana* (see DUCK).

BALEARICINAE: see CRANE.

BAMBOO-WREN: substantive name of the TAPACULO *Psilorhamphus guttatus*.

BANANAQUIT: *Coereba flaveola* (Passeriformes, suborder Oscines), a widespread bird of tropical America, especially well known in the West Indies where it is the commonest bird on many islands and has acquired many local names. The Bananaquit is a small bird (about 11 cm long), mainly dark grey above and yellow below, with a white superciliary stripe (except on St Vincent and Grenada, where most individuals are blackish), and a sharply pointed decurved bill and tubular tongue adapted for sucking nectar and fruit juices. Its systematic position has been controversial. Formerly placed with the honeycreepers (see HONEYCREEPER (1)), FLOWER-PIERCERS and CONEBILLS in a family, Coerebidae, it has



Bananaquit *coereba flaveola*. (*R.G.*)

since been shown that this is almost certainly not a natural group and that the honeycreepers and flower-piercers are specialized tanagers (see TANAGER) while the Bananaquit and conebills may be closer to the American warblers (see WARBLER (2)). This is by no means certain, however, and the Bananaquit is here provisionally placed, with the conebills, in a reduced family Coerebidae. It may well be that future research will modify the present arrangement.

One of the features that distinguishes the Bananaquit from the tanagers is the form of its nest, which is roughly globular with a small doorway opening obliquely downwards. Both sexes build, constructing dormitory nests which are used only for sleeping as well as the more substantial breeding nests. Separate dormitory nests are used by the male and female of a pair. The breeding season tends to be very long, being at its height (like that of hummingbirds) when nectar-producing flowers are most abundant. The clutch consists usually of 2, less often 3, brown-spotted eggs. The incubation period is 12–13 days, and the fledging period 17–19 days, the nestlings being fed mainly by regurgitation. D.W.S.(1)

Skutch, A.F. 1954. Life histories of Central American birds. Pacific Coast Avifauna No. 31.

BANDING: see MARKING.

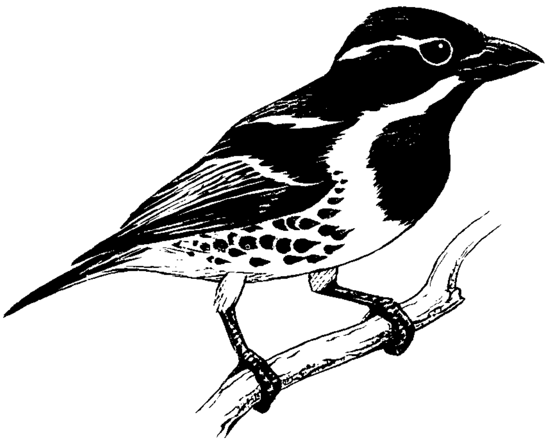
BANTAM: a miniature breed of domestic fowl.

BARB: alternatively 'ramus', a lateral branch of the rachis of a feather, i.e. a constituent unit of the vane (see FEATHER).

BARBET: substantive name of the species of Capitonidae (Piciformes, suborder Galbulae); in the plural, general term for the family, the name 'barbet' coming from the feathers and bristles around the base of the bill. Barbets are usually divided into 13 genera and 76 species and inhabit mainly the tropical forests of the Afrotropical, Oriental and Neotropical Regions. The majority (42 species in 5 genera) occur in Africa where several species have exploited much more arid habitats than those in other continents. Thus the small savanna tinker-birds (*Pogoniulus* spp.) and 3 ground nesting species (*Trachyphonus*) found in Africa do not have counterparts in Asia or tropical America. In contrast, only 12 barbets in 3 genera are found in South America. Speciation has resulted in notable instances of convergence; thus the Black-backed Barbet *Lybius minor* of central Africa is similar in several aspects to the White-mantled Barbet *Capito hypoleucus* in South America. Again each continent has produced a small-medium species with a predominantly brown plumage and each is highly social (Goodwin 1964). Although there are considerable differences in habit and external form between the small, agile and energetic members of the family, the slim longer-legged ground-nesting barbets of Africa, and the larger Asiatic forms, there seems ample justification for grouping them in one family.

Characteristics. Barbets are strongly built, thickset birds with rather large heads, ranging in size from about 9 cm in the tinker-birds of Africa to more than 33 cm in the larger members of the Asiatic genus *Megalaima*. The bill is stout, conical, and sharply tipped, proportionately longer and more formidable in some of the larger species. Several have notches in the bill to assist grip and this is well developed in the Double-toothed Barbet *Lybius bidentatus* and in the Pied or White-headed Barbet *Lybius leucocephalus*, both found in the African savanna. The legs are comparatively short and the feet are zygodactyl and well adapted for clinging woodpecker-fashion to trees; when doing this the tail is often used as a support, although the feathers are not stiffened for the purpose. The large barbets appear heavy, clumsy birds, but some of the smaller ones, such as the Red-headed Barbet *Eubucco bourcierii* of South America, are very agile. While foraging, it frequently hangs head downwards probing and boring into rotten wood. The wings are rather short and rounded, and flight, although rapid, is not usually sustained for long distances and appears weak. Progression on the ground is by rather clumsy hops.

Most of the barbets are brightly coloured, some of the Asian and South American species being the most beautifully plumaged of all birds. In these, green predominates, with red, blue and yellow markings around the head. In African barbets, black, yellow and red predominate, green is essentially absent, and there is a greater tendency towards spotting and barring than is found in species elsewhere. Although in most South American species the sexes are dimorphic and readily distinguishable in the field, this is generally not the case in Africa and Asia. Only the Red and Yellow Barbet *Trachyphonus erythrocephalus* in Africa and the Gaudy Barbet *Megalaima mystacophanes* in Asia have marked sexual dimorphism.



Spotted-flanked Barbet *Lybius lacrymosus*. (*P.J.K.B.*).

Movements. Barbets are comparatively sedentary and any movements seem to be governed by the availability of food rather than by seasonal migration.

Food. Barbets feed chiefly on fruits, berries, and buds but most species include some insects in their diet and the larger species occasionally take young birds, mice, and lizards. In many species a switch of diet, from frugivorous to insectivorous, takes place during the breeding season, and this is particularly the case in captive barbets. The African 'ground barbets' are mainly insectivorous as is the Red-headed Barbet. Some barbets work over the bark of trees like woodpeckers and bore into rotten wood in search of insects. Although most indigestible matter, such as insect wings and legs and vertebrate remains, are regurgitated as 'pellets', the skins and seeds of grapes, berries, and other fruit are passed in the faeces.

Fruit-eating barbets are very wasteful feeders, plucking and rejecting many of the berries and small fruits which they attack, while they so persistently shake their heads and wipe their bills to rid themselves of pieces of fruit which adhere to them that more seems to be cast away than is swallowed.

Behaviour. Most barbets live singly or in pairs, although some of the smaller species may, out of the breeding season, be seen in the tree-tops in parties, sometimes in the company of other birds. Little seems to be known about their territorial requirements, although many savanna species, at least, hold territories and respond vigorously to a playback of their calls. Some species of barbets when in captivity are extremely pugnacious towards conspecifics of either sex except when breeding. They usually roost in holes, often boring a special roosting hole which may be later used for breeding. In some of the smaller species a large number of birds may roost together in 'dormitories', such as woodpecker holes, that sometimes contain as many as 16 individuals. In some African barbets co-operative breeding takes place (see later).

Voice. Most barbets can hardly be described as possessing a song in the usual sense of the word, uttering instead an oft-repeated single note or a series of very monotonous notes, in many cases quite un-musical, and resembling honks, chirps or the tapping of a hammer on a hollow object. In some species the males utter a very rapid version of the *poo-poo-poo* of the Hoopoe *Upupa epops*. Duetting has been studied in several species of African barbets and reported in both Asian and American species (Payne 1971, Kunkel 1974). One of the most notable is the East African Red and Yellow Barbet. A pair of birds, usually sitting close together, will simultaneously burst into loud, cackling songs, composed of different notes and not necessarily in the same tempo but which rhythmically synchronize so well that it is difficult to tell which bird is producing which notes except by the bobbing and tail wagging display which accompanies the duet. Although usually described as a 'duet', it is sometimes a chorus of the combined efforts of a family party. In the field this duet is very similar to that of the closely related D'Arnaud's Barbet *Trachyphonus darnaudii*.

Breeding. In most cases there is little formal courtship apart from the chasing of the female by the male, although in the 'ground barbets' the male struts and postures around the female with his erectile crown feathers raised.

Barbets nest in holes, usually excavated by themselves in rotten trees, euphorbia stems, termite mounds and sand or earth banks, in which case several pairs may nest close together, forming a small colony. The nest-hole entrance of the smaller species is circular but may be quite ragged and irregular in the larger species such as the Double-toothed Barbet and *Megalaima* species. The Double-toothed Barbet often uses the same nest-hole for several consecutive seasons. D'Arnaud's Barbet bores a tunnel almost vertically downwards into level ground, swinging horizontally at the bottom to form a nest-chamber. The Pied Barbet appears to be the only species which, in the absence of suitable trees for boring, will take over deserted nests of other birds, such as swallows and martins.

No nest material is used, the 2–5 white eggs resting on the bottom of the nest-hole. Incubation (12–15 days) and rearing are shared by both parents, food being carried direct to the young in the bill except for a few of the smaller species, such as the Red-fronted Barbet *Lybius diadematus*, which regurgitate semi-digested food deep into the throats of the nestlings.

Nest sanitation varies between species and at different stages of development of the young. Faeces are sometimes swallowed whole by the parents, sometimes pounded with the wood dust at the bottom of the nest into a bolus which is carried away. This latter behaviour may account for the persistent tappings that are sometimes heard from within the nest-hole and referred to below.

The fledging period is not known with certainty for any species in the wild, but has been estimated in 2 species at more than 17 days. The young emerge well-developed and, in most cases, able to fly well, although they continue to demand food from their parents long after they appear well able to fend for themselves. Young males of the South American Red-headed Barbet emerge from the nest in almost full adult plumage with a red head.

Co-operative breeding has been proved to occur in 4 species of African barbets and suspected in others (Grimes 1976). Up to 4 adult Red and Yellow Barbets have been observed taking food to a nest-hole and ringing has shown that young of a first brood will assist in rearing a second.

Unlike, for example, the woodpeckers, there is little actual nest-chamber and not only may the adult birds incubate in what appears to be a most uncomfortable position, but the young are extremely cramped. Persistent tapping from within the hole may indicate an attempt by the growing young to enlarge the nest-chamber. This may well be one of the explanations for the extraordinary 'lesions' which occur on the heels of nestling barbets, serving as a protective grip in place of the claws which are necessarily 'folded' upwards through the cramped position. These disappear shortly after the young leave the nest. It is noteworthy that similar 'heel-pads' are present in some species of honeyguides which are parasitic on African barbets. Several instances have been recorded in captivity of the fledgling young being 'released' by the parents boring into the tree at nest-chamber level. (J.T.D.) M.D.E.

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BARBICEL: a process on a barbule (radius) of a barb (ramus) of a feather; the hooked barbicels on the distal side of a barbule engage with the spoon-shaped proximal barbicels of the next barbule, thus maintaining the coherence of the vane (see FEATHER).

BARBTAIL: *Premnoplex brunnescens* (see OVEN-BIRD (1)).

BARBTHROAT: substantive name (sometimes 'hermit') of *Threnetes* spp. (for family see HUMMINGBIRD).

BARBULE: alternatively 'radius', a lateral branch of a barb (ramus) (see FEATHER).

BARE-EYE: substantive name of *Phlegopsis* spp. (see ANTBIRD).

BARE PARTS: the areas of the body surface which are not covered by feathers, namely the bill, eyes, legs and feet, together with any unfeathered skin (see INTEGUMENTARY STRUCTURES).

BARRANCOLINO: *Teledromas fuscus* (see TAPACULO).

BARWING: substantive name sometimes used for the tropical Asian BABBLERS of the genus *Actinodura*.

BASIC PLUMAGE: in species which wear the same plumage the whole year round, this is the basic plumage. If two different plumages are worn per year, the basic is usually the dull plumage worn outside the breeding season. The term is part of a modern American terminology. The equivalent of basic plumage in the classical terminology is annual or non-nuptial plumage (see PLUMAGE).

BASIOCCIPITAL: a paired bone of the SKULL.

BASIPTERYGOID: see SKULL.

BASISPHENOID: a paired bone of the SKULL.

BASSIAN: see AUSTRALASIAN REGION.

BASTARD WING or **ALULA:** also called 'ala spuria', consists of a number of small quill feathers attached to the first digit (see WING).

BATELEUR: *Terathopius ecaudatus*, an aberrant African harrier-eagle (see HAWK).

BATESIAN MIMICRY: when a relatively scarce, palatable and vulnerable species resembles an abundant, relatively unpalatable or well-protected species, and gains protection thereby. See COLORATION, ADAPTIVE; MIMICRY.

BAT-HAWK: *Machaerhamphus alcinus* (see HAWK).

BATHING: see COMFORT BEHAVIOUR and photo.

BATING: term used in FALCONRY.

BATIS: substantive name sometimes used for the puff-back flycatchers of the genus *Batis* (see FLYCATCHER (1)).

BAYA: name sometimes used alone for the Baya Weaver *Ploceus philippinus* of India and elsewhere (see WEAVER).

BAZA: substantive name of Asiatic *Aviceda* spp. (see HAWK).

BEAK: synonymous with BILL.

BEARDED TIT: *Panurus biarmicus*, for family see PARROTBILL.

BEAU GESTE HYPOTHESIS: the hypothesis, named after the novel by P.C. Wren, that territorial male songbirds may simulate the presence of many individuals by singing a repertoire of song variants. The advantage to the singer of this hypothesized deception is that potential rivals are discouraged from intruding into the singing bird's territory by the apparent high density of occupants. The deception could only work if intruders use the number of song variants heard to assess bird density in an area. The hypothesis has been criticized on a number of grounds. First, it has been said that the deception would not last long in evolutionary time, since listeners would evolve the capacity to 'correct' for large repertoires in assessing density of songsters. Second, many songbirds sit conspicuously in one position while singing many different variants, a mode of behaviour which does not seem compatible with deception.

BECARD: substantive name of the 16 species of *Pachyramphus* (with which the genus *Platypsaris* is now merged), a group of arboreal, mainly tropical, American birds formerly placed in the Cotingidae but now, on anatomical grounds, considered to be closer to the Tyrannidae (see FLYCATCHER (2)), of which, with the TITYRAS, they are currently considered to constitute a subfamily, Tityrinae.

Becards are compact, medium-sized (13–19 cm), mainly insectivorous birds, with broad, somewhat hooked bills. Most species lack bright colours, but in two, including the Rose-throated Becard *P. aglaiae*, the only species extending as far north as the southern USA, the male has a pink throat-patch. In males only, the 9th primary is highly modified, being narrow and pointed and much reduced in length. Becards build large globular and often conspicuous nests, typically high in a tree or, if lower, near the tip of an outer branch; some species habitually nest in close association with wasps' nests (see NESTING ASSOCIATION).

BECCAFICO: a familiar Italian name ('fig-eater') applied almost indiscriminately to small passerine birds frequenting gardens in autumn and often caught for the table—perhaps particularly Garden Warbler *Sylvia borin* (see WARBLER (1)).

White-throated Bee-eater *Merops albicollis*. (*N.A.*).

BEE-EATER: substantive name of all species of Meropidae (Coraciiformes, suborder Meropes); in the plural, general term for the family. A homogeneous, essentially Paleotropical family (15–38 cm in length) specializing on flying venomous Hymenoptera (ants, bees, wasps) for food. Bee-eaters forage principally by sallying, like flycatchers, and occasionally in continuous flight, like swallows, and most species take non-volant prey only exceptionally. There are 24 species, in 3 genera; *Nyctyornis* (2 species) and *Meropogon* (1 species), inhabit south-east Asian rain-forests; the species of *Merops* (including the formerly-recognized genera *Melittophagus* and *Aerops*) are mainly open-country birds of Africa and southern Asia.

Characteristics. The beak is rather long, slender, laterally compressed and decurved to a sharp point; legs are weak and the feet syndactylous. Most bee-eaters have bright, non-iridescent plumages of green, buff and chestnut, with a black line through the eye, usually a black or blue pectoral band and a contrasting yellow or red throat; but 1 species is mainly black, 2 dark blue and 2 carmine. The sexes are alike. The young hatch naked and most of them fledge in plumage like the adults'. All species nest in tunnels which they excavate in cliffs or flat sandy ground, many breeding colonially. They are sociable birds with melodious voices; several larger species are migratory and have a buoyant, wheeling flight, rather long, pointed wings and elongated central rectrices. Species weights range from 14–70 g. The largest bee-eaters are *Nyctyornis amicta* and *N. athertoni*, stout-beaked primitive birds with green plumage, loose, elongated throat feathers, rounded wings and croaking voices.

Habitat. Three species of *Merops* and the genera *Nyctyornis* and *Meropogon* inhabit the middle storeys and canopy of lowland tropical rain-forests, which is probably the ancestral habitat of the family. Other bee-eaters inhabit forest edges and secondary growth; all manner of savannas and timbered open country; marshes, grassland, farmland; and arid sub-desert steppe. They are partial to waterside situations (reed-beds, riverine woods, flooded abandoned excavations), particularly where there are also cliffs and sand-banks suitable for nesting. They perch freely on vegetation and wires, and sometimes on the ground.

Distribution. *Meropogon forsteni* is endemic to Sulawesi rain-forest and *Nyctyornis* to Oriental rain-forest from Wallace's Line to Nepal (the southern *N. amicta* just overlapping the northern *N. athertoni* in Tenasserim). *Merops viridis* and *M. leschenaulti* are Oriental and *M. orientalis* ranges from Indochina to Senegal. The *M. ornatus*/*M. philippinus*/*M. persicus* superspecies inhabits Australia, New Guinea, the Oriental Region, Madagascar and the borders of the Sahara. *M. apiaster* breeds from the Mediterranean basin at least to 50°N and 75°E, and in southern Africa. All other bee-eaters are African.

Movements. All *Merops* species except the forest forms (*M. breweri*, *M. muelleri*, *M. gularis*) and a few small nonforest forms are migratory, *M. apiaster* and the *M. philippinus* superspecies travelling thousands of km.

Food. Investigating bee-eater diets is fairly simple, and numerous studies have been made. When an insect is caught the bird generally returns to a perch to immobilize it; it is then swallowed or carried to the nest, and in either case can be identified readily. Several times a day bee-eaters regurgitate firm pellets of insect sclerites, which can easily be collected near nests and favoured perches for analysis. With few exceptions, *Merops* species prey on flying insects and 60–95% of the diet of each species are bees, wasps, hornets and related stinging insects. Honey-bees *Apis mellifera* are sought after to the extent that bee-eaters have been persecuted as pests at apiaries; a collection of pellets from any African locality nearly always contains honey-bees, which commonly form about 25% numerically (more by volume) of the entire diet and may comprise over 90% of a large sample. Only occasional drones (which are not venomous) are taken, and bee-eaters seem to distinguish the stinging workers and to select them. Venomous Hymenoptera are held at the tip of the abdomen and rubbed against the substrate until venom is discharged, when they are further beaten and then swallowed whole. The behaviour is innate but improves with practice, and the birds seem to have some immunity to venom. Carmine Bee-eaters *Merops nubicus* can evidently devenom *Apis* workers in flight, without having to return to a perch. In most bee-eaters the next largest dietary portion after Hymenoptera is beetles, then grasshoppers, bugs, flies, termites, butterflies, up to the size of cicadas *Platypleura*, dragonflies *Anax* and carpenter-bees *Xylocopa*, (each about 1 g).

The large green bee-eaters (*M. persicus*, *M. philippinus*) take Hymenoptera but specialize on Odonata (dragonflies, demoiselles) which comprise three-quarters of their diets. Carmine Bee-eaters eat many grasshoppers flushed by fire, and they sometimes use bustards, ostriches, grazing mammals, and tractors as 'animate perches'. White-throated Bee-eaters *M. albicollis*, which breed in sub-desert steppe, take some non-volant prey—insects, spiders, small lizards—from the sand, and in their forest-zone 'winter' quarters they catch in flight nutritious strips of oil-palm epicarp discarded by squirrels feeding in the crowns above them. The only other recorded vegetable matter is berries eaten during exceptionally cold weather by European Bee-eaters wintering in Zimbabwe. Rarely, some bee-eaters pluck small fish from the surface of ponds, as has recently been established by videotape analysis and pellet studies.

Behaviour. Forest bee-eaters breed solitarily, and for the rest of the year occur solitarily or in pairs, accompanied by the young for some weeks after fledging. Of the open-country bee-eaters, the smaller species in general breed solitarily then form family parties which may aggregate into small, wide-ranging flocks. But most species are gregarious the year round and breed in loose aggregations or in dense colonies of tens, hundreds, or (Rosy Bee-eaters *M. malimbicus*) tens of thousands of nests. Within their large home-ranges the more solitary species are weakly territorial when breeding; in colony-breeding species an individual distance of only a few cm is maintained and that distance around the nest burrow entrance is defended. Individuals of the more sedentary species often have favoured foraging patches which may be defended. Infringement of all of these territories is commonplace and causes vocal and postural bickering; rarely, two birds fight with interlocked beaks in the air or on the ground. *M. apiaster* and the red-throated bee-eaters *M. bullocki* and *M. bullockoides* (the only species adequately investigated) have life-long monogamy, but these and some other species have nest helpers which are the pair's progeny of a previous year and which, remaining all year with their parents, maintain a filial bond. Helpers may copulate with a parent and effectively replace it if it dies. Only a minority of pairs have one (usually) or more helpers; but *M. albicollis* probably has helpers at most nests and there may be up to 6 helpers at any one (see CO-OPERATIVE BREEDING).

Voice and display. *Merops* bee-eaters are very vocal, mostly with a variant of the pleasing liquid, monotonous *crüük*, *crüik* of *M. apiaster*. Separate functions can be ascribed to 6 common calls of *M. bullocki*, and to 5 additional copulation, food-delivery and begging calls. Vocal greeting, accompanied when intense by raised crown feathers and fanned and vibrated tail, is a daily event. Courtship displays are not elaborate and comprise an exaggerated greeting ceremony with a ritualized modification of prey-immobilizing behaviour; courtship feeding occurs. Bee-eaters roost in vegetation or, in cold weather and when breeding, in the nest; the pair, family party or even flock clusters tightly together.

Breeding. Nest holes are oval chambers at the end of a tunnel which birds dig in the soil with their beaks, kicking loosened soil out backwards. They excavate in flat ground or in a slight slope, ridge or bank. The soil may be sandy but is often hard-baked. African savanna bee-eaters breed in the rainy season, mostly in its first half, but *M. bullocki* is exceptional and breeds in the dry season. But it digs its nest burrows at the end of the previous wet season, before the soil becomes hard-baked. This species is an obligate cliff-nester; the burrow is about 6 cm diameter and 1 m long, and inclines slightly to a lip beyond which is the egg chamber. Other species have declining tunnels, 0.5–3 m long. There is no nest material, but the eggs receive some protection from an accumulating carpet of insect sclerites, from pellets. Eggs are laid and hatch after *c.* 20 days at intervals from 0.6 days (*M. pusillus*) to 1.7 days (*M. nubicus*), and clutch sizes vary from a mean of 2.9 (*M. bullocki*) to 4–9 (*M. apiaster*). Nestlings, which fledge in 20–25 days, have swollen papillae on the ankles, on which they move rapidly forwards and backwards in the nest chamber and the tunnel. Death by starvation of the younger birds in a brood is common. Accidental destruction of eggs by adults is frequent and there is some predation by reptiles; otherwise breeding success is high. See photo FEEDING HABITS. (A.L.T.) C.H.F.

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BEGGING DISPLAY: see BEHAVIOUR, DEVELOPMENT OF; PARENTAL CARE.

BEHAVIOUR: the integrated pattern of movement or other overt response of an animal to internal and external stimuli. Behaviour is the product of the action of the nervous and muscular or other effector systems. See BEHAVIOUR, DEVELOPMENT OF; BEHAVIOUR, HISTORY OF.

BEHAVIOUR, DEVELOPMENT OF: the elaboration of behaviour from its first occurrence to a more perfect state. The term development in its broadest sense refers to the ontogeny of an organism from the fertilized egg cell to its death. For the study of behaviour, the most interesting part of ontogenetic development is between shortly before birth and the age at which sexual maturity is reached, because this is the period when most developmental processes and changes occur.

The study of behavioural development derives from one of the questions asked in behavioural research in general: 'How does this behaviour develop in the life of the individual?'

Research on the development of bird behaviour in particular has to cope with two features which characterize this class of vertebrates:

(a) The development of birds as compared, for example, to mammals is characterized by its remarkably high speed. Birds may reach their adult size and weight within about 1% of their total life expectancy, whereas some mammals need 30% or more, as is the case for most of the higher primates. Such speed in general development, which has been understood as an adaptation to a quick acquisition of the ideal ratio between body weight and a constant wing surface, is reflected in the evolution of some traits peculiar to the behavioural development of birds, such as the occurrence of rapid learning or the relative scarcity of play behaviour (see below).

(b) Birds lay eggs which are usually incubated by one or both parents. The embryos, like those of other egg-laying species, are much more open to various influences from the environment than are the embryos of viviparous animals, e.g. mammals. In addition, the occurrence of intensive brood care offers the opportunity for at least acoustic communication between the mother or, in some species, both parents and the developing embryo. Birds, therefore, represent ideal subjects for the study of topics such as prenatal learning or the interaction between genetic and environmental influences in general. These fields of research have received increasing attention in recent years.

Although no sharp distinction can be made in every case, two categories of behaviour which occur during ontogenetic development should be distinguished: those which are precursors of adult behaviour and, as a rule, are retained for the remainder of life, and those which have evolved in relation to the specific needs of the young bird and, as a consequence, disappear again in the course of development. (Some of the latter, however, may reappear, with different functions, in the adult, such as wing quivering in many passerine birds which is part of the begging behaviour of fledglings and part of the precopulatory behaviour of the adult female.)

Behaviour peculiar to the young bird. Special behaviour patterns of young individuals naturally show great differences between precocial and altricial species. The young of precocial species hatch with fully developed sense organs and motor skills and are able to leave the nest immediately or shortly after hatching. Altricial birds, such as parrots and passerines, hatch at a less advanced stage of development and spend a greater proportion of time in or, later, very close to the nest. They require much more intensive care by their parents in terms of food, brooding, nest sanitation and protection. Within the precocial birds, however, some variation occurs, ranging from the Anseriformes and Galliformes, the offspring of which live on yolk sacs for the first day or two and afterwards find their own food, never being fed by adults, to the gulls and auks the young of which leave their nest for short distances but return to it to be fed by their parents. The extreme situation is represented by the mound-building Indo-Australian MEGAPODES in which the hatchling lives on its own from the moment it emerges from the surface of the mound and no parental care is provided whatsoever.

(a) Hatching. The eggshell is broken by a series of blows from the bill with the egg-tooth. Blows often alternate with periods of rest, and hatching itself may take anything from a few minutes, e.g. in woodpeckers and grebes, to several days (Sooty Shearwater *Puffinus griseus*).

An exceptional way of breaking the egg-shell is found in the megapodes (Megapodiidae). In their embryos, the egg-tooth its functionless, and the eggshell is broken with the legs which in this group of gallinaceous birds are especially strongly built.

(b) Begging behaviour and adult feeding. In extremely precocial birds the change from the feeding behaviour of the young to that of the adult is gradual. In the intermediate forms, the young bird begs for its food but uses the adult movement of pecking in feeding. Thus in the Herring Gull *Larus argentatus* begging first occurs a few hours after hatching and consists of repeated pecks at the parent's bill-tip, but even at this age pecks may be directed at regurgitated food on the ground. However, in those species in which the parent puts food into the nestling's gape, as in all passerine birds, the behaviour used by the young in feeding is so different from that used by the adult that the second does not develop out of the first.

In such altricial birds, begging may be divided into three developmental stages. During the first days, the nestling gapes vertically, often with a special call in response to very varied auditory and tactile stimuli, or sometimes apparently spontaneously. Several days later, the bird begins to gape in response to visual stimuli. For about a day it may still direct the gape vertically, but gradually it begins to turn the gape towards the visual stimulus. Wing vibration and characteristic head movements (if present) appear at this stage.

During the later part of the nestling period adult feeding responses are developing quite independently. The first pecks are directed at almost any distinct object. When hungry the birds always beg; they even beg at food that has fallen to the floor, instead of pecking at it. Later the bird gets some food by pecking but begs whenever the parent appears. The parents' unwillingness to continue feeding probably helps to terminate begging. Adult feeding behaviour usually shows progressive improvements, both in its form and in the efficiency and appropriateness of food selection, and learning may well be involved. Experience seems to be of particular importance in birds which capture live prey, e.g. raptors and owls.

(c) Defaecation. Many altricial birds have a specialized method of defaecation. The nestling turns round when it has been fed, raises its cloaca and extrudes a dropping enclosed in a mucilaginous envelope, which is taken by the parent and dropped in flight some distance away from the nest. Adult defaecatory behaviour appears when the fledgling leaves the nest; at the same time the envelopes cease to be produced. Such 'nest-sanitation' does not, however, occur in all species of altricial birds: in most Estrildid finches, for example, the young defaecate within the dome-shaped nest, the interior of which is covered with faeces when the young fledge.

In addition to the behaviour patterns described so far which serve specific purposes during early developmental stages, there are other phenomena which are also restricted to or occur mainly in young birds but which may, in addition, exert an influence on adult behaviour. This is the case, for example, in play behaviour and in vocalizations called subsong.

(d) Play behaviour. One aspect of behaviour development which has recently received increased attention among mammalogists but has been rather neglected with regard to birds is play behaviour. Play is characterized by a number of criteria. It appears to be 'without purpose' since the behaviour patterns involved do not seem to fulfil the biological function for which they have been developed during their phylogenetic history; its components can be combined in various ways; and there is no mutual inhibition and no strict temporal correlation of individual behaviour patterns. Finally there seems to be no habituation since many behaviour patterns occur during play for considerable periods of time without any sign of fatigue.

For birds the occurrence of play behaviour in this sense has been recorded only rarely. This may be because in birds it seems to be more difficult to distinguish play from other activities. A more likely explanation, however, is that young birds do indeed spend less time at play than do young mammals. Such differences might be a consequence of the above-mentioned general speed of avian ontogenetic development, which leaves less time for play activities.

As in mammals, one has to distinguish between locomotory and object play. Examples of each category have been described for birds: Adélie Penguins *Pygoscelis adeliae* have been observed to ride on small ice floes on a tide run, only to come back to the starting point to repeat the process; object manipulation with dead prey, twigs, stones or feathers has been seen in many species with the object often carried into the air, dropped and then caught again. For a third category of play, frequently observed in mammals, the so-called social play, there is no sound evidence, although young birds often show some low-intensity or incomplete sequences of aggressive or sexual behaviour which have sometimes been classified as play behaviour. The most complex play known for birds is found in the corvids, mainly in the Raven *Corvus corax*, in which it probably has an important function in adapting the young to their future life in a wide variety of habitats.

(e) Subsong. In many species of birds, adult males utter a type of song which is different from territorial or courtship song and is characterized by low volume, a high degree of variability, a large number of elements and a broad frequency range. Such subsong occurs mainly in autumn as well as in early spring, before territorial song develops (see VOCALIZATION). In young birds subsong, which is often called 'recording', is particularly frequent during the late summer and autumn of the first year of life. Several authors have considered it to be a kind of play as it apparently lacks any immediate function and also shows some other remarkable similarities with the characteristics of non-vocal play (e.g. re-ordering of sequences, incomplete sequences, repetition of patterns or elaboration of new patterns).

The biological function of both play behaviour and subsong has frequently been discussed but no definite conclusions have been reached so far. It seems certain, however, that both activities provide practice for adult behaviour by enhancing muscular development and improving cognitive abilities and that, in addition, play may also provide some experience on how to adjust social relationships. (See also PLAY.)

Learning. In principle, early learning in birds does not differ from other vertebrates; and their main categories of learning have also been described for birds. One difference, however, concerns the phenomenon of IMPRINTING. It is certainly not by chance that imprinting and the occurrence of early sensitive phases for learning were not only first discovered but also are especially widespread among birds. Such a comparatively rapid and early learning process may have a selective advantage in organisms which are characterized by a speedy ontogenetic development and early dispersal of the young. They may have to acquire relevant information very early, and the long-term retention of such information may be important, not only so that it may be available when they have to look for mates and suitable habitats in adult life, but also to avoid the acquisition of 'wrong' information when they have to live in less suitable habitats or when they come into close contact with other species (e.g. in their winter quarters or during migration). Early and temporally restricted sensitivity to social and other environmental stimuli, as well as a high degree of stability in the storage of early information will, therefore, confer a definite selective advantage. Sensitive phases and stability are characteristics of imprinting processes, and this may be a reason why different kinds of imprinting, such as filial, sexual, habitat or locality imprinting, are especially widespread in birds.

Behaviour embryology. The behaviour patterns of young birds discussed so far all refer to the postnatal stage. It has long been known, however, that behaviour starts well before hatching. Although it has been suggested that embryonic activity is merely a by-product of neural maturation, some recent studies indicate that it also may have its own adaptive function. Such function may refer to the regulation of muscle and joint development, to meeting the special requirements inside the egg and also to the creation of adequate preconditions for the hatching and early post-hatching periods.

For example, embryos use behavioural activity to attain the appropriate position for breaking the eggshell. Many species of precocial birds start vocalizing days before hatching. Their vocalizations have been found to facilitate post-hatching species-recognition (see below) or to enhance the synchronization of hatching which is important for an early and synchronous departure from the nest. In the Guillemot *Uria aalge*, the young in the egg even learn to distinguish, through mutual and contingent acoustic contact, between the calls of their parents and those of other birds. This enables the offspring to react selectively to their parents immediately after they have left the egg, such an ability being an adaptation to breeding in densely packed colonies where the young come into close proximity not only to their parents but also to many other adult birds as soon as they leave the egg (see DEVELOPMENT, EMBRYONIC; GROWTH).

Development of adult behaviour. In addition to the study of behaviours which are important for the developing individual, birds have also been—perhaps again as a consequence of their high speed of ontogenetic development—favourite tools for the study of developmental processes which are important mainly for the adult organism, and which are of relevance for the understanding of regularities in behaviour development in general. During the early stages of ethology, interest concentrated on the ontogeny of what at that time was called innate or instinctive behaviour or fixed action patterns (FAPs) (see BEHAVIOUR, HISTORY OF). Later there was a shift in interest towards a more detailed analysis of the exact interplay between genetically determined predispositions and the influence of early environmental stimulation.

The reason why early studies on 'innate' behaviour have been carried out, in great detail, on birds (and fish) may be that bird behaviour, perhaps being more influenced by hereditary factors and owing to the more permanent effects of early experience (see above), seems to be less flexible than the behaviour of mammals, so that it seemed better suited for the study of relatively fixed behaviour patterns.

Some early studies have indeed shown that there are behaviour patterns which for their development do not depend on being performed. This developmental process was called maturation. The most frequently cited example was provided by Grohmann, who prevented young pigeons from using their wings whilst they were reared and found that they flew as well as controls when released. Another example of a very strong genetic component concerns the migratory behaviour of Garden Warblers *Sylvia borin*. Hand-reared individuals, held in captivity, nevertheless attempted to fly in the natural south-westerly direction and after about a month spontaneously changed the direction to south-south-east. This is in exact accordance with their free-living conspecifics which make the same course correction at exactly the same time, a correction which prevents them from flying out into the open ocean once they have arrived over southern Spain or north-western Africa. Some evidence for genetically determined behaviour, finally, comes from behaviour embryology (see above). Embryos of various species of birds start to show active movements at a time when the reflex arc between sensory organs and muscles is not yet completed. As a consequence no input from the sensory organs can yet be transferred to the muscles and the movements occurring at this time must therefore be programmed and regulated endogenously.

Such behaviours in which obviously no learning is involved are very rare, however. In the majority of cases, there is a very subtle interplay between many internal and external factors. In bird research, this has been demonstrated in three areas among others: in studies on song learning, imprinting and prenatal development.

In song development (see VOCALIZATION), three different types of constraints have been found which contribute to restrict the learning process to elements of the species-specific song. (1) In many species, some basic outline of the song as a sequence of syllables with, for example, a certain approximate duration and/or tonal quality or structure, has been found to exist independent of experience with the species' song. (2) In addition, several species, for example the Chaffinch *Fringilla coelebs* and White-crowned Sparrow *Zonotrichia leucophrys*, have a predisposition to learn species-specific song patterns in preference to those of other species. If during song learning they are exposed to different acoustic stimuli they selectively respond to those of the appropriate tonal quality, which they include in their song repertoire. (3) In other species there is a predisposition to learn the song of birds with which an 'emotional' bond of some kind exists. They may pick up preferentially song elements of a territorial neighbour, as in the Crested Lark *Galerida cristata*, or of the father, as in the Bullfinch *Pyrrhula pyrrhula*, Bengalese Finch *Lonchura striata* (domestic form) and Zebra Finch *Poephila guttata*. In these species the young male develops a copy of its father's or foster father's song even if the latter belongs to another species and/or sings an alien song, and even if 'correct' song types are heard in close proximity and perhaps more frequently than the song of the tutor. Within these constraints, however, which seem to be genetically determined, environmental factors, i.e. the particular kind of acoustic stimulation the young bird is exposed to, determine the exact type of song it will finally develop.

In imprinting, the genetical constraints are temporal. A comparison of different species reveals that the onset and duration of the sensitive phase for, for example, sexual imprinting, is different in different species and obviously adapted to the specific conditions under which the offspring grow up (e.g. duration of parental care, age at dispersal etc.). Experimental studies, however, have shown that within these temporal limits, which obviously are again genetically determined, actual imprinting can occur earlier or later during the course of the sensitive phase, according to the particular conditions, e.g. the time of exposure to the imprinting stimulus. Again, environmental factors determine the exact outcome of ontogenetic development.

The most elegant studies on the interactions between genetical and environmental factors have been done with embryos. In ducklings *Anas platyrhynchos*, for example, it has been found that birds hatched in isolation in incubators are able to respond preferentially to the maternal call of their own species as compared to the call of another species, even if they have never heard the species-specific call before. This finding suggests a strong genetical background for such selectivity. However, as the developing embryo is of course able to listen to its own vocalizations, which begin several days before hatching, some exogenous influence via feedback through the auditory system cannot be excluded. To investigate this possibility, the preferences of ducklings which had been mechanically prevented from vocalizing prior to the onset of their own vocalizations were tested. Even these ducklings showed a high degree of preference for the species-specific maternal call, thus demonstrating the high degree of innate predisposition for selective responses. The devocalized-isolated ducklings, however, presumably due to an overlap in certain acoustic features, failed in one of the discrimination tests whereas the sham-operated controls did not. Obviously, selectivity in the responses to auditory stimulation is not perfect if no auditory experience is possible at all. It can be concluded that even such strongly predetermined responses are open to some, although minor, enhancement through sensory stimulation. Such stimulation may be very brief indeed. The deficiency in discrimination ability could be avoided if the devocalization procedure was delayed so that the embryos had about 24 hours of exposure to their own vocalizations before they were muted.

In order to classify the different ways in which environmental factors influence behavioural development, a number of distinctions have been made. For example a distinction is made between environmental stimuli which have more general effects and those which have specific effects. Another distinction is between three sorts of factors: those which initiate a developmental process which without such stimulation would not have begun; those which facilitate processes that are already in operation; and those which maintain the end-products of the developmental process, the relevant parts of the behavioural repertoire.

Mechanisms. The mechanisms for the changes in behaviour occurring during ontogenetic development are difficult to assess. Some behaviour patterns may be impossible to perform at first, simply because certain sense organs and muscles are not yet functioning. Thus, a newly hatched altricial bird may be deaf and blind, with only the muscles extending the neck and legs adequately developed. In such cases, some changes in behaviour may be seen as simple consequences of sensory and motor development.

Two important mechanisms which are involved in behavioural development are changes in the central nervous system and changes in the hormone level in the blood. The former may involve the proliferation and differentiation of neurons, 'remodelling' of axons, dendrites and synapses, or changes in the biochemical synthetic pathways for neurotransmitters. One process of neurogenesis which also seems to be of importance for behavioural development, e.g. the regulation of sensitive phases, is the phenomenon of neuronal cell-death. Thousands of cells in many parts of the central nervous system undergo differentiation including axonal growth and the formation of synapses, only to be subject to complete degeneration subsequently. The function of neuronal cell-death is not yet completely understood. It seems to be a mechanism, however, which ensures the adequate innervation of post-synaptic neurons or other targets (see NERVOUS SYSTEM).

Changes in the hormone level in the blood are of particular importance with regard to sex hormones and the ontogenetic development of reproductive behaviour. For example, cockerels normally first show treading at 80 days, but testosterone injections will induce it at 15 days and crowing at 4 days. In the Herring Gull, androgen injections will produce courtship display well before the end of the first year instead of after 3 years, and in male Zebra Finches, which normally start singing at about 34–37 days of age, it has been possible to advance the onset of song to an age of only 18–19 days if testosterone is applied at day 16.

Despite the examples listed, one must mention, in conclusion, that the number of experimental studies on neural and hormonal influences on behavioural development is still rather small. Much has to be done before we come to a better understanding of the mechanisms underlying behavioural development in birds. (R.J.A.) K.I.

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BEHAVIOUR, HISTORY OF: broadest definition includes all kinds of movement and responses to changes in the environment, ranging from simple reflexive movements such as breathing to complex learned skills such as playing the piano. The behaviour of birds studied by ornithologists and comparative psychologists is generally towards the more complex end of this spectrum and includes COURTSHIP, AGGRESSION, and PARENTAL CARE. This survey traces the early history of the study of behaviour leading to the emergence of ethology and comparative psychology as the two major disciplines devoted to animal behaviour, and is followed by an account of some of the major issues addressed by students of behaviour during the 20th century.

Early history: Aristotle—18th century. The earliest systematic accounts of animal behaviour are in Aristotle's *Historiai peri ta zoa*

(Enquiries about Animals). Among many aspects of bird behaviour described by Aristotle are territorial behaviour and variations in territory size from species to species, pair bonding, and the development of bird song, in which Aristotle notes that some species of birds sing abnormally when reared in the absence of their parents, a phenomenon which has been the subject of much research during the last three decades (see VOCALIZATION). Aristotle's writings remained as the definitive account until the post-renaissance, although there were some writers in the middle ages such as Frederick II of Hohenstaufen (1194–1250), author of an extensive work on bird behaviour and FALCONRY.

In the 17th and 18th centuries two major lines of development occurred in the study of behaviour. First, philosophers such as Descartes (1596–1650) and Locke (1623–1704) debated the relationship between the behaviour of animals and that of man; and second, field naturalists such as C.G. Leroy (1723–89) in France, F.A. Pernau (1660–1731) in Germany, and Gilbert White (1720–93) in England made detailed descriptions of the behaviour of animals, especially birds, in their natural environment. Leroy was the first to emphasize the value of complete catalogues of the species' repertoire of behaviour as a starting point for research (nowadays such a catalogue is referred to as an *ethogram*), while White is famous *inter alia* for his recognition that the three British *Phylloscopus* warblers, although very similar in plumage, could be readily distinguished by their songs.

The 19th and early 20th centuries. The event of overwhelming importance in the 19th century biology was the widespread acceptance of the theory of evolution, and of NATURAL SELECTION as a major force causing evolutionary change. Charles Darwin, who towered above his contemporaries as a proponent of the theory of evolution, also wrote extensively on animal behaviour. For example, he formulated the theory of SEXUAL SELECTION to account for the extremely elaborate courtship displays and flamboyant nuptial plumages of some birds, and discussed how the postures of animals may reflect their motivational state, in his book *On the expression of emotions in animals and man*.

The latter half of the 19th century also saw the beginnings of a split between laboratory-oriented students of animal behaviour and those who preferred to watch animals in the field. The former were dubbed 'comparative psychologists' by the Frenchman P. Flourens (1794–1867) and the latter were named 'ethologists' by another Frenchman, I. Geoffroy St Hilaire (1801–1865). It is worth noting parenthetically that the English philosopher John Stuart Mill used the word ethology to refer to the 'science of character formation', a definition still given in the *Concise Oxford Dictionary*, but not the one used when referring to the study of animal behaviour in the natural environment.

Particularly influential in the establishment of laboratory experiments on behaviour were D.A. Spalding's (1840–77) studies of imprinting in chicks and C. Lloyd Morgan's (1852–1936) book *An introduction to comparative psychology* (1894). In this book Lloyd Morgan enunciated his famous canon: 'In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty if it can be interpreted as the outcome of one which stands lower in the psychological scale'. In other words we should not jump to conclusions such as 'magpies get together for magpie weddings' unless we can rule out all possible simpler explanations such as 'magpies get together at good feeding sites'. This variant of Occam's razor had a seminal influence on comparative psychology, especially in North America where it led indirectly to a long succession of highly controlled rigorous experimental studies of mechanisms of learning by B.F. Skinner, and many others. In much of this work it was assumed that the behaviour of animals could be reduced to simple mechanistic laws of response to reward and punishment. For zoologists most of this work appeared to focus too narrowly on a few species (mainly rats and pigeons) and it addressed questions far removed from the behaviour of animals in the wild, in which adaptation to ecological conditions and differences between species were prevailing themes.

While comparative psychologists focused their attention on behaviour produced in response to reward and punishment, zoologists were impressed with the fact that the behaviour of animals is generally organized into well-coordinated sequences leading to a particular end point. This observation was formalized in 1918 by an American, Wallace Craig (1876–1954), in his account of 'instinctive behaviour'. Craig pointed out that many behaviour sequences consist of a rather flexible, partly learned, 'appetitive' phase in which the animal appears to seek out a particular stimulus situation (e.g. a hungry lion searching for a gazelle or a territorial bird patrolling its boundaries) followed by a more rigidly pre-programmed, stereotyped 'consummatory act' which brings the sequence to an end. In the case of the lion this would be the act of prey capture; with the territorial bird it would be meeting and chasing or displaying at a rival. In other words, for Craig animals were not passive responders to events in the outside world, but were actually driven by internal motivation to search for stimuli that would trigger off a consummatory act. Similar views were propounded by the German zoologist Oscar Heinroth (1871–1945), who also suggested that consummatory acts, or FIXED ACTION PATTERNS as he called them, were species-specific traits that could be used as taxonomic criteria in the same way as morphological features.

The writings of Craig, Heinroth, and another American, C.O. Whitman, set the stage for the emergence of ethology as a major discipline in the study of behaviour. Particularly influential in this were Konrad Lorenz (b. 1903) and Niko Tinbergen (b. 1907). (It is interesting to note as an aside that in spite of its strong tradition in natural history, the stuff of ethological science, Britain lagged behind continental Europe in the establishment of ethology as an academic discipline, perhaps because natural history was viewed as being the domain of amateurs such as Eliot Howard. Julian Huxley (1887–1975), one of the few professional zoologists in Britain to take an interest in ethology early on, did not pursue it as his main line of research.)

Lorenz's theory of instinct. In addition to being trained as a medical doctor and for a short while holding a chair of philosophy at Königsberg, Lorenz made major contributions to almost every aspect of ethology. His work on the evolution of displays, on imprinting in ducks and geese, on human behaviour in relation to that of animals, are all impressive, but in some ways his major contribution was to formulate a unified theory of instinctive behaviour, building on the work of Craig and Heinroth.

According to Lorenz, each fixed action pattern in a species repertoire is innate (i.e. pre-programmed by the genes and unmodified by ontogeny) and driven from within by an 'action specific potential' or specific drive. This drive was viewed as arising from within the nervous system and it was thought to cause the animals to perform the sequence of appetitive behaviours leading to the consummatory act. The latter allowed the drive to be dissipated, so that a quiescent phase was likely to follow. Lorenz's picturesque analogy was with the flushing of water from a lavatory cistern. The 'hydraulic model', as it was called, also embodied the notion that without performance of the appropriate consummatory act, drive would 'build up' inside the animal (like the lavatory cistern filling up with water) until eventually the consummatory act could occur even in the absence of any suitable external stimulus (a so-called 'vacuum activity'). One of Lorenz's favourite examples of this was a pet Starling *Sturnus vulgaris* that hawked for non-existent flies on the ceiling as a result (Lorenz would say) of build-up of the action specific potential for hunting. The more usual discharge of a drive occurred when the animal encountered a suitable stimulus to trigger the consummatory act. Lorenz argued that for each consummatory act there existed a specific trigger stimulus (*sign stimulus*, or in a social context, *releaser*) that could 'unlock' the act. This idea was borrowed from the writings of Jacob von Uexküll. The sign stimuli were thought to be detected in the central nervous system by special inbuilt sensory mechanisms (innate releasing mechanisms or IRMs), each one specific to a particular sign stimulus.

This theory of instinct, combining as it did ideas about the ontogeny of behaviour (in the concept of innateness), perception of stimuli, and internal control of behaviour, was a masterly synthesis. It had a major influence on ethologists, as well as affecting the research of neurophysiologists, endocrinologists and even some psychiatrists, such as John Bowlby. The theory was modified and improved by a number of authors, notably Tinbergen in his hierarchical model (1951), and Lorenz himself in his most recent book on ethology (1981).

In spite of its intuitive appeal and its ability to account for many everyday 'facts' about behaviour—after all lions do set out to hunt for prey, chase and capture the victim and rest after eating—Lorenz's theory eventually fell into disfavour in the 1950s and 1960s. Part of the reason, as W.H. Thorpe pointed out, is that the theory stimulated so much new research that it rendered itself obsolete. This is, of course, to be seen as a strength and not a weakness of theory. The point can be illustrated with reference to the concept of IRMs. The early work of Tinbergen and Lorenz showed that often simple models containing only a few components of the real stimulus were sufficient to trigger a response: gull chicks would peck at a pencil as readily as at a complete model of the parent's head and stickleback males would attack any model with 'red below' even if quite unfishlike in other respects. They interpreted these results as suggesting that the perceptual pathways are equipped with special detectors tuned in to key stimulus features. In the last two decades neurophysiologists have discovered the cellular analogues of some of these IRMs in the shape of single cells receptive to particular environmental features. In the visual system of the frog, for example, there are detectors that respond only to small dark moving objects ('bug detectors') and others that respond to moving lines or edges. Thus the general concept of IRM can be replaced with a more accurate account in terms of neural processes in the visual system.

However, in other respects Lorenz's theory failed to hold up to close scrutiny. Two examples are as follows. (a) Associated with the theory was the concept of 'innate behaviour', by which Lorenz originally meant (he later altered his ground) behaviour patterns that were completely fixed by genetic instruction and therefore appeared in the adult even in the absence of any environmental input. It is now recognized that all traits, including behaviour, develop through an interaction between genetic and environmental influences, and that any dichotomy into innate and learned behaviour is therefore artificial. Rather than asking whether a behaviour is innate or learned, one should ask to what extent variation between individuals in behaviour reflects genetic or environmental variation. (b) In formulating his ideas on action specific potential, Lorenz was much influenced by the work of von Holst showing that spontaneous rhythmical activity is generated in the central nervous system of invertebrates, even in the absence of any sensory feedback whatsoever. While it is true that some motor patterns (e.g. walking in insects) can be centrally generated, this does not mean that each activity has a specific drive that builds up with time since the last performance. In fact experimental evidence shows that Lorenz's prediction does not always hold. While hunger does seem to fit (at least at a superficial level; the threshold for feeding drops with time since the last meal until, as Charlie Chaplin found, shoelaces make an acceptable substitute for spaghetti) the same is not true for other activities such as aggression. In Lorenz's controversial book *Das sogennante Böse* (1963) translated into English as *On Aggression* (1966) he argued that aggression in animals and man is motivated by a specific drive that builds up if not released. However, careful experiments with a variety of animals have shown that sometimes exactly the opposite is true; aggression builds up consequent upon performance of aggressive acts rather than declining.

Tinbergen's four questions. While Lorenz's major contribution was in the study of mechanisms and ontogeny of behaviour, Tinbergen, at least in his later years, focused on experimental studies of the survival value of behaviour. A classic example of this approach is his study showing that eggshell removal (when the parent carries the broken shell from the nest shortly after hatching) by Black-headed Gulls *Larus ridibundus* is a method of maintaining the camouflage of the nest. Other experiments of this genre include a test of the survival value of spacing-out as a defence against predators in cryptic animals, experiments on the enhancement of foraging efficiency as a result of feeding in a flock, and observations on the survival value of colonial nesting in gulls.

One of the most influential papers written by Tinbergen is his *On the aims and methods of ethology* (1963). In this paper he spelled out the distinction between four different kinds of question asked in behavioural research, and in biology in general. Tinbergen's four questions are as follows: (a) Function: 'How does this behaviour contribute to survival or reproduction of the individual?' (b) Causation: 'What are the proximate internal and external factors causing the animal to behave in a particular way at a particular time?' (c) Ontogeny: 'How does this behaviour develop in the life of the individual?' and (d) Evolution: 'What is the evolutionary history of this behaviour pattern and under which selective forces did it evolve?' Note that while this fourth question is related to the first, it addresses past history rather than the present day.

Although Tinbergen stressed the importance of distinguishing between these four questions, he also saw that research often moves from one to another. One of his favourite illustrations was that Karl von Frisch started with the functional question "Why are flowers coloured?' and this led him to demonstrate that insects have colour vision and to elucidate a great deal about the mechanisms of insect vision (a question related to causation of behaviour).

Ethology in the second half of the 20th century. It is less easy to pinpoint the current highlights of ethology than it is to trace the main points of its historical development, and what follows is necessarily no more than an illustration of the issues under investigation in recent years in the four areas specified by Tinbergen.

(a) Function. Investigations of the function or survival value of behaviour have close ties with ECOLOGY since it is the environment that ultimately generates selection pressures on behaviour, and with population GENETICS since the consequence of natural selection is a change in the frequency of genes in a population. Ecological pressures may cause closely related species to evolve differences in behaviour related to differences in habitat as well as leading to the convergent evolution of similar behavioural traits among unrelated species living in similar habitats. For example, J.H. Crook and D. Lack showed in the 1960s that, irrespective of taxonomic affiliation, birds feeding on insects or other animal food tend to be territorial while those feeding on plant material such as fruit and seeds tend to be gregarious, living in flocks and nesting in colonies. (These are, of course, statistical trends and there are many exceptions, e.g. seabirds). These results suggest that diet and habitat have an important moulding influence on social organization. Plant foods tend to occur in large patches, which facilitates gregariousness by reducing competition; living in a group may actually enhance the likelihood of finding patches of food (more pairs of eyes are better than one) and/or it may provide protection from predators (see FLOCKING, COLONIALITY). In contrast, insect food does not usually occur in great enough local abundances to be exploited by groups, so individuals or pairs defend territories to keep away competitors and secure enough for themselves. Analogous arguments have been put forward to account for correlations between diet, habitat and MATING SYSTEMS and PARENTAL CARE.

More detailed studies of the relationship between behaviour and environmental resources in individual species have borrowed the terminology of micro-economics. In this approach the costs and benefits of behaviour are measured in some suitable currency such as time or energy, and these measurements are used to account for observed variations in behaviour. For example, hummingbirds and sunbirds sometimes defend winter feeding territories but at other times they do not, and it transpires that individuals generally abandon their territories when the extra energetic gain (calories of nectar) from excluding rivals is less than the energetic cost of defence (calories spent in chasing rivals). In other words the economic defendability of the resource determines whether or not the birds are territorial (see TERRITORY; OPTIMAL FORAGING).

A third important development is the realization that many details of complex social interaction within a group can be analysed in terms of KIN SELECTION. The essential idea is that various forms of co-operation or aid-giving (see CO-OPERATIVE BREEDING, ALTRUISM) might be favoured by natural selection if the individuals involved are close relatives. For example, by helping to protect or feed its young siblings a bird may, under the appropriate ecological conditions, be able to perpetuate its own genes (some of which it shares with its siblings) as effectively as it could if it were to attempt to breed itself. The sub-discipline of SOCIOBIOLOGY is largely concerned with elucidating the ways in which altruism might be favoured by selection. Another suggested mechanism for its evolution is reciprocity: if A helps B (e.g. by sharing food) at a small cost to itself and considerable benefit to B, and B later returns the favour, both individuals have made a net gain, even though A and B are unrelated. Some evidence from primates indicates the occurrence of reciprocal altruism in Nature. A moment's thought reveals a potential difficulty for the evolution of reciprocity. If A helps B there may (to put it anthropomorphically for shorthand) be a temptation for B not to reciprocate, in which case A pays a net cost while B gains a bigger benefit than it would if it reciprocated. In general terms, the benefit to A depends on the response of B. This feature of social interaction is widespread and not just restricted to reciprocity; it has led to the extensive use of GAMES THEORY by sociobiologists as an appropriate theoretical tool for finding the 'best' STRATEGY in this kind of situation.

(b) Causation. By its nature the study of proximate causes of behaviour leads to analyses of the physiological mechanisms underlying behaviour. For example, much has been done to elucidate the hormonal control of reproductive behaviour in birds (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM). In the female Canary *Serinus canaria*, external stimuli, such as increasing daylength and male song, initiate, via control centres in the brain, development of the ovaries which produce estrogen, the hormone that stimulates nest-building. Subsequently tactile stimuli from the nest on the sensitive brood patch (itself developing under the influence of estrogen) cause a change to softer nesting materials such as feathers (the nest lining) and eventually to a decrease in nest building and

the onset of the next phase of reproduction. This small example serves to illustrate the complex way in which hormones, external stimuli, and behaviour interact in the causation of reproductive behaviour.

Some aspects of causation cannot yet be studied at the physiological level and are more fruitfully analysed in the behavioural terms. Although, for example, a great deal is known about the physiological basis of hunger, this information does not necessarily give any indication of how hunger interacts with other comparable motivational systems such as thirst or sex. Does high sexual motivation enhance or inhibit hunger? The answer to this kind of question has been primarily studied at the behavioural level, using behavioural indices, such as rate of working by pecking a key to get food, to indicate how hungry the animal is. Such studies reveal that in general motivational factors are specific in their effects (i.e. food deprivation, while increasing hunger, does not increase sexual motivation) but that there are some general aspects of motivation (e.g. a hungry animal is generally more active or 'aroused' than a satiated one).

A related question concerns the way in which behaviour is organized to cope with the problem of conflicting motivational demands. Often animals are motivated to do more than one activity at any given moment, but generally one activity suppresses all the others, so that motivational conflict is not apparent to the observer. A flock of hungry sparrows leaves the bird table and flies to a bush as soon as a cat appears (fear inhibits feeding) and to the observer arriving to see sparrows in a bush the conflict between fear and hunger may not be readily apparent.

In this example the transition from one activity to a new one was caused by an increase in the causal factors for the second activity (i.e. the appearance of the cat). This kind of transition is said to be due to motivational competition. An alternative kind of transition is one that occurs as a result of motivational disinhibition. A hungry Barbary Dove *Streptopelia risoria* provided with access to food does not simply feed until it is satiated. Instead it interrupts feeding from time to time and switches to other activities such as preening. But increasing the level of causal factors for preening (by sticking a paper clip on the bird's wing) does not alter the time of the first transition from feeding to preening. In other words the transition occurs because feeding disinhibits preening rather than because preening outcompetes feeding.

Sometimes animals show overt signs of motivational conflict, for example by rapid alternation between two activities, by INTENTION MOVEMENTS and DISPLACEMENT ACTIVITIES (see also RITUALIZATION). Displacement activities have been of particular interest to ethologists since they appear to be irrelevant to the ongoing behaviour (for example birds engaged in a fight may break off and preen or peck at the ground when fear and aggression are in conflict). It seems likely that displacement activities form a heterogeneous group in terms of their motivational mechanisms. Some can be explained as 'low priority' activities temporarily disinhibited by major ongoing activities, in much the same way as the preening response of hungry doves referred to above. The disinhibition may come about because the major activity is thwarted or because it is in motivational conflict with another activity. Other displacement activities, however, seem to be attributable to a high level of general arousal (see above) arising from motivational conflict, and they may even serve to reduce arousal although the mechanisms underlying this are not understood.

(c) Ontogeny (see also BEHAVIOUR, DEVELOPMENT OF). In the broadest sense all behaviour has its ontogenetic roots in the genes. Some behavioural differences between individuals can be ascribed to specific effects of simple genetic differences (for example the difference in mental development between normal children and those suffering from phenylketonuria (PKU) is due to a single gene difference—see GENETICS), while in other cases the link between behavioural differences and genetic differences is more tenuous and complex (e.g. differences between children in ability to play the piano). Even when the link between genes and behaviour differences is simple, the environment during development can have a dramatic modifying effect on behaviour—PKU sufferers can be behaviourally normal in spite of their genetic abnormality if reared on an appropriate diet from birth.

The proportion of variation in behaviour or any other trait that is due to genetic variation is sometimes expressed as a measure called heritability, a measure which is often abused and misunderstood. One common misconception is that a high heritability score implies that the trait is genetically fixed and resistant to environmental change. The PKU example above illustrates the fallacy of this notion: without dietary control the difference in mental ability between PKU and normal humans is largely genetic (high heritability), but the effects of the genetic difference are very much modifiable by the environment.

The student of behavioural ontogeny addresses the question of exactly how genetic and environmental factors interact in the unfolding of behaviour during development. One of the classic methods used is the isolation or Kaspar Hauser experiment in which an individual is reared in the absence of certain environmental influences to see if its behaviour still develops normally (see VOCALIZATION for such studies on bird song). These experiments have played an important role in understanding ontogeny but their results must be interpreted with caution. Sometimes, for example, the isolated animal generates its own environmental cues for development, so the isolation experiment has not isolated the animal as fully as might be thought at first. A case in point is bird song: isolated Chaffinches *Fringilla coelebs* use auditory feedback from their own vocalizations in developing their songs.

One of the important general principles to emerge from isolation experiments is that of the sensitive phase. Animals are often more sensitive to environmental effects at some ages than at others: White-crowned Sparrows *Zonotrichia leucophrys* seem to be capable of learning their song only in a short period during the first few months of life and young precocial birds are most likely to become imprinted on an object in the environment if exposed to it in the first few days after hatching (see IMPRINTING). Not all instances of LEARNING, however, are restricted to short sensitive periods and in some ways ontogeny can be said to continue until the animal dies.

(d) Evolution. There is virtually no fossil record of behaviour, the few exceptions being such things as footprints or other tracks and artifacts. Therefore inferences about behavioural evolution have to be drawn largely from comparisons of living species. Such comparisons may be used in any of three endeavours. The first is to identify homologous behavioural traits and distinguish them from analogous traits. The former are common to a taxonomic group and reflect the evolution of the group from a common ancestor; as an example, almost all passerines scratch the head by putting the foot over the wing, while non-passerines scratch from underneath the wing. Over-wing scratching probably reflects the common ancestry of passerines and is therefore homologous. In contrast, bats, cetaceans and oilbirds all use ECHO-LOCATION to find their way about, but this is not because they have all evolved from a recent common ancestor but because all three groups have independently solved the problem of orienting in the dark by evolving echo-location—the trait is analogous rather than homologous.

A second use of comparisons is to trace the probable path of evolution of a behavioural trait. For example present day shorebirds (in North America) show four kinds of mating system: (a) *Monogamy* (e.g. Western Sandpiper *Calidris mauri*); (b) *Double-clutching*, in which a female lays a first clutch of eggs which is incubated and reared by the male, while the female lays a second clutch and cares for it herself (e.g. Sanderling *Calidris alba*); (c) *Sequential polyandry* in which a female pairs with a number of males in succession, laying a clutch for each one to look after, and helps the last male herself (e.g. Spotted Sandpiper *Actitis macularia*); (d) *Simultaneous polyandry*, in which a female lays clutches for several males, leaving each of them to do the parenting (e.g. Northern Jacana *Jacana spinosa*). It is a reasonable inference from these observations that polyandry evolved from monogamy via double-clutching.

Finally, as discussed earlier, behaviour patterns can be used as an aid in taxonomy. Probably the best example of this is still Lorenz's classic work on the taxonomy of the Anatinae based on their DISPLAYS.

Conclusion. In the past many of the major advances in the study of behaviour have come from work on birds. Their conspicuousness and accessibility, together with their reliance on visual and auditory senses, their ease of maintenance in captivity and their aesthetic appeal are among the features that have led ethologists to study birds. No doubt birds will continue to occupy a central place on the ethological stage, even though the methods used to study them are rapidly changing from gumboots and binoculars to radiotelemetry, electrophoresis, and sophisticated field experiments. J.R.K.

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BELLBIRD: substantive name of *Procnias* spp. (see COTINGA); also of the Crested Bellbird *Oreoica gutturalis* (see THICKHEAD); and name of *Anthornis melanura* (see HONEYEATER).

BELL-MAGPIE: see CURRAWONG.

BELL-MINER: *Manorina melanophrys* (see HONEYEATER).

BELL-SHRIKE: sometimes used as substantive name of certain *Laniarius* spp. (see SHRIKE).

BELLY: the ABDOMEN; or the ventral surface area roughly corresponding thereto (see TOPOGRAPHY).

BELLY-SOAKING (1): specialized behaviour associated with the carrying of drinking water for the chicks by species of Pteroclididae (see SANDGROUSE).

BELLY-SOAKING (2): specialized behaviour associated with incubation by charadriiform birds, especially Charadriidae, nesting in tropical and sub-tropical environments. Belly-soaking is most frequent between about 10.00 and 13.00 h and is characteristically performed by a bird about to relieve its mate at the nest; a sitting bird does not usually leave its eggs to belly-soak unless its mate has failed to arrive for duty when called by the on-duty bird. The usual method for wetting the feathers is to walk into shallow water and repeatedly dip the underparts into the water by bending the legs. Dips may be momentary or may be prolonged into immersions. Up to 11 separate dips/immersions, sometimes interspersed with short runs during which the belly feathers are kept in the water, are used to saturate the belly feathers, the whole process taking up to a maximum of 10 min. Water may be carried up to 100 m. The African Skimmer *Rynchops flavirostris* achieves a similar end result by flying over water with dangling feet and splashing water onto its underparts.

For purely physical reasons, belly-soaking must result in evaporative cooling of both bird and eggs (which, incidentally, are often shaded rather than incubated properly); the stimulus for it is probably the combination of high ground surface temperatures (60°C on some Skimmer *Rynchops* breeding beaches) and comparatively high (30°–40°C) air temperatures just above the ground that result from intense solar radiation in calm conditions. Most published accounts of belly-soaking conclude that its primary function is to cool the eggs but the work of Howell and Bartholomew (1962) suggests that, even under conditions of intense solar radiation, the temperatures of eggs kept covered/shaded by parent birds are unlikely to reach lethal values. Since belly-soaking is a normal feature of incubatory behaviour in *Hoplopterus* spp. and *Charadrius* spp. (e.g. White-headed Plover *H. albiceps*, Yellow Wattled Lapwing *H. malabaricus*, Kittlitz's Sand Plover *C. pecuarius*, Three-banded Plover *C. tricollaris*) and is not specially associated with a return to eggs left exposed during an enforced absence, its function is probably primarily to assist heat loss from the adult rather than the eggs though the two are not mutually exclusive. Cloud and/or wind may reduce the heat load to below the threshold for releasing belly-soaking in those species in which the behaviour is, on present evidence, sporadic (Little Ringed Plover *C. dubius*, White-fronted Sand Plover *C. marginatus*, Chestnut-banded Sand Plover *C. pallidus*, Blacksmith Plover *H. armatus*, Spur-winged Plover *H. spinosus*, Black-winged Stilt *Himantopus himantopus*, Avocet *Recurvirostra avosetta*). J.F.R.


White-headed Plover *Vanellus albiceps* bringing water to its eggs. Note wing spurs and wattles. (*Photo: J.F. Reynolds*).


Namaqua Sandgrouse *Pterocles namaqua* male wetting its belly feathers. (*Photo: G.L. Maclean*).

Howell, T.R. & Bartholomew, G.A. 1962. Temperature regulation in the Sooty Tern *Sterna fuscata*. Ibis 104: 98–105.
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BELT: a broad band, in some plumage patterns, across the breast or belly (see TOPOGRAPHY).

BENGALESE: see CAGE BIRD.

BENTBILL: *Oncostoma cinereigulare*, a small tyrant-flycatcher with a curiously thick, arched bill (see FLYCATCHER (2)).

BERGMANN'S RULE: that, among the forms of a polytypic species, body-size tends to be larger in cooler parts of the total range and smaller in the warmer parts (see also ALLEN'S RULE; ENERGETICS; WING).

BERRYEATER: substantive name of *Ampelion* spp. (for family see COTINGA).

BERRY-PECKER: substantive name sometimes used for the New Guinea FLOWERPECKERS of the genus *Melanocharis*.

BEWIT: term used in FALCONRY.

BIBLE, BIRDS OF THE: less than 40 species are mentioned in the Bible, out of over 400 resident in or migrating through Israel. Half of the names are included in the lists of the unclean birds mentioned in Leviticus 11 and in Deuteronomy 14; the two lists are very similar, with several variations in the order and only one name mentioned in one list and not in the other. The other names, some of which are difficult to identify, are scattered through the books and include names of birds (and other creatures) characteristic of deserts and other lonely places. Doves and young pigeons are connected with the ritual sacrifice in the Temple, and they are most frequently mentioned in the Bible. Passages striking in their beauty refer to such migrating birds as the Turtle Dove and White Stork (Song of Songs, 2, 12; Jer. 8, 7)—see also under QUAIL.

The identification of the names of birds and other animals met with difficulties as early as the time of the translation of the Bible into Greek, in the 3rd century BC. It is quite possible that in different parts of the Land of Israel different tribes, or even smaller population units, used different names for the same creatures; and when these names were included in the books of Law and the books of the Prophets they could

Table showing English names used in translating from the Hebrew as compared with the modern identifications made by Israeli zoologists.

The first column gives the names used in King James's Bible—the Authorised Version (Old Testament); where a name is widely at variance with the modern identification it is placed within quotation marks. More than one entry for the same name indicates that different Hebrew words are represented. Where the name used in the recent translation issued by the Jewish Publication Society of America is different, it follows within brackets. The second column gives selected references to the use of the name in King James's Bible; 'L' = Leviticus, chapter 11, 'D' = Deuteronomy, chapter 14.

	BIBLICAL REFERENCE	ZOOLOGICAL IDENTIFICATION
'arrowsnake' (great owl)	Isa. 34, 15	Long-eared Owl *Asio otus*
'bittern'	Isa. 14, 23; 34, 11; Zeph. 2, 14	Long-eared Owl (Aharoni) *Asio otus*
birds	Gen. 7, 14; Ps. 104, 17	general
birds, ravenous	Ezek. 39, 4	eagles *Aquila* sp.
bird, speckled (speckled bird-of-prey)	Jer. 12, 9	eagle *Aquila* sp.
'cormorant'	L; D	Fish Owl *Ketupa zeylonensis*
'cormorant' (pelican)	Isa. 34, 11; Zeph. 2, 14	pelican *Pelecanus* sp.
'crane' (swallow)	Isa. 38, 14; Jer. 8, 7	Swift *Apus apus pekinensis*
'cuckow' (sea-mew)	L	gull *Larus* sp.
'doleful creatures' (ferrets—*sic*)	Isa. 13, 21	Eagle Owl *Bubo bubo aharonii*
dove	Gen. 8, 8; Isa. 38, 14; 59, 11; 60, 8; Hos. 7, 11; 11, 11; Ps. 55, 6; Song of Songs 2, 14; 5, 2; 5, 12; 6, 9; Nah. 2, 7; Ezek, 7, 16; Jer. 48, 28	pigeon *Columba* sp.
dove, turtle	Gen. 15, 9; Lev. 1, 14; 14, 30	Turtle Dove *Streptopelia turtur*
'eagle'	Exod. 19, 4; Deut. 32, 11; Isa. 40, 31; Jer. 4, 13; Ezek. 17, 3; Ps. 103, 5; Pr. 30, 17; Lament. 4, 19	Griffon Vulture *Gyps fulvus*
'eagle' (vulture)	Hab. 1, 8; Job 39, 27	Griffon Vulture *Gyps fulvus*
'eagle' (great vulture)	D	Griffon Vulture *Gyps fulvus*
'eagle, gier' (carrion vulture)	L; D	Egyptian Vulture *Neophron percnopterus*
fowl	Gen. 7, 14	general
fowl	Ps. 8, 8	general
fowl; fowls of the mountains (birds-of-prey; ravenous birds of the mountains)	Gen. 14, 11; Isa. 18, 6	eagles *Aquila* sp.
fowl, fatted	Kings I, 4, 23	swan *Cygnus* sp.
glede	D	kite (Aharoni) *Milvus* sp. or buzzard (Margolin) *Buteo* sp.
hawk	L; D; Job 39, 26	hawk *Accipiter* sp.
'hawk, night'	L; D	falcon *Falco* sp.
heron	L; D	herons Ardeidae spp.
kite	L	Black Kite *Milvus migrans*
'kite' (falcon)	L; D	buzzard, or kite (Aharoni) *Buteo* sp. or *Milvus* sp.
'lapwing' (hoopoe)	L; D	Hoopoe *Upupa epops*
'ospray'	L; D	Black Vulture *Aegypius monachus*
ossifrage (bearded vulture)	L; D	Lämmergeier *Gypaetus barbatus*
ostrich	Lament. 4, 3	Ostrich *Struthio camelus*
'ostrich' (stork)	Job 39, 13	White Stork *Ciconia ciconia*
'owl' (ostrich)	L; Isa. 13, 21	Ostrich *Struthio camelus*
owl, great; owl	L; Isa. 34, 11	Short-eared Owl *Asio flammeus*
owl, little; owl of the desert (owl of the waste places)	L; D; Ps. 102, 6	Little Owl *Athene noctua*
owl, screech (night monster)	Isa. 34, 14	Tawny Owl *Strix aluco*
partridge	Sam. I, 26, 20; Jer. 17, 11	partridge (See-see) *Ammoperdix heyi*
'peacock'	Kings I, 10, 22	parrot Psittacidae sp.
'peacock' (ostrich)	Job 39, 13	Ostrich *Struthio camelus*
pelican	L; D; Ps. 102, 6	pelican *Pelecanus* sp.
pigeon, young	Gen. 15, 9	pigeon *Columba* sp. (juv.)
pigeon, young	Lev. 14, 30	pigeon *Columba* sp. (juv.)
quail	Exod. 16, 13; Num. 11, 31; Ps. 105, 40	Quail *Coturnix coturnix*
raven	L; Kings I, 17, 6; Song of Songs 5, 11	raven or crow *Corvus* sp.
'raven' of the valley	Pr. 30, 17	Magpie *Pica pica bactriana*
singing of birds	Song of Songs 2, 12	Nightingale *Luscinia megarhynchos*
sparrow	Ps. 102, 7	House Sparrow *Passer domesticus biblicus*
stork	L; D; Jer. 8, 7; Zach. 5, 9; Ps. 104, 17	White Stork *Ciconia ciconia*
swallow (crane)	Isa. 38, 14; Jer. 8, 7	swallow (Aharoni) or crane (Margolin) Hirundinidae sp. or Gruidae sp.
'swan' (horned owl)	L; D	Barn Owl *Tyto alba*
turtle (turtle dove)	Num. 6, 10; Song of Songs 2, 12; Jer. 8, 7	Turtle Dove *Streptopelia turtur*
'vulture' (kite)	D; Isa. 34, 15	Black Kite *Milvus migrans*
'vulture' (falcon)	Job 28, 7	buzzard *Buteo* sp.

obviously give rise to controversy. The discussion in the Talmud, centring on the difficulty of identifying birds subject to ritual prohibitions, shows that there were localities where certain birds were eaten which were considered to be unclean elsewhere (E. Billig).

The divergence in the identification of the names mentioned in the Bible grew immensely when translators and expositors came to be persons who lived outside of the Land of Israel and imagined that the animals of their own countries were identical with those mentioned in the Bible. The ever-growing number of languages into which the Bible is being translated reflects the difficulties regarding such identifications for people of countries with different flora and fauna from that of the Land of Israel. Even in revised English translations (e.g. King James's Bible) the same Hebrew names are sometimes translated in various ways, as can be seen from the appended Table; this is also true of a more recent translation such as that of the Jewish Publication Society of America. There is no unanimity even among Israeli scientists regarding the meaning of some of the Biblical names and their uses in modern Hebrew. However, the differences over the names of birds are few in comparison with those over the names of mammals.

The Table presents English translations of the names of the birds mentioned in the Hebrew Bible, along with their scientific identification as generally accepted in Israel today. The English names are those used in King James's Bible, with those in the J.P.S.A. Bible (where different) for comparison. The list of quotations is not complete, but it includes the most typical and commonly cited passages.

Two Hebrew names, *zipor* and *of*, are used for birds in general. It was admitted by some scholars, and generally accepted in Israel, that the first denominates small birds and the second the large ones. It is doubtful, however, whether such a distinction was carefully followed in the Bible. Another reservation concerns the frequent combination of two Hebrew names for Turtle Dove (*tor*) and young pigeon (*yona*—also *gozal*). There are also names which might have been used for birds but are of doubtful meaning, e.g. *sechvi* (rooster or soul), *thinshemeth* (chameleon or owl), *kipod* (owl in translation but hedgehog in colloquial Hebrew), and *atalef* (now considered to refer to a bat). The name *hogla* is commonly used now in Israel for the Stone Partridge; in the Bible it is used as a place-name (Beth Hogla).

Canon Tristram was the first man to try to base the identification of the flora and the fauna of the Bible upon their study in the Land of Israel. During several journeys, spread over some 20 years, he studied the habits of the beasts and birds as well as the local names still in use by the population. His excellent work was of value to the J.P.S.A., which undertook a new translation of the Bible on behalf of Jewish authorities in the years 1892–1915. The next step was made by Aharoni, the first zoologist to live and work permanently in Palestine. When writing a first zoological school text in Hebrew, he introduced into the everyday usage of the Hebrew-speaking school-children names which later became commonly accepted. Margolin increased the general knowledge of the flora and fauna of the Bible in Israel by teaching schoolmasters in his institution and through his books. Although Bodenheimer doubted the possibilities of exact identification of the animals of the Bible, the use of names introduced into everyday life became so widespread that now it is in practice less important whether the names used by Israelis today are or are not the same as those used by their forefathers. The living Hebrew now spoken in Israel has brought the names of birds and other animals mentioned in the Bible into common use; in this way names again attach to observable realities instead of being disputable scholastic terms.

There are few references to birds in the New Testament and they are mainly to domesticated species—hen, pigeons or doves—or to commensals such as sparrows *Passer* and the Raven *Corvus corax*, with single references to 'great eagle' and 'vulture'. This may be explained by Christ's preaching mainly to the inhabitants of villages and small towns. A.S.

Tristram, H.B. 1911. The Natural History of the Bible. London.
Aharoni, J. 1941–1942. [Key to Palestine Birds—in Hebrew.] Jerusalem.
Margolin, J. 1947. [Zoology—in Hebrew.] Tel-Aviv.
Bodenheimer, F.S. 1956. Animal Life in Biblical Lands. Jerusalem.

BIBLIOGRAPHY: the most useful guide for the ornithologist is the section 'Aves' of the *Zoological Record*, published annually by the Zoological Society of London (see ZOOLOGICAL RECORD). Also giving short summaries as well as titles, but with a less complete coverage of ornithology, are the volumes of *Biological Abstracts* published since 1927 under the auspices of the Union of American Biological Societies. Many ornithological periodicals publish reviews, abstracts, or lists of titles of current literature. In an attempt to keep pace with the proliferation of books and papers on birds, the American Ornithologists' Union and the British Ornithologists' Union began publication in January 1983 of *Recent Literature*, a supplement to their respective journals *Auk* and *Ibis*. This gives titles and in some cases short abstracts of papers.

For lists of birds of the world see references under CLASSIFICATION. A list in French under the title *Projet de Nomenclature Française des Oiseaux du Monde* is being published by P. Devillers (1976–19—) in sections in *Le Gerfaut*, journal of L'Institut royal des Sciences naturelles de Belgique.

Several bibliographies (listed below) were published in the first part of the 20th century, but to embark on an up-to-date one would be a most formidable task.

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BICEPS: see MUSCULATURE. The presence or absence of a 'biceps slip', a division of the humeral head of this flexor of the forearm, has been used as a taxonomic character.

BILL: alternatively 'beak' and technically 'rostrum', the projecting jaws of a bird, with their horny sheaths. The whole consists of the upper mandible (or maxilla) and the lower mandible: the former is based on the facial bones, especially the premaxillae, and the latter on the composite jaw-bones (see SKULL). The horny coverings of both are formed by the outer layers of the Malpighian cells of the epidermis (see SKIN). The whole horny structure is known as the rhamphotheca, the upper and lower portions being sometimes separately designated rhinotheca and gnathotheca.

Upper mandible. For descriptive purposes this may be divided into the culmen, or dorsal ridge from the tip (dertrum) of the bill to the forehead, and the upper mandibular tomia, or lateral cutting edges. In most birds the external covering is fused into a single hard sheath; in parrots, however, there is limited vertical movement on a 'hinge' between the premaxillae and the skull. In a few families, such as the albatrosses, division of the mandible into distinct horny sections is apparent. Most limicoline birds (Charadrii) have relatively soft 'leathery' coverings to their bills; in geese (*Anser* spp. etc.), while much of the sheath is soft, the tip forms a hard 'nail' well adapted to cropping vegetation. The proximal portion of the mandible may be soft and thickened, forming a sensitive cere, as in diurnal birds-of-prey, in which it is naked, and in parrots, in which it is usually feathered; or it may have a soft, swollen operculum above the nostrils, as in pigeons.

The nostrils or external nares with circular, oval, or linear openings, are usually separated by a cartilaginous or ossified medial septum, as in e.g. the owls, but in certain families such as the gulls and cranes this feature is absent (see NARIS). In the fulmars and shearwaters (Procellariidae) the nostrils are in paired tubes separated by a septum on top of the culmen, but in the storm petrels (Hydrobatidae) they are in a single tube. Darters and cormorants have only rudimentary nostrils that close after the young leave the nest; gannets, which plunge into the sea after fish from a considerable height, have no external nostrils but wide inner apertures communicating with the mouth and, like adult cormorants, they breathe through the mouth. The nostrils of most small passerine birds open into a slight superficial depression, the nasal fossa. The position of the nostrils relative to the base of the bill shows considerable differences; but only in the kiwis, nocturnal species with a highly developed olfactory system, are the nostrils located at the tip of the bill (see SMELL).

Lower mandible. The chief characters of the lower mandible are the lower mandibular tomia, or cutting edges, the mandibular ramus, extending posteriorly on either side of the jaw, and the gonys, or ventral ridge formed by the junction distally of the two halves of the jaw, as clearly seen in gulls for example. The full-length apposition of the closed mandibles is known as the commissure. The gape or rictus is the mouth

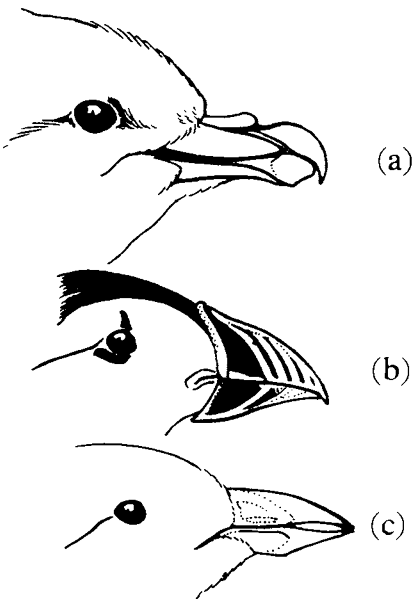

Fig. 1. (a) Fulmar *Fulmarus glacialis*, compound bill and tubular nostrils; (b) Puffin *Fratercula arctica* in breeding season; (c) Puffin in winter, showing bill after sheath has been moulted. (*C.E.T.K.*)

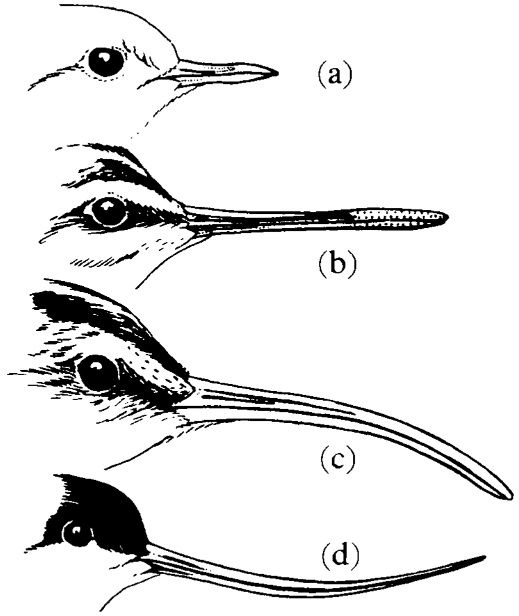

Fig. 2. (a) Golden Plover *Pluvialis apricarius*, bill of moderate length; (b) Snipe *Gallinago gallinago*, long straight bill; (c) Whimbrel *Numenius phaeopus*, long decurved bill; (d) Avocet *Recurvirostra avosetta*, long recurved bill. (*C.E.T.K.*).

opening, formed in the angle between the two mandibles when the lower jaw is dropped.

Regeneration and moult. Regeneration of the rhamphotheca of both mandibles and even of the bones of the bill damaged in combat has been recorded in storks and in the domestic fowl. As a result of damage and imperfect regeneration, or possibly genetic defect, various deformities occur. The effects of normal wear, occurring particularly at the tip of the bill in many species, are compensated by additional growth. The external surfaces of the bills of parrots and some other species are renewed by a process of irregular 'peeling'. In puffins *Fratercula* spp. the much enlarged and laterally flattened and decorated outer sheaths are shed after the breeding season, leaving smaller, unembellished bills of a different shape during winter. Laterally compressed bills occur in other genera of the Alcidae and many are brightly coloured in summer.

Appendages. Seasonal ornamentations or appendages to the bills of male birds occur in many species. Some pelicans, for example, grow several erect horny plates, which are cast after breeding; these birds also show maximum development of the membranous gular sac, which extends the whole length of the lower mandible and embraces the chin, gular region, and jugulum. In many birds, such as coots *Fulica* spp., turacos *Musophaga* spp., a megapode *Megacephalon maleo*, and scoters *Melanitta* spp., the base of the culmen and the forehead are swollen to form ornamental plates, knobs, or humps. These embellishments are seen in extreme form in the hornbills. The swellings are in most instances of light and spongy tissue, but in the Helmeted Hornbill *Rhinoplax vigil* the bones of the enlarged forehead have a dense epidermal covering with the consistency of ivory.

Sexual dimorphism. Notable dimorphism in structure is uncommon, but it is well illustrated in the bill of the Huia *Heteralocha acutirostris*, the male's being relatively short, stout, and almost straight, and the female's slender, decurved, and nearly twice as long (see WATTLEBIRD (2)). Dimorphic bills can also be seen in certain hornbills, in some of which the disparities in size and shape are considerable (e.g. the Rufous-necked Hornbill *Aceros nipalensis*). Differences between the colours of the bills of males, females, and young occur in many species; there are also seasonal changes in colour (see also SEXUAL DIMORPHISM).

Early development. The bills of embryo birds develop a calcareous, scale-like EGG-TOOTH on the tip of the upper mandible with which the eggshell is later perforated; this feature is shed within a few days of hatching. In some species, e.g. American Woodcock *Scolopax minor*, there is another egg-tooth on the lower mandible. Nestling honeyguides possess a pair of sharp mandibular and maxillary hooks which are shed about the time the eyes open; with these interlocking 'teeth'—a unique adaptation—the young parasite kills the nestlings of its host species. The linings of the mouths of altricial nestlings are usually vividly coloured, and both the plate and tongue are often embellished with coloured spots (see TONGUE). The rictal regions are first much swollen; this swelling and the soft operculum found above the nostrils of nestlings of certain species disappear as the bill hardens and assumes adult proportions. Species with highly adapted bills, such as curlews *Numenius* spp. and flamingos, have bills of generalized form in the early nestling stage.

Functions. The bill serves many of the purposes of a 'hand', the specialized forelimbs of birds being little available for these. Notably it is used in nest building, which in some instances demands a high degree of dexterity, and in preening the feathers (see COMFORT BEHAVIOUR; NEST BUILDING). It is also a weapon; and, as already noted, it may bear ornamental or other colouring, excrescences, or appendages. Above all it is used in feeding, being in effect an extension of the jaws, and it is to this function that its structure shows the greatest variety of special adaptations (see FEEDING HABITS).

Adaptation to feeding habits. The external characters of the bills of different species vary greatly in accordance with feeding behaviour. Some reveal high degrees of adaptation, in both shape and proportionate size. The following are typical examples, the characters described being not necessarily exclusive to the groups or species mentioned.

The long, dagger-shaped bills of most herons and bitterns are well adapted to seizing quick-moving prey in shallow water or among reeds. A more perfected development for grasping fish is seen in the bills of mergansers *Mergus* spp., which have saw-like tomia; the bills of toucans have similar toothed serrations for securing food. The elongated, slender bills of most wading birds of the Charadriiformes are adapted to probing in mud or sand, typical straight and pliable examples being seen in the Snipe *Gallinago gallinago* and Woodcock *Scolopax rusticola*; deeply decurved examples occur in the curlews *Numenius* spp. The avocets feed largely on the surface of shallow water and have slender, much recurved bills. In the Wrybill Plover *Anarhynchus frontalis* the whole of the distal half of the bill is curved to the right. A highly specialized mode of feeding is illustrated by the Spoonbill *Platalea leucorodia*, which has the tip of the bill flattened and enlarged in spatulate form, and in the Shoveller *Anas clypeata*, which has a wide, spoon-shaped bill. The boat-shaped bills of the Shoebill *Balaeniceps rex* and the Boatbill *Cochlearius cochlearius* are other examples. An even more extreme adaptation occurs in the skimmers, in which both the lower mandible and its supporting jaw-bones are much elongated, to serve as a projecting scoop (although laterally

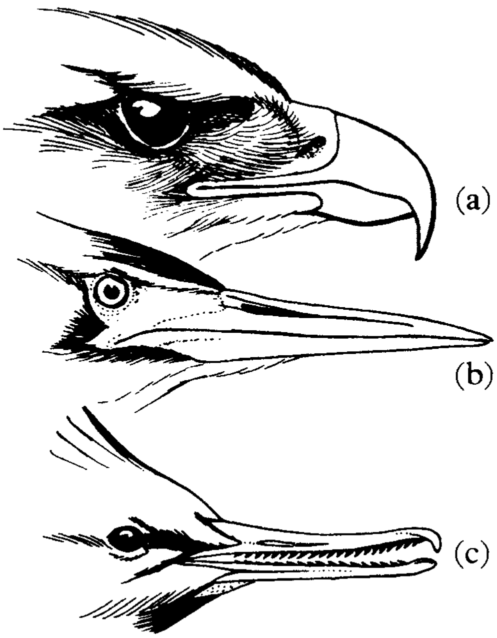

Fig. 3. (a) Golden Eagle *Aquila chrysaetos*, raptorial bill; (b) Bittern *Botaurus stellaris*, spear-like bill; (c) Red-breasted Merganser *Mergus serrator*, saw bill. (*C.E.T.K.*)

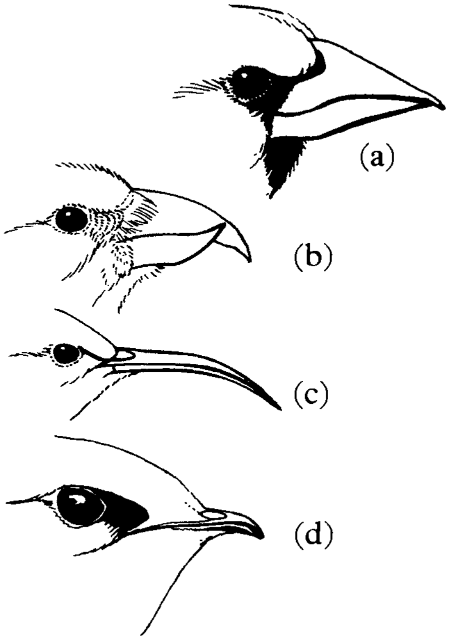

Fig. 4. (a) Hawfinch *Coccothraustes coccothraustes* strong bill; (b) Crossbill *Loxia curvirostra*, tips of mandibles crossing; (c) Scarlet-breasted Sunbird *Nectarina senegalensis*, bill adapted to nectar-feeding; (d) Alpine Swift *Apus melba*, weak bill in a bird that catches insects with open gape. (*C.E.T.K.*)

compressed) in skimming food from the surface of the water in flight. The bills of flamingos are angled downwards in the middle and equipped with a series of elaborate plates or lamellae, which sieve food from muddy water, the bill being held in an inverted position (see FLAMINGO). Lamellae are present also in the bills of swans, geese, and ducks and in prions *Pachyptila* spp. The maximum development of lamellae is seen in the brush-like mass inside the bill of the Openbill Stork *Anastomus oscitans*; this species shows a further peculiarity in that it has a gap halfway along the closed mandibles.

The finches and grosbeaks, the buntings, the weavers and sparrows, and others have stout bills, conical in section, and well adapted to cracking seeds. The commissures in this group of birds are characteristically angulated. A notably wide range of variation in the bill is found in the Reed Bunting *Emberiza schoeniclus* (see BUNTING). A species showing remarkable specialization is the Hawfinch *Coccothraustes coccothraustes*, which has a very highly developed musculature of the jaws and skull, and ridged bosses or 'anvils' on the palate and inside the lower mandible, enabling it to crack the stones of cherries and even of olives. Somewhat similar, but transverse, rasp-like ridges are found inside the bills of certain parrots; with these the hardest fruit-stones are reduced to fine particles. Another striking adaptation is illustrated by the bills of adult crossbills *Loxia* spp., the mandibles being sharply pointed and widely crossed over (to right or left in about equal numbers) to aid the rapid extraction of seeds from fir-cones.

Birds-of-prey, both diurnal and nocturnal, have powerfully hooked and sharply pointed bills, well adapted to killing and tearing up their food. The small, chiefly insectivorous members of the Falconidae have bills of delicate proportions, but in the larger eagles such as *Haliaetus* the proportions are massive. The bills of shrikes are sharply hooked at the tip and the upper mandibular tomium has a distinct 'tooth'; several 'teeth' are apparent in the upper mandibles of trogons.

Small insectivorous birds, typified by the Old World and New World warblers (see WARBLER (1) and (2)), have small and usually slender bills. Treecreepers, which seek small insects in the bark of trees, also have slender but longer and decurved bills. The long and, in some species, finely curved bills of hummingbirds are adapted to probing the corolla-tubes of flowers for nectar, as in varying degree are those of the sunbirds, the honeyeaters, the Hawaiian honeycreepers (Drepanididae), and some flowerpeckers. Some insectivorous families such as the nightjars, which are crepuscular feeders, and some birds of smaller size such as the flycatchers of the Muscicapidae and Tyrannidae, have forward-pointing rictal bristles; like the swifts and swallows, they have very broad gapes which facilitate the capture of flying insects. An adaptation to a highly specialized method of feeding is found in the Buphaginae (see OXPECKER).

Woodpeckers are equipped with sturdy chisel-tipped bills for the excavation of nest-holes in tree-trunks and for reaching wood-boring insects. G.M.

BILL ABNORMALITIES:

Types. Abnormalities are usually confined to the outer covering of the bill (the rhamphotheca, see BILL). A wide variety of abnormalities has been observed, the commonest being elongation, which is often associated with some degree of down curving. Lateral curvature, normal in the Crossbill *Loxia curvirostra*, occurs quite commonly as an abnormality in other species. Abnormalities such as these which involve distorted growth are believed to have genetic origins, although the evidence for this in wild birds is circumstantial. (In domestic fowls, there is detailed evidence for inheritance of similar deformities.)

Another common type of abnormality involves elongation of only one mandible, often accompanied by evidence that the other mandible has been broken. In some cases, at least, such birds are obliged to change their method of feeding (see below), resulting in reduced wear of the tip of the undamaged mandible. Its subsequent elongation results from normal growth. In species whose normal mandibles are unequal, such as parrots and raptors, overgrowth of the upper mandible is rare in the wild, but common in captives eating comparatively soft foods.

Frequency. Abnormalities of the bill have been reported for numerous species of many families. There is some evidence that they are more frequent in passerines than non-passerines, and there are not unexpectedly more records for species which have become commensal with man. Where large samples are available, the frequencies for individual species can be calculated: they are usually between 0.1 and 1.0%.

Behaviour and survival. In view of the close correlation between the shapes of birds' bills and their normal methods of feeding, it is remarkable that some individuals survive with bills that differ so markedly from the normal for their species. The survivors often show considerable changes in behaviour, for example turning the head on one side to feed and drink. Clearly this is difficult unless the food is on a firm surface (e.g. the ground). It may be significant that there are very few records of abnormalities in gleaners (such as warblers), despite the huge numbers handled by ringers. In such species, individuals with serious deformities would seem unlikely to survive.

Survival may be easier for commensal species that rely in part on food

Robin *Erithacus rubecula* with crossed mandibles. (*Photo: N. van Swelm*).

provided by man. Some of the grossest deformities of wild birds have occurred in Starlings *Sturnus vulgaris* and House Sparrows *Passer domesticus*. Yet a number of records concern apparently healthy wild birds of species with specialized diets which could not possibly have fed normally—for example, records exist of a Hawfinch *Coccothraustes coccothraustes*, and a Pink-footed Goose *Anser brachyrhnchus*, both lacking the distal half of the upper mandible. Their survival is evidence that feeding behaviour can show considerable improvisation. There are a few records of modification of a quite different kind; where a bird with an abnormal bill was being fed by another individual, presumably its mate.

Other effects. Whilst some birds with abnormal bills not only survive but also appear healthy, with normal weights, others fare less well. In particular, many have difficulty in preening; their plumage is in poor condition and they carry numerous ectoparasites, especially feather lice.

D.E.P.

Pomeroy, D.E. 1962. Birds with abnormal bills. Br. Birds 55: 49–72.

BILL-CLAPPERING, -CLATTERING, -FENCING: see MECHANICAL SOUNDS.

BILLING: caressing with the bill.

BILL SOUNDS: see MECHANICAL SOUNDS.

BIMACULATION: the occurrence of two spots, e.g. in the facial plumage of certain ducks (Anatidae)—see PLUMAGE.

BIMODAL: see under BIOSTATISTICS.

BINDING-TO: term used in FALCONRY.

BINOCULAR VISION: see VISION.

BINOMINAL or **BINOMIAL SYSTEM:** see NOMENCLATURE.

BIOCENOSIS: ecological term (plural 'biocenoses') for an association of living things inhabiting a uniform division of the 'biosphere'; in other words, the ecological community found in a particular 'biotope' (see under BIOSPHERE).

BIOCHORE: see under BIOSPHERE.

BIOCYCLE: see under BIOSPHERE.

BIOLOGICAL CLOCK: see RHYTHMS AND TIME MEASUREMENT.

BIOLOGY: the science of life—the study of animate nature. The antithesis is with the physical sciences, apart from the applications of these to the study of living matter. The term 'biological' does not exclude the study of dead specimens as one of the approaches to the problems of the living organism, although sometimes loosely used as if it did.

BIOMASS: quantitative term used in ecology—the total weight of organisms per unit area of land, or the total weight of organisms of a specified kind (e.g. birds).

BIOME: term for a major biotic community, i.e. one existing in a wide area defined by certain general environmental features (and possibly including both land and fresh water)—contrast LIFE ZONE. An equivalent term in respect of animal life only is 'zoome' (and in respect of plants only, 'phytome').

BIOMETRICS: see BIOSTATISTICS.

BIONOMICS: term equivalent to ECOLOGY.

BIOSPECIES: see under SPECIES.

BIOSPHERE: ecological term for the sum total of the environments capable of supporting life, i.e. the 'habitable globe' as regards animals and plants. The biosphere is divisible into 3 'biocycles'—ocean, fresh water, and land. These in turn are divisible into 'biochores'; thus the main biochores in the terrestrial biocycle are forest, dry open land, moist open land, high montane and polar areas. Biochores are in turn made up of 'biotopes', which are particular areas substantially uniform in their environmental conditions and living inhabitants (see ECOLOGY).

BIOSTATISTICS: the application of statistical methods to the solution of biological problems. The topic is also known as *biological statistics* and sometimes as *biometry*, though this latter term is usually reserved for the study of morphological measurements of animals. Statistics have a relatively more important role in biology than in the physical sciences because of the existence of NATURAL SELECTION. Natural selection operates on the natural variation between animals: individuals with different values for the characters selected reproduce differentially into future generations. Because of this, the ability to study variation between individuals is fundamental to the study of evolutionary processes within biology, which can therefore never be exact in the sense of the physical sciences. The subject matter of biostatistics is therefore data arising from populations or groups of animals. Whilst repeated measurements on a single bird may be of interest in providing insight into a biological problem, they are of little value as conclusive evidence, even when supported by statistical treatment.

Because biostatistics has to treat of variability amongst animals, it cannot provide exact answers. There is no unique answer to questions such as 'Are male House Sparrows *Passer domesticus* heavier than female House Sparrows?' A large number of factors outside the control of the ornithologist intrude on the measurement process: factors such as season, ambient temperature, food supply, breeding physiology, and body size all influence body weight and it will therefore be in general impossible to acquire samples of individuals differing only in sex. Instead, we must work with samples of males and females and, to questions such as that posed, confine our answers to probabilistic statements as to the results of the comparison, i.e. how *likely* it is that a male sparrow will be heavier than a female, all else being equal. If the probability of a result is high enough, of course, the result can be accepted as an established fact and as a general feature of the population concerned.

Some statistical terms. Data in biostatistics are generally based on individual observations, measurements made on the smallest sampling unit. These units will often be individual birds, with each bird yielding one observation or measurement. Such individuals may be referred to as2 cases. In other studies, repeat measurements may be made on the same individual bird, so that each case yields two or more observations. For example, in avian endocrinology the same measurement may be made before and after a hormone injection: here, the case remains the individual bird but there are two observations, one 'before', the other 'after'. Similarly, in a ringing study, the two observations of the bird's location at ringing and at recovery constitute paired observations pertaining to a single case.

An observation consists of recording a character or variable for the bird. Typical examples are a measurement of wing length or body weight, noting the colour of a particular part of the plumage, or noting a food item brought to a nestling.

The term *statistical population* has a definite meaning within biostatistics and one distinct from the normal biological definition of the population as the collection of all the individuals of a given species in the specified area and time. A statistical population is the total set of observations under analysis and about which some inference is to be made; a synonym of the statistical population is the *universe*. For a very small number of species the population to be sampled may be quite definable, as for example with the population of Whooping Cranes *Grus americana* in the USA. In general, though, the biological population will be so large that the universe of possible measurements is prohibitive of analysis and a *sample* is taken from it for study. From the behaviour of this sample under statistical treatment we infer what the behaviour of the entire population is likely to be.

The term *variable* is used in biostatistics to define any characteristic in respect of which individual birds can be established to differ. The detail with which these differences can be established characterize particular classes of variables: (1) measurement variables (which may be either continuous or discrete), (2) ranked or ordinal variables and (3) nominal (or categorical) variables or *attributes*. The statistical treatment which may be afforded these different variables varies substantially between these classes.

Measurement variables are those whose values for individual birds can be ordered in a numerical fashion. *Continuous variables* are those which can, at least in theory, take an infinite number of values between any two fixed points. Thus, body weights may be measured to a precision limited only by that of the measuring instrument. For example, whilst an egg weight may be measured to only 0.1 g with a spring balance it might be measured to 0.01 g with an electrical balance or to 0.001 g with a micro-balance: the actual value is limited only by the measurement precision. Examples are weights, lengths, areas, volumes, temperatures, durations, and rates.

Discrete variables are those which can take only fixed numerical values. Thus, clutch size can take values only of 1, 2, 3, etc. eggs. It is meaningless to talk about a clutch of 2.7 eggs. In general, discrete variables are the result of counting procedures rather than of measurement procedures.

Ranked or *ordinal variables* are those which can be placed in sequence or ranking according to their value but which cannot otherwise be measured. Thus, the age of a bird increases as one goes through the sequence neonate, nestling, fledgling, juvenile, immature, and adult, so that the birds can be ranked in age according to these categories. One cannot, however, make any statement about the absolute differences in age between these categories. Thus, although one might rank the birds according to these categories as 1 = neonate, 2 = nestling, 3 = fledgling, etc., there is no implication that a bird of rank 2 is twice as old as a bird of rank 1. Furthermore, equality of differences in rank does not imply equality of differences in age.

Nominal (or *categorical*) *variables* or attributes are those which cannot be measured but which can be unequivocally described by some quality. For example, the sex of a bird is such an attribute: a bird may be characterized as a 'male' or 'female' but the sequence (male, female) is as valid as the sequence (female, male). Other examples of attribute data include species lists for a census plot (each species identity being an attribute), colour polymorphisms, behaviours. The values or names attached to these categories (whence the term 'nominal variable') are not amenable to statistical treatment such as averaging. Counts of the frequencies with which these categories occur in a sample are, however, amenable to statistical treatment.

The term *variate* is used for an individual value taken by a particular variable.

Accuracy and precision. The term *accuracy* is used to describe how close a measured value is to its true value. Any reproducible difference between the two reflects the presence of a *bias* of measurement. The term *precision* refers to the degree of similarity amongst repeated measurements of some quantity. A measurement may therefore be quite precise but inaccurate because of the presence of reproducible bias in the measuring process. The precision of an estimate can be increased by taking more readings but the accuracy of a measurement can be improved only if it is possible to assess the bias quantitatively.

In ornithology the most precise data usually arise when whole numbers are involved. Counts of clutch-size, for example, can be precise. Counts of such small numbers are also likely to be accurate. In a census of a wood the counts of Robins *Erithacus rubecula* or of Treecreepers *Certhia familiaris* may be precise but nevertheless inaccurate: not all birds may be seen in the course of searching the wood.

Measurements of continuous variables are in general approximations. The extent of this approximation is implied by the number of decimals quoted. The usual convention is that the last digit quoted represents the precision of the measurement: the statement that the weight of a Great Tit *Parus major* was 19.5 g implies that the weight is in fact somewhere between 19.45 g and 19.55 g; had it been just outside these limits we would have quoted the weight as 19.4 g or 19.6 g as appropriate. Similarly, a statement that a weight was 19.523 g implies the bird was weighed with a precision of 1 mg. This convention is frequently incorrectly ignored by ornithologists citing a spuriously large number of decimal places.

What precision of measurements should one seek? Clearly, if one weighed birds to only 1 g whilst the birds' weight ranged over only, say, 3 g, one has very little chance of detecting any seasonal or sexual differences in weight. On the other hand, measuring the weights of all birds to 1 mg is wasteful of time and effort (and the readings are probably biased in addition as a result of excretion and the like). Sokal and Rohlf (1973) suggest that the precision of measurement used should be such that the *range* (difference between the smallest and the largest measurement values) has between 30 and 300 identifiable steps. According to this, the bird with the weight range of 3 g should be measured with a precision of at least 0.1 g but not more than a precision of 0.01 g. But with a larger bird with a weight range of, say, 15 g a precision of 0.5 g would suffice.

Trailing zeros imply precision if decimal points are present. Thus, a measurement reported as 3.20 cm means the measurement is correct to within 0.1 mm. However, this convention is rarely observed in the absence of decimal points: the figure 2700 strictly means 1 more than 2699, but is widely taken as meaning an estimate determined to ±50.

Ratios. A ratio is the proportion obtained by dividing the value of one variable by the value of a second variable. Ratios are widely used in taxonomy, particularly in describing shape. The ratio obtained by dividing bill depth by bill length has been used to separate sexes amongst Herring Gulls *Larus argentatus*, for example. Although used in this form, ratios have a number of disadvantages, notably that their distributions are frequently non-normal and therefore require either transformation or the use of relatively less powerful *non-parametric statistics* in studying them. In addition, a bird with average dimensions for the two variables which enter the ratio does not have an average value for that ratio. Probably most importantly, much information is lost through the use of ratios: plots of y against x are much more informative in identifying sexual or seasonal groupings than is a simple scrutiny of the ratio of y/x.

Frequency distributions. The results of tabulating (or graphing) the counts of occurrences of the individual values of a variable against those values (Fig. 1). Where the variable concerned is categorical in type, the order of presentation of the different values is arbitrary and may be interchanged without loss of information. When the variable is ordinal, however, they are arranged in descending or ascending order. The shape of a frequency histogram of such ordinal data can be informative. Many such distributions have a bell-shaped curve, frequency falling off symmetrically on either side of some central category (Fig. 2). But distributions may be distinctly asymmetrical, the tail of the distribution being excessively extended in one direction or in the other. Such skewed distributions usually reflect either selection for or against birds with those particular values or the presence of some bias in the measurement scale. Similarly, the presence of two peaks in a bimodal distribution (Fig. 3) indicates the possible presence of discrete populations of birds.

Distributions are frequently displayed graphically (Figs 1–3) so that

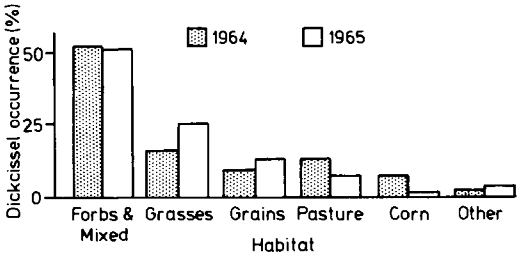

Fig. 1. Typical bar-diagram displaying qualitative data, where frequencies have been converted to percentages. Note (by comparing the results for the 2 years) that there are no constraints on the left-to-right sequencing of these categorical data. (After Wiens & Rotenberry 1981, Studies in Avian Biology).

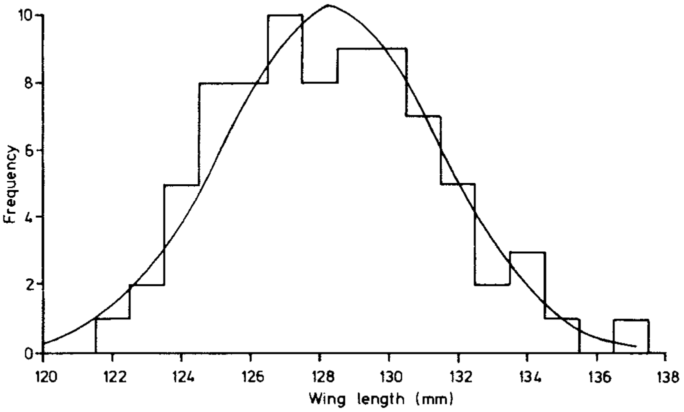

Fig. 2. Typical histogram of near-normally distributed interval data, showing the bell-shape characteristic of this distribution. The data are for wing-lengths of first-year Sanderlings *Calidris alba* trapped in autumn in Surinam (South America). (After Spaans 1980, Wader Study Group Bull.).

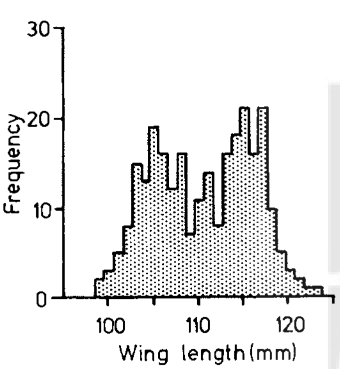

Fig. 3. A bi-modal distribution typical of a mixture of two distinct sample populations, here of male (long-winged birds) and female (short-winged birds) Skylarks *Alauda arvensis* trapped at Gibraltar Point (England) bird observatory. (After Davies 1981, Ringing & Migration).

their shape may be easily assimilated. There are two conventional ways of presenting the material. Where discrete variables are involved, so that only certain values may be found, a *bar-diagram* is used for the display (Fig. 1). Note that the bars do not touch one another, thereby indicating the non-continuity of the variable. Where the data are continuous, on the other hand, they can be presented as a *histogram* (Fig. 3), the height of each bar indicating the frequency, and the width of each bar indicating the class interval. To construct such a histogram the values of the continuous variable are tallied into specified class intervals defined by specified upper and lower limits, the upper limit of one class serving as the lower limit of the adjacent class. The class interval is usually held constant across the histogram, except perhaps at the beginning and final steps, but its width may be chosen according to convenience. Typically there are 12–20 classes displayed on a histogram.

Descriptive statistics. The first task of biostatistics is to provide some form of summary description of the data. If one measures 200 bird weights it is impracticable to describe the population by quoting the raw data: some form of summary is required. For an ordered frequency distribution two descriptive statistics are particularly important: a measure of *central tendency*, and a measure of *dispersion*. If appropriately chosen, these statistics more economically describe the data than do the histograms or bar charts previously presented.

Statistics of location or of central tendency indicate the whereabouts of the distribution as a whole (Fig. 4). The figure shows the position of three separate measures of central tendency, the mode, the median, and the mean. Which measures may best be used depend on the nature of the data (whether nominal, ordinal or continuous).

The *mode* is the most frequently represented value within the histogram or bar chart, i.e. there are more observations at that value than at any other, whether the value be discrete or that of a class interval. It is thus the highest point on a frequency distribution. The mode may be used with data of all three types, though with interval data it is of relatively little use other than as an indicator of the most commonly occurring class.

The *median* is that measure of location which splits a frequency distribution ranked by order into two equal halves. It follows that it is inapplicable to attribute data. With ordinal and continuous variables the data may be ranked by size, whereupon the median is the point at which half the observations lie below and half above. Where the number of observations is an even number, its value is conventionally computed as the mid-point of the two central members of the ranked frequency distribution. With discrete data and with interval class data several observations may fall into the central class containing the median value. In such cases it is usual to assume that the data are distributed evenly across the class and, with class interval data, to assign the median to the corresponding proportional point between the class limits. With discrete data the corresponding enumeration is performed.

The median is a particularly useful statistic wherever frequency distributions are skew: because the median depends only on the frequency representation of unusually high or unusually low values and not on the value of the variate at those observations, the position of the median is relatively insensitive to such outlying points.

The *mean* or *average* is a parametric statistic of location, computed by summing the observations made within the sample and dividing the total by the number of such observations. This summation results in extreme observations receiving considerable weight, so that the mean moves in the direction of any asymmetry in the frequency distribution.

Measures of dispersion. Frequency distributions may vary substan-

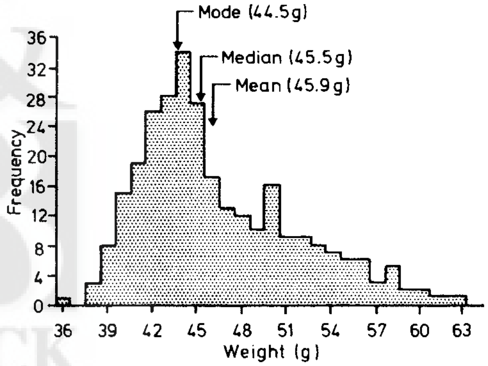

Fig. 4. An example of a skew distribution, here of weights of female Corn Buntings *Miliaria calandra*, showing the effect of the (here positive) 'tail' in moving the mean value away from the median and modal values (which are themselves separated). (Modified from Boddy & Blackburn 1978, Ringing & Migration).

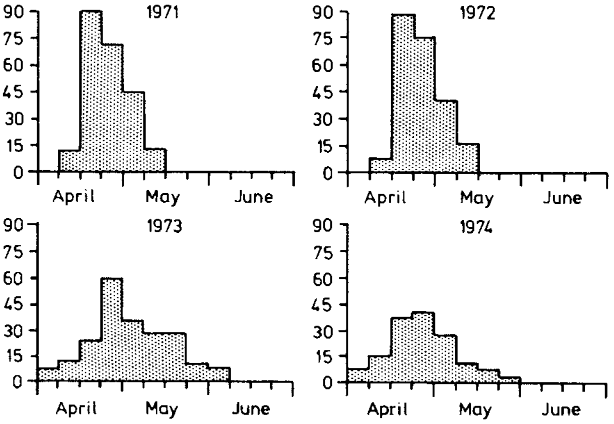

Fig. 5. Annual distributions of egg-laying dates in a New Forest (England) population of Lapwing *Vanellus vanellus* showing year-to-year variation in distribution width ('dispersion'). (After Jackson & Jackson 1975, Ringing & Migration).

tially in their apparent 'width' independent of their central location (Fig. 5). Some measure of the width of the distribution is therefore desirable.

The *range* is the simplest form of characterizing distributions and is calculated as the difference between the largest and the smallest item in the sample. This measure is obviously sensitive to outliers and is therefore only an approximate measure of the dispersion. It is worth noting in particular that as sample size increases the probability of detecting an observation with a still more extreme value increases, thereby increasing the range.

The *standard deviation* is the most widely used measure of dispersion for symmetrically distributed data. It is computed as

$$S = \sqrt{\frac{\Sigma(x - \bar{x})^2}{n - 1}}$$

or equivalently as

$$S = \sqrt{\frac{\Sigma x^2 - n\bar{x}^2}{n - 1}}$$

where x is an observed value, $\bar{x}$ is the average of all values in the sample, and n is the sample size. The former version shows that the standard deviation is a root mean square index of dispersion. That is, it is calculated by computing the deviations of each point from the mean, squaring them, weighting them for sample size and taking their square root. The squaring procedure ensures that positive and negative deviations are given equal weight and avoids the problems caused by the average deviation being zero; the squaring process has other advantages on mathematical grounds. The use of the factor $(n - 1)$ in the denominator instead of dividing by n to compute an average mean square deviation has been shown by statisticians to be necessary to obtain an unbiased estimate of the spread of the population from which the sample has been drawn.

The term *variance* is used to describe the square of the standard deviation.

The *coefficient of variation* is a statistic which expresses dispersion (in the form of standard deviation) as a percentage of the sample mean. That is,

$$CV = 100\,s/m$$

where s is standard deviation and m is sample mean.

This measure of *relative variation* allows for the fact that large animals are more likely to vary individually by any absolute amount than small animals: a Wren *Troglodytes troglodytes* will not show the same absolute variation in measurement as will an Ostrich *Struthio camelus*. The coefficient of variation provides a scale of relative variation with which meaningful comparisons between species of different size can be attempted.

Statistical significance. Because animals are inherently variable as to the characteristics ornithologists may wish to measure, statements about them are necessarily expressed (at least in principle) in probabilistic terms. That is, we are rarely in a position to assert that, say, males are larger than females; what we must say, in strict pedantry, is that males are *more likely* to be larger than females. Were there no convention amongst scientists as to how a phrase such as 'more likely' is to be interpreted there would be considerable variation in individual ornithologists' interpretations of its meaning. Conventionally, therefore, such results are assessed in terms of statistical significance, meaning the probability that a particular result would have arisen by chance were the supposed hypothesis untrue. In the example of the male-female weight difference, for example, we start with the assumption or *null hypothesis* that there is no difference between males and females. We then compute the probability that two samples drawn from this common pooled male/female population would in fact differ by the amount found in the samples actually taken. If these chances are low enough we regard the probability of the male and the female sample having been drawn from a common pool as being so low as to be unlikely and prefer the alternative hypothesis that there are in fact differences between male and female.

What is 'low enough' in this context? The conventional probability for scientific purposes is 0.05, meaning that we have five chances in a hundred of getting the two (or more) samples drawn from the common pool yielding a difference as big as that observed. Two points must be made about this limit. First, it is a purely conventional limit accepted as a working tool by scientists. Secondly, in working to this conventional value one is accepting a one in twenty chance of a sampling artefact, there really being no difference between the male and female distributions. When there is great importance attached to getting the results correct a one-in-twenty chance of error may be too high and it is possible to work to higher levels of significance, such as 0.01 or 0.001, meaning respectively a one-in-a-hundred and a one-in-one-thousand risk of falsely asserting the existence of a difference between the two samples.

This approach to testing hypotheses has a further consequence. If one conducts 100 tests of differences between males and females on the basis of a 5% significance level, as many as five of these tests are likely to yield 'significant' results by chance alone. Consequently, where repeated testing of samples is involved, it is necessary to avoid such a 'Type I' error by working to a higher level of significance than would otherwise be appropriate. On the other hand, such an approach to probability testing of hypotheses is more likely to fail to recognize real differences between male and female samples as the significance level is raised (a failure known as Type II error). That is, in protecting ourselves against the chances of falsely asserting the presence of a male/female difference, whilst the samples were in fact drawn from distributions similar for males and females, we are increasing our chances of failing to detect sex differences when male and female distributions are not identical.

Testing a significance level. How does one assess the probability of two samples drawn from a common distribution in fact differing by the amount observed in the experimental samples? One approach is to draw repeatedly from a model population with the desired characteristics, and to examine the differences between the two samples of pseudo-males and pseudo-females drawn from this population. Such a course would be extremely tedious and one normally has recourse instead to certain test statistics whose critical values are conveniently tabulated. As these test statistics have been computed only for distributions obeying certain assumptions, it is important that the data under test also obey these distributions. Thus, a test statistic calculated for a normally distributed population is inappropriate to a population whose distribution is non-normal.

To accommodate the wide variety of problems regularly encountered, statisticians have evolved a number of test statistics meeting particular problems. The rationale behind these test statistics is that they represent quantities which can be calculated for samples repeatedly taken from some underlying distribution. Corresponding to repeated sampling from the population will be a distribution of values of these test statistics, the distribution being defined either analytically or, in the case of complex population distribution, by computer simulations. It is therefore possible to examine these distributions and to establish values of the test statistic corresponding to, say, 50% of all observations lying between the chosen values, 90% of all observations lying between the specified values, 95% lying between them, etc. Of particular interest are the values corresponding to 95% of the observations defined by the critical values since this corresponds to the conventional 0.05 significance level. Were two samples drawn from a single underlying population and the corresponding test statistic computed, 95% of the drawings would yield test values within the specified critical values. Were the computed value outside these limits, one would be dealing with the rare set of 5% of the drawings from a common population. Given real samples for which such a test statistic value was calculated, one has a nineteen to one chance against the value being derived from samples belonging to the distribution concerned.

Such critical values will vary according to the size of the samples drawn. Consequently, it is possible to tabulate these values as a function of sample size. Armed with such a table, an ornithologist faced with a real sample or samples can compute the same test statistic and enquire whether the value exceeds the conventional 5% significance level.

Confidence limits. The aim in sampling is to describe the population by inferring from the observations which were taken as a sample. How good is the resulting inference? Suppose one is interested in the weights of individuals of a species just before migration. If one could weigh all individuals of the species one would know the 'true mean' (M) and the 'true variance' (σ^2) for the population. In practice one has a sample of these birds with some average weight $\bar{x}$ and sample variance S^2. One may set *confidence limits* to the estimated average $\bar{x}$ to allow statements of the form 'The probability that *limit 1* $< \bar{x} <$ *limit 2* is at least 95%' by using certain statistical methods to calculate the *lower confidence limit limit 1* and the *upper confidence limit limit 2*. Such statements claim that conventional statistical procedures have been followed and that estimates of the confidence limits would encompass the true mean in at least 95% of the experiments analysed with such procedures.

The theory behind such statements is complicated but an understanding of the methods may be obtained as follows. Suppose we took, as before, a sample of observations from the parent distribution of all observations and computed some test statistic for the sample. We could repeat this process as often as we wish, tabulating the resulting values of the test statistic for each drawing of the sample. After, say, 1,000 such samples, we would have a good idea as to the distribution of the test statistic scores and, in particular, what values of the statistic would arise in only 5% (or 1% or 0.1%, as we wish) of the samples. If we now examined a sample of real observations satisfying certain criteria (discussed below) we could likewise compute a sample test statistic. If this were so extreme as to arise in 5% or fewer of the sample drawings just discussed it would be rather improbable that these real data belonged to the parent distribution. Note that we have reached a conclusion—that the real data do not belong to the parent distribution—on the basis of comparing a computed test statistic for the sample with a critical value (for 5%, 1%, etc.) already established by simulated drawings from the parent population. These critical values depend on the size of the sample used but it is nevertheless possible to prepare tables of these critical values, both with respect to different significance levels and with respect to sample size.

If these tables had to be prepared from the results of large numbers of sample drawings as outlined above, with different procedures for each different problem, the tables would be excessively voluminous. In practice analytical expressions for the distribution of particular test statistics can be formulated and many problems can be analysed in such a way as to generate such a statistic. Examples of widely used statistics of this type include Student's t, the variance ratio F, and chi-squared (χ^2).

Parametric and non-parametric statistics. Test statistics based on analytical expressions necessarily make assumptions about the distribution of the population sampled. If these assumptions are correct, the test statistic will be correctly calculated and the conclusions valid; if incorrect, the statistic is inappropriate and the conclusions invalid. Since the population assumptions turn on values given to parameters within their algebraic expressions these methods are called *parametric*.

Many statistical techniques more recently in fashion are independent of such assumptions and are called *distribution-free* or *non-parametric* methods. These techniques are particularly valuable with ordinal and categorical data, which fail to satisfy parametric assumptions. These techniques may also prove helpful with skew or otherwise unsatisfactory distributions of continuous variables. In many instances non-parametric procedures result in an evaluation of the exact probability of getting as extreme an event as that observed. That is, this probability is directly calculated rather than inferred via a statistic subject to assumptions. This is especially valuable with very small samples, for which the validity of assumptions as to distribution is difficult to check. They are also useful in testing differences between populations known to differ in distribution. The main drawback of non-parametric methods is that they require rather larger samples than do equivalent parametric tests for which all assumptions are satisfied.

Statistical testing. Siegel (1956) summarizes the process of statistical testing into six stages: (1) state the *null hypothesis*; (2) choose an appropriate statistical test with its associated statistical model; (3) specify the target significance level and sample size; (4) find (or assume) the sampling distribution of the statistical test for the assumption that the null hypothesis is correct; (5) define *region of rejection*; and (6) compute the value of the test for the sample data and accept or reject the null hypothesis accordingly.

The *null hypothesis* is one temporarily assumed for the purposes of the statistical test. Since it is impossible to prove a negative we try to recast the problem as a positive; e.g. the surest way to prove that a colour-ringed Blackbird *Turdus merula* is not breeding in a particular forest is to show that it *is* breeding somewhere else; otherwise, however well one searched the forest one has always a residual possibility of having missed the bird. For a null hypothesis, therefore, we assume the absence of what we expect to find and seek to establish the presence of a consequential discrepancy.

The choice of statistical test depends primarily on (a) the validity of the assumptions to be made if the chosen test is to be used and (b) the type of data involved, particular tests being inapplicable to certain types of data (see above).

The *level of significance* associated with a test is necessitated by the variation inevitably associated with random sampling. Repeated sampling on the same question will give different results on different occasions, with the extent of the variation determined by measurement errors and by the natural variation of biological populations. Consequently, the results of a test are only probabilities, not determinants, and one is at risk both of falsely deciding in favour of and of falsely deciding against one's hypothesis. By convention—and one must emphasize it is convention, not an inescapable rule—we accept at maximum a one-in-twenty risk of incorrectly rejecting the null hypothesis (and thus of falsely concluding in favour of the research hypothesis under test). For some purposes we may wish to reduce this risk (a so-called 'Type I' error) to one in a hundred or even to one in a thousand. This is equivalent to demanding stronger evidence for the research hypothesis and therefore carries increasing risk of making the alternative ('Type II') error, of falsely accepting the null hypothesis and concluding one's research hypothesis is wrong. In general the chance of correctly rejecting the null hypothesis increases with sample size.

Glossary of some common statistical tests. It is not possible to describe within the scope of the present article how to conduct the various statistical tests available. For information on these readers are referred to the references below. What follows is a brief glossary of some of the commoner statistical tests, primarily to indicate their respective functions.

Analysis of variance A general class of statistical tests used for assessing the significance of differences between two or more samples. The principle used is to compare the between sample and within sample variances: if the average differences between samples are large enough relative to the variation within each sample, it is likely that biological effects are present. The implementation of this principle varies, however, according to the assumptions that one can (or must) make about relationships between the individual birds measured in each sample. For an excellent introduction see the book by Parker.

ANOVA (Anova) A synonym of analysis of variance.

Bartlett's test of homogeneity of variances A test of whether three or more samples are equally variable (see F-test for two sample case)

Binomial test A test for whether in a sample the number of birds possessing some particular attribute corresponds to the proportion expected (according to some quantitative, e.g. genetical-hypothesis) to have that attribute.

Chi-square (χ^2_{X}) A test for assessing the significance of differences in ratios between samples, e.g. do the proportions of male and female sparrows taken by Sparrowhawks and cats respectively differ? The test can accommodate more than two samples and more than two attributes, e.g. here one might also use chi-square analysis to compare Sparrowhawk, cat and small-boy-with-catapult mortality of male and female sparrows or to compare the incidence of mortality of these types in different months.

Concordance A method of testing the consistency of several sets of rank orders, e.g. in comparing the effectiveness of, say, five types of scarecrows in inhibiting crop consumption by three species of bird: is the relative effectiveness of each scarecrow the same for all three species?

Correlation A test for the presence of trend in a sample, e.g. are Blackbirds heavier in months of lower temperatures? The Pearson or product-moment correlation tests for linear trend between normally distributed variables but non-parametric correlation coefficients (Kendall's, Spearman's) are also available and can accommodate non-linear trends in which rank order and not linearity is maintained.

Covariance analysis A technique related to analysis of variance which accommodates the situation where classification of samples on some criteria has to be continuous rather than discrete (as in ANOVA).

F-test A test of whether two samples are equally variable.

g-test A test for whether a distribution is significantly skewed.

Goodness of fit test The use of chi-squared (usually) to test whether an observed frequency distribution accords with that expected on some theoretical basis.

Kendall's tau A non-parametric test of correlation (*q.v.*).

Least squares A general class of statistical computation, common to many of the tests listed here, in which the best estimate of some statistic is taken as that which minimizes the squared deviations between statistic and observations. See 'standard deviation' in the main text for a simple example.

Linear regression See *Regression.*

Mann-Whitney U-test One of the most commonly used tests of differences between the central values of two samples in which the data are not normally distributed.

Median test Performs the same function as the Mann-Whitney U-test but can be extended to comparing central values of three or more samples.

Paired sample test A term used to describe a class of test in which known relationships exist between the individuals contributing to two samples of measurements, e.g. 'before' and 'after' measurements on birds injected with hormones.

Partial correlation A method of testing the trend between two variables, say x and y, when either or both may also be correlated with some other variable z. By first correcting for the effects of z the partial correlation analysis tests whether x and y are mutually correlated in their own right rather than via common correlation with z.

Rank correlation A non-parametric test of trend, where trend is measured between the ranks of the variable concerned rather than between their absolute values. See also *Correlation.*

Regression A test for trend between two variables which assesses the rate of change of one variable (the dependent) with changes in the other (independent) variable. The technique is applicable only to normally distributed variables. Where several independent variables are present an extension—multiple regression—is available to describe the simultaneous dependences of the dependent variable on the several independent variables.

Sign-test A non-parametric test for trend measured in paired samples. If enough individuals in samples show the same trend (up or down) between two sampling occasions, probability of a real movement up or down would be high.

Signed rank-test A more powerful extension of the Sign-test which takes into account the sizes of the differences recorded of the members of a paired sample.

Spearman's correlation See *Rank correlation.*

Stepwise regression A variant of multiple regression (see regression) in which the independent variables are considered in turn for inclusion (step-up) or exclusion (step-down) from the multiple regression equation, until the equation contains only those variables that contribute significantly to the explanation of the variation in the dependent variable. It is possible for step-up regression to give a different set of independent variables from those obtained by step-down regression and these sets may, in general, differ from the set that would be obtained by an exhaustive search of all possible combinations of independent variables.

Student's t-test A test for the presence of a difference between two sample means, where the data in each sample are normally distributed and equal in variance. A special modification applies where the samples differ in variance.

Transformation The technique of applying some mathematical manipulation to data to make them conform more closely to the assumptions to be made in a particular statistical test. The statistical computations may then be validly applied to the data but the final results will require a reversal of the transformation procedure, so that, for example, symmetrical confidence intervals computed for the transformed data will yield asymmetric confidence intervals when expressed in terms of the original data. Common transformations include taking the logarithm, square root or arc-sine of the data values, the exact transformation adopted depending on the nature of the non-normality in the original data. R.J.O'C.

Parker, R.E. 1973. Introductory Statistics for Biology. London.
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Snedecor, G.W. & Cochran, W.G. 1967. Statistical Methods. Ames, Iowa.
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BIOTA: term coined to comprehend both the fauna and the flora of an area (see FAUNA).

BIOTELEMETRY: see RADIO TRACKING AND BIOTELEMETRY.

BIOTIC: term applied to the organic element in the environment.

BIOTOPES: particular areas which are substantially uniform in their environmental conditions and flora and fauna.

BIOTYPE: a population of the same genotype (in the proper sense of the latter term)—see GENOTYPE.

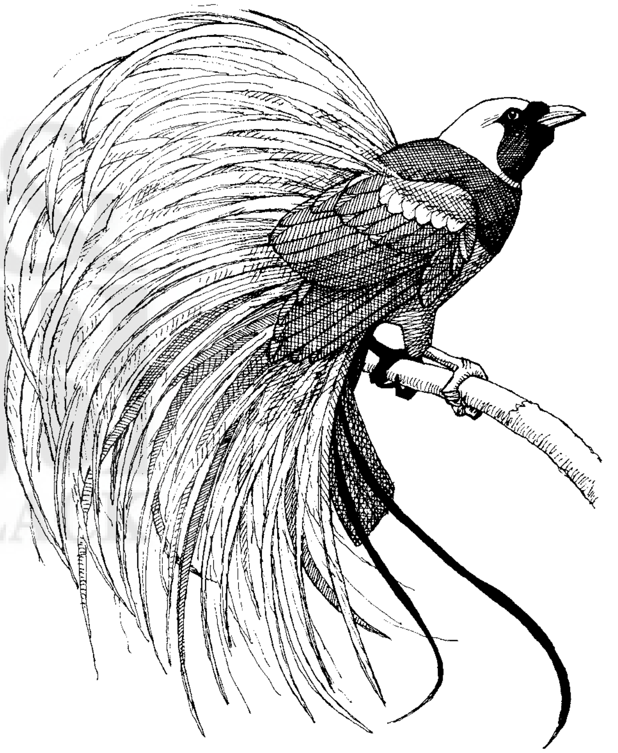
BIPEDAL: two-footed, in the sense that the forelimbs are not used for walking; but compare the special meaning of TETRAPOD, also applied to birds.

BIRD: term applied, in different contexts, either to an individual animal or to a species (or subspecific form) belonging to the class Aves; occasionally to an imaginary generalized type; also used adjectivally (e.g. bird song), or as part of the name of a species or group (e.g. tropicbird, bird-of-paradise)—see AVES.

BIRD FANCIER: see AVICULTURE.

BIRD LIME: see CONSERVATION.

BIRD OBSERVATORY: see OBSERVATORY, BIRD.



Raggiana Bird-of-paradise *Paradisaea raggiana*. (*N.W.C.*).

BIRD-OF-PARADISE: substantive name of most species of Paradisaeidae (Passeriformes, suborder Oscines) and, in the plural, general term for the family. Birds-of-paradise are most closely related to the bowerbirds (Ptilonorhynchidae). On the basis of their cranial anatomy, Bock (1963) placed the 2 groups in separate families, but Gilliard (1969) and Schodde (1976) combine them into Paradisaeidae. Bock defined 2 subfamilies, the Cnemophilinae (comprising *Loria*, *Loboparadisaea*, *Cnemophilus* and *Macgregoria*) and the Paradisaeinae containing all other genera. He concluded that birds-of-paradise and bowerbirds evolved from the primitive Cnemophilinae which are probably derived from the Sturnidae. *Macgregoria* has subsequently been transferred to the Paradisaeinae (Gilliard 1969, Diamond 1972, Schodde 1976). The Meliphagidae, Callaeidae, Cracticidae, Corvidae and the problematical *Lamprolia* of Fiji (see SILKTAIL) have also variously been considered ancestral to and/or close relatives of the birds-of-paradise.

The 43 Paradisaeidae species are usually ascribed to 20 genera. The 17 genera of Paradisaeinae contain 1–7 species while those in the Cnemophilinae are monotypic. Diamond proposed extensive alterations to this classification involving the merging of genera to reduce Cnemophilinae to 2 and Paradisaeinae to 8, but his proposals have been largely ignored in the face of a lack of information about the biology of many of the species involved.

Characteristics. Birds-of-paradise are stout-billed and strong-footed, rather starling- or crow-like in general appearance and size (lengths 12.5–100 cm including variable tail lengths) and are renowned for their spectacular plumages and courtship displays and their diverse mating systems.

Habitat. Birds-of-paradise inhabit wet forests ranging from tropical lowland to sub-alpine types.

Distribution. The family very probably originated in New Guinea, to which most species are restricted. However, the monotypic genera *Lycocorax* and *Semioptera* are confined to islands in the Moluccan Archipelago and *Ptiloris paradiseus* and *P. victoriae* to north-eastern Australia. The predominantly New Guinean ranges of *Manucodia* (*Phonygammus*) *keraudrenii* and *Ptiloris magnificus* also extend into extreme north-eastern Australia. Most mainland New Guinea species have restricted and/or patchy montane distributions and are confined to discrete altitudinal zones. Some *Manucodia*, *Paradisaea* and *Diphyllodes* species are restricted to offshore islands, although other members of these genera have extensive mainland distributions at low altitudes.

Birds-of paradise were formerly hunted intensively to provide ornate feathers for the European millinery trade. Today hunting is limited to providing material for traditional native adornment and an extensive barter trade, conducted mainly with shotguns which are rapidly replacing traditional methods and weapons, and is essentially self-regulated at unharmful levels. However the restricted ranges of several species render them vulnerable to habitat destruction accompanying agricultural expansion and modernization.

Food. The feeding ecology of most birds-of-paradise is poorly documented. A few are known to be and many others presumed to be mainly frugivorous. However, *Ptiloris* species are predominantly insectivorous, probing into and tearing apart dead wood, and bill morphology and limited feeding observations suggest that *Semioptera*, *Seleucidis*, *Drepanornis* and *Epimachus* take mainly animal food. Some *Paradisaea* species and *Cicinnurus* also take much animal food and frequently forage for insects in mixed-species flocks. Animal foods eaten by birds-of-paradise include arthropods, annelids, frogs and nestling birds; plant resources include fruits, leaves, succulent stems and nectar.

Behaviour. All *Manucodia* and *Macgregoria* species are sexually monomorphic, monogamous and both parents care for the young. *Lycocorax* and 2 *Paradigalla* species are probably monogamous too. All other species of Paradisaeinae are markedly sexually dimorphic and known or presumed to be polygamous, probably promiscuous, the female alone caring for the young. The mating systems of the 3 sexually dimorphic species of Cnemophilinae are unknown, although a brief observation of uniparental female brood-care in the Sickle-crested Bird-of-paradise *Cnemophilus macgregorii* indicated that this species may be polygamous as well.

Courtship and agonistic displays of monogamous males comprise static performances with wing and tail movements and flight chases. Cnemophiline display is undocumented, but polygamous paradisaeine males perform elaborate sequences of ritualized displays involving spectacular exhibition and manipulation of the colourful plumages. Intense sexual selection in the polygamous species has led to the evolution of diverse and highly modified species-specific male plumages. The genetic homogeneity obscured by this is reflected in the large number of inter- and intrageneric hybrids recorded from the wild in polygamous genera (Gilliard) (see HYBRID).

Males of most polygamous species display in the upper or middle vegetation layers of the forest but a few species display terrestrially. Polygamous males also exhibit arena behaviour ranging from the stripping of foliage around arboreal display perches (Frith 1981) to clearing ground courts (e.g. *Diphyllodes* and *Parotia* spp.) (see LEK). Communal lek display is typical of some or most *Semioptera*, *Astrapia* and *Paradiseaea* species, but male *Ptiloris*, *Lophorina*, *Pteridophora* and *Cicinnurus* display solitarily in trees, male *Diphyllodes* on vertical perches above a cleared ground court, and male *Parotia* on horizontal perches above a cleared ground court or actually on it (Frith and Frith 1981). Polygamous birds-of-paradise apparently show sexual bimaturism. Males typically acquire adult plumage at 4 to possibly 7 years old and females are thought to breed when much younger (Bishop and Frith 1979).

Voice and mechanical sounds. These vary from soft, often drawn-out calls to loud, explosive sounds reminiscent of gunfire. Some species exhibit limited vocal mimicry in captivity although this has not been noted in the wild. Non-vocal sounds include bill-snapping by displaying males and rustling made by modified primaries during flight and display (see MECHANICAL SOUNDS).

Breeding. Nests are typically bulky, shallow or deep cups made of leaves, ferns, twigs and vine tendrils on an external foundation of stouter sticks, but *Cnemophilus* and probably the other species of Cnemophilinae build domed nests (Gilliard). Birds-of-paradise nests are generally placed in tree forks, although *Cicinnurus* uses tree hollows.

Background colours of eggs vary from cream and grey-white to pink and reddish brown and most have contrasting, dispersed coloured markings. However, the somewhat aberrant egg of *Cnemophilus* is fine-shelled and white with a wreath of dark markings near the blunt end. Clutch size is 1–3, usually 1 or 2 eggs. Eggs range from 27.5–45.5 mm long and 21–30.6 mm wide. Recorded incubation periods for captive and wild birds range from 17–21 days and nestling periods from 17 to about 20–30 days. Fledgling Magnificent Birds-of-paradise *Diphyllodes magnificus* attain independence after about 21 days. The Trumpet Manucode *Manucodia keraudrenii* may be an occasional brood-parasite or merely breed in the nests of other species occasionally. The nests and eggs of some 12 species remain undiscovered. (A.L.R.) C.B.F.

Bishop, K.D. & Frith, C.B. 1979. A small collection of eggs of Birds of Paradise at Baiyer River Sanctuary, Papua New Guinea. Emu 79: 140–141.

Bock, W.J. 1963. Relationships between the birds of paradise and the bower birds. Condor 65: 91–125.

Cooper, W.T. & Forshaw, J.M. 1977. The Birds of Paradise and Bower Birds. Sydney.

Diamond, J.M. 1972. Avifauna of the Eastern Highlands of New Guinea. Publ. Nuttall Orn. Club (12).

Frith, C.B. 1981. Displays of Count Raggi's Bird of Paradise *Paradisaea raggiana* and congeneric species. Emu 81: 193–201.

Frith, C.B. & Frith, D.W. 1981. Displays of Lawes's Parotia *Parotia lawesii* (Paradisaeidae), with reference to those of congeneric species and their evolution. Emu 81: 227–238.

Gilliard, E.T. 1969. Birds of Paradise and Bower Birds. London.

Schodde, R. 1976. Evolution in the birds of paradise and bowerbirds, a resynthesis. Proc. XVI Int. Orn. Congr. 1974: 137–149.

BIRD-OF-PREY: in the most general sense, a species that hunts and kills other animals (particularly the higher vertebrates) for food; in a more specialized sense (and regardless of habits) a member of the ACCIPITRIFORMES, CATHARTIFORMES or FALCONIFORMES; in the plural, general term for these 3 orders (see FALCON; HAWK; OSPREY; SECRETARY-BIRD; VULTURE (1); VULTURE (2)); sometimes extended to cover the Strigiformes, the qualifications 'diurnal' and 'nocturnal' then being used to distinguish the 2 groups (see OWL). The term 'raptor' is sometimes used in similar senses.

BIRD PROTECTION ACTS: see CONSERVATION.

BIRD'S NEST SOUP: see EDIBLE NESTS.

BIRD STRIKE: collision between birds and aircraft.

BIRD-WATCHING: a general term for almost all forms of admiring, observing or studying birds in the field; once chiefly confined to those who looked at birds for their own personal enjoyment. The change has come about as a result of the increased general interest in birds, stimulated by the mass of books, radio and television programmes; for instance, in Britain the membership of the Royal Society for the Protection of Birds grew from 20,000 in 1960 to 375,000 in 1984. For many people, too, the term bird-watcher is more easily understood than ornithologist, which, strictly, is confined to one who studies birds scientifically, and it has meant that many who are really amateur ornithologists now call themselves bird-watchers.

The way that people watch birds varies enormously: some are satisfied with identifying birds seen from the kitchen window; for others the ability to name birds adds enormously to the enjoyment of a country walk. Some may use special field lists to record the names of birds and even attempt to assess numbers (see CENSUS; COUNTS) that they have seen on their walks so that they may discover seasonal or local population changes on different visits to the same locality. Excellent field guides designed especially to assist in quick identification now accompany the birdwatcher virtually all over the world. For some, this type of bird-watching may be a leisurely occupation but for others it can become obsessive. Tally hunters or 'twitchers', as they have been recently called in Britain ('birders' in North America), seek to identify and list as many species as they can on each field trip, in the course of a year, and so on.

In the USA, this type of bird-watching is highly organized and the American Birding Association, founded in 1969, is the chief organization for promoting the sport and hobby of bird-listing. The magazine *Birding* has become indispensable for all serious American birders. Members list the species they have seen in various categories of time and geography. The most popular category is the life list of birds seen in North America north of Mexico, but year lists, world, provincial and state lists are amongst others published in the magazine. 'Rare bird alerts' are also highly organized. In Britain a code of conduct when observing rarities has been published by the journal *British Birds*.

Bird-listing for many is the be-all and end-all of their bird-watching. Others go on to ask questions about all aspects of bird life and try to find answers for themselves by collecting facts, testing the theories and publishing results—thus meriting the title of bird-watcher-naturalist or, more properly, ornithologist.

Early amateur bird-watchers made many interesting discoveries and by their example encouraged others. In Britain the prototype is Gilbert White (1720–1793), the curate of Selborne, who in his journal and correspondence kept a record of events in his parish, not only of his fellow countrymen but what he observed of bird and plant life. He was the first to distinguish between the Willow Warbler *Phylloscopus trochilus*, Wood Warbler *P. sibilatrix* and Chiffchaff *P. collybita*, and was one of the first to realize that Swallows *Hirundo rustica* migrated southwards rather than hibernated in the bottom of ponds. Charles Waterton (1782–1865) not only kept records of his observations in Britain but also on his travels in South America. Thought of as a somewhat eccentric landowner, he experimented with many kinds of artificial nest sites in the grounds of Walton Hall, Yorkshire, where he lived. H. Eliot Howard (1873–1940), a businessman whose bird-watching was restricted to the early morning, was the first to enunciate clearly the theory of territory.

Perhaps the best known of the early American bird-watchers were Alexander Wilson (1766–1813), often called the first modern ornithologist, and John James Audubon (1785–1851), a naturalist and painter whose work has been the inspiration of one of the world's largest conservation movements. Together they set a tradition for bird study in America. Henry D. Thoreau (1817–1862) wrote about the New England countryside and its affairs, but he was acquainted with the best American ornithologists and many of his books showed him to be a keen and accurate observer of birds. Rather like Eliot Howard, Mrs Margaret Morse Nice (1883–1974) was strictly an amateur whose 5-year study of the Song Sparrow *Zonotrichia melodia* was highly scientific and stimulated many amateurs and professionals to study the life histories of birds. But probably no one has helped more people, on both sides of the Atlantic, to an enjoyment of birds and bird-watching than Roger Tory Peterson through his field guides, paintings and writings.

Comparable in the USA to the Royal Society for the Protection of Birds is the National Audubon Society, founded in 1902 as a bird-watching organization and now with over 350,000 members. It publishes *Audubon* magazine which over the years has reflected the Society's broadened emphasis and concern for environmental matters. But of greater interest to the strict bird-watcher is the Society's *American Birds* (formerly *Audubon Field Notes*) which is published 6 times a year. The US Fish and Wildlife Service collaborates in the production of the region by region compilation of bird notes primarily from the USA and Canada. *American Birds* also reports on various nationwide surveys such as the Winter Bird Population Study, the Breeding Bird Census and the better known Christmas Bird Count which normally takes place in the second half of December each year. To make counts from various parts of America comparable, strict rules regulate the date of the count, the size of the area covered and the number of people in each group. Special reporting forms must be used and a fee is payable by all those taking part, to cover cost of analysis and publication.

'For transportation they rely mostly on their feet, but anything that will get you there is legal. And in past years they have used dog team, helicopter, canoe, airboat, hovercraft, horse and golf cart. In 1979–80 a new mode was added: the birding team at Grandfather Mountain, N. Carolina, logged a mile and a half by hang-glider' (*Audubon*, March 1980).

Whilst the Royal Society for the Protection of Birds, founded 1898, can hardly be called a bird-watching club, it does provide hides (or blinds) on some of its 80 or so reserves where its members may often see shy and rare birds at close quarters. Its colourful magazine *Birds* contains much to interest and inform bird-watchers. The RSPB also sponsors the Young Ornithologists' Club, with a membership of 80,000 young bird-watchers up to the age of 18, which publishes *Bird Life* 6 times a year.

In almost every country where there is a widespread interest, bird-watchers form clubs in towns, counties or states, which arrange regular indoor lectures and field excursions. Often the main scientific purpose of the club is the study of the birds of the club's area. The collection of records of migrants, breeding birds or unusual birds, for publication in the annual bird report for the area is by far the most common corporate manifestation of a more or less individual activity. These reports are used by historians of local avifaunas, and of the distribution of the breeding birds. In the USA there are estimated to be over 800 of such clubs whilst in Britain the figure stands at about 200.

Ad hoc groups of scientific organizations, in which the amateur bird-watching organizations have played a significant role, have often been able to collect evidence to combat threats to important avian habitats such as the impoundment of estuaries. Throughout the world there are at least 6 groups whose members concentrate their energy on counting breeding seabirds, studying seabird movements or other aspects of seabird ecology. In at least 7 countries there are Beached Bird Surveys which monitor the death-roll amongst seabirds from the effects of oil pollution, or sometimes the effects of dangerous chemicals which have been deliberately or accidentally spilled into the sea.

The speed of air travel has enabled the bird-watcher to travel the globe. The place of the former explorers, overseas civil servants and servicemen has been taken by the young bird-watchers, sometimes working for commercial firms, for example on oil rigs at sea, or reserve wardens and university students on expeditions taking advantage of the cheaper air fares to travel to distant places, partly to increase their own knowledge of birds but also to bring back descriptions of avifaunas of areas often unvisited by bird-watchers for many years. The 'special interest' tours arranged by several travel agents give for a short time their bird-watcher clients the thrill of sampling exotic avifaunas, but few such tours go far from the good class hotels and a relatively well-beaten track. See also ORNITHOLOGICAL SOCIETIES; ORNITHOLOGY; PHOTOGRAPHY. P.J.C. (1)

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BISHOP: substantive name of some *Euplectes* spp. (see WEAVER).

BITTERN: substantive name of the species of the Botaurinae, a subfamily of the Ardeidae (Ciconiiformes, suborder Ardeae); in Britain commonly used without qualification for the sole native species; in the plural, general term for the subfamily. The other subfamily is the Ardeinae, which includes the so-called 'tiger bitterns' or 'tiger herons' (see HERON). The bitterns are closely related to the herons and some authorities do not separate the 2 subfamilies.

Usually 2 genera are recognized (*Botaurus*, 4 species, and *Ixobrychus*, 8 species); recently, it has been proposed that the Zigzag Heron *Zebrilus undulatus* should be included in this subfamily (Payne and Risley 1976), but here it is retained in the Ardeinae, following Bock (1956) and others. All *Botaurus* species are allopatric and many authors treat them as one superspecies, even considering some of them conspecific; skeletal differences, however, suggest that only the Eurasian Bittern *Botaurus stellaris* and the Australian Brown Bittern *B. poiciloptilus* are close enough to be regarded as a superspecies. Three species of *Ixobrychus* (the Least Bittern *I. exilis*, the Little Bittern *I. minutus* and the Yellow or Chinese Little Bittern *I. sinensis*) also form a superspecies. The Dwarf Bittern *I. sturmii* was placed in its own genus *Ardeirallus* by Curry-Lindahl (1971), but there are no marked skeletal differences to sustain this suggestion. The

Bittern *Botaurus stellaris* regurgitating food to young. (*Photo: E.J. Hosking*).

Black or Mangrove Bittern *I. flavicollis* is polymorphic with 6 distinct plumages (black, reddish, or partly white morphs occurring in the same population) and has been generically separated in *Dupetor*, but the absence of morphological differences between it and the other smaller bitterns supports its retention in *Ixobrychus*.

Characteristics. In general, bitterns have shorter necks and legs and stouter bodies than herons. The inner toe is longer than the outer (the reverse in herons); they have 8 or, more usually, 10 tail feathers (12 in herons), and only 2 pairs of powder-down patches on the breast and rump (3 or 4 in herons including the thighs and, sometimes, the back). Their bills are strong and pointed, and the toes are long and slender with the middle toe pectinated (as in herons). In addition, the majority nest solitarily (herons are usually colonial) and they largely lack the exaggerated head, breast and scapular plumes so characteristic of the Ardeinae.

The sexes are alike in *Botaurus* (as in herons), but dimorphic in most *Ixobrychus*, the exceptions being the Dwarf Bittern and the Stripe-backed Bittern *I. involucris*.

Botaurus are large (range 60–80 cm in length) and heavy (mass not less than 370 g, with some males reaching 1,900 g). Their soft plumage is beautifully variegated with browns, buffs, blacks and yellows in a cryptic pattern of streaks and bars. The South American Pinnated Bittern *B. pinnatus* differs from the other 3 in having barring on the crown. In contrast, *Ixobrychus* are mostly much smaller (range 25–40 cm in length, apart from the Black Bittern which reaches 55–60 cm), with dove-sized bodies (mass not greater than 170 g and some as little as 45–65 g). Females are generally rather streaked above (or spotted with white in the case of Schrenk's Little Bittern *I. eurhythmus*), but 4 of the males (*exilis, minutus, sinensis, eurhythmus*) have plain backs (dark except *sinensis*) and pale wing-coverts contrasting with dark flight-feathers; 3 (*sturmii, flavicollis*, Cinnamon Bittern *I. cinnamomeus*) show uniformly coloured backs and wings; and only 1 (*involucris*) is broadly streaked on the back. The Black Bittern has the feathers of the crown and lower neck somewhat developed as plumes.

Botaurus usually walk deliberately with feet lifted and lowered slowly; they rarely perch in trees, but are able to climb reeds, if not particularly nimbly. In marked contrast, *Ixobrychus* run rapidly on the ground and readily climb in reeds, shrubs, and trees.

Distribution and habitat. The subfamily has a wide distribution: 2 species breed in Europe (*B. stellaris, I. minutus*), 2 in North America (American Bittern *Botaurus lentiginosus, I. exilis*), 3 in Africa (*B. stellaris, I. minutus, I. sturmii*), 3 in South America (*B. pinnatus, I. exilis, I. involucris*), 3 in Australia (*B. poiciloptilus, I. minutus, I. flavicollis*), and 6 in Asia (*B. stellaris, I. minutus, I. sinensis, I. eurhythmus, I. cinnamomeus, I. flavicollis*). Thus there is a fairly even scatter throughout the zoogeographical regions, but *Botaurus* are found mainly in temperate zones and both genera are largely confined between 60°N and 40°S.

Bitterns are marsh birds, feeding and breeding in wetlands with a dense cover of high sedges or long grass and scattered low shrubs. The Dwarf Bittern and the Black Bittern prefer more open situations than the often sympatric Little Bittern, and are found at the fringes of reed beds and in mangrove swamps where roots and branches of trees and bushes hang into the water.

Movements. The majority of bitterns are at least partial migrants, the northern Holarctic populations mostly moving southwards after the breeding season. Many Eurasian Bitterns winter in southern Asia, the Mediterranean basin and even Africa. Palearctic populations of the Little Bittern winter largely in Africa, apart from a few in Iraq and Iran. The American and Least Bitterns likewise move south and stragglers even turn up along the western fringes of the Old World. Within Africa, the Dwarf Bittern is markedly migratory, being present in the southern and probably the more northern parts of its range during their respective wet seasons; nearer the Equator the populations are more sedentary. A Black Bittern ringed in Malaya was recaptured 2,400 km north-west in India.

Food. Both large and small bitterns take a wide variety of prey, especially fish, amphibians, and insects, but also including crustaceans, molluscs, worms, leeches, reptiles, and even birds and small mammals. Some species or populations are almost exclusively fish-eaters, while others are largely insectivorous.

Behaviour. Bitterns are secretive and solitary (being at best only loosely colonial, and usually not at all). Although *Botaurus* may be seen flying or even feeding during the day, they are essentially crepuscular, being most active at dawn and dusk. *Ixobrychus* are also often crepuscular, but at least some species are rather more diurnal as well.

Several habits are almost or entirely peculiar to the group. Most striking is the concealment posture shared only with the tiger herons. In this the bird becomes completely rigid with the bill and neck pointed stiffly skywards and the feathers tightly compressed so that the whole body appears elongated; it keeps its underside towards the source of danger, watching with unwinking yellow eyes swivelled downwards, and revolves slowly (or whirls with great rapidity) if the observer or other threat moves around. The striped undersides (or plain dull underparts of some *Ixobrychus*) fit in remarkably with a background of dead reeds, and the bird in this posture is almost invisible. In a light breeze, at least some species will sway with the reeds. *Ixobrychus* may even let itself be picked up; W.H. Hudson described how *I. involucris* allowed him to push its head down until this touched its back and, when he removed his hand, the head and neck flew up to the original position like a steel spring. This protective posture is adopted even by downy young only a few days old.

Bitterns use their powder-down patches and pectinated middle claw to clean their plumage. Percy (1951) observed that the head is rubbed in these patches until covered with the powder, which is then allowed to soak up fish slime and oil (probably also excess preen oil) before being combed off by vigorous movements of the toothed claw.

Botaurus are highly territorial throughout the breeding season. They will even attempt to stab one another in aerial combat, and are occasionally found dying or dead from wounds. Flight activities involving 4–6 birds and lasting up to 10 min at heights up to *c.* 65 m during the middle of the breeding season may have either territorial or courtship significance. *Ixobrychus* also drive off intruders by chasing and flight-attack to the border of the territory. There is probably no real pair bond in *Botaurus*, but pairs are formed in *Ixobrychus*.

Voice. The male *Botaurus* bitterns are well known for their distinctive and far-carrying 'booming' or 'thunder-pumping' territorial calls, which may be heard both by day and by night but mostly in the evening before and during the breeding season. They usually boom from inside a reed bed, but sometimes at the edge and more rarely from a perch high in a tree. The male's oesophagus is especially modified before the breeding season so that it can be inflated and act as a resonating chamber: the bird utters a series of clicks or coughs, breathes in deeply with its head thrust forward and whole body vibrating, and then produces the deep resonant boom in a great exhalation. It is audible to the human ear at distances of 1–5 km, depending on climatic conditions; the performance is commonly repeated several times. A comparable noise is uttered by the tiger herons.

The pre-breeding calls of male *Ixobrychus* are guttural cooing and croaking sounds uttered in long sequences and are used to attract the female to the nest: apparently the only species that 'booms' is *I. flavicollis* and then only in India and Sri Lanka (Curry-Lindahl 1971).

Breeding. All bitterns nest in freshwater reed, sedge and other aquatic vegetation in marshes, lakes or the margins of large rivers. *Botaurus* build up a platform of reeds and sedges some 10–15 cm above the water level, while *Ixobrychus* make more of a nest at heights of 3–60 cm (sometimes as high as 3–6 m) above shallow water in dense vegetation or occasionally in trees. Nest building is by the female in the Eurasian and American Bitterns (*Botaurus*) but mainly by the male in the Little and Least Bitterns (*Ixobrychus*). Whether this distinction in roles applies to all species in the 2 genera is not known. Nests are solitary in *Botaurus* (except that some males are polygamous) and most *Ixobrychus*, but *I. sturmii* and *I. flavicollis* occasionally breed in small loose colonies, the latter sometimes among egrets.

The clutch size varies in those species (e.g. *I. exilis*, *I. minutus*) which have a wide latitudinal distribution, being smaller in the subtropics and tropics (2–3) than at higher latitudes (*c.* 4–7); the common range is 4–6 for the whole subfamily, but up to 10 eggs have been recorded for *Ixobrychus*. The eggs, which are smooth but with little or no gloss, vary in colour from white to bluish or greenish in *Ixobrychus* and buffish-brown to olive-brown in *Botaurus*; they generally lack markings although there may sometimes be a few fine brown speckles near the large end. The laying intervals, so far as known, are 2–3 days for the Eurasian Bittern and 1 day for the Little Bittern (sometimes 2), American Bittern and Least Bittern. Incubation generally lasts 24–26 days in *Botaurus* (females only incubating) and 17–19 days in *Ixobrychus* (both sexes incubating); it begins usually with the first egg, so hatching is asynchronous and, indeed, may be spread over as long as 12–13 days in the Eurasian Bittern. The majority of bitterns are single-brooded, but 2–3 broods have been recorded in *I. sinensis* and 2 in *I. flavicollis*.

Young bitterns are fed by regurgitation by the female in *Botaurus* and by both sexes in *Ixobrychus*. The young begin to wander from the nest at the age of 14–20 days in *Botaurus* and as early as 5–7 days in *Ixobrychus* (*minutus*, *sturmii*, *exilis*). Recorded fledging periods are in the ranges of 50–55 days (*B. stellaris*) and 25–30 days (*I. minutus*). See photo PARENTAL CARE. I.J.F.-L.

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BITTERN, SUN-: see SUNBITTERN.

BLACKBIRD (1): in Britain, *Turdus merula*; also used as substantive name of some congeners elsewhere (see THRUSH). See photos COMFORT BEHAVIOUR; PARENTAL CARE; SUNNING.

BLACKBIRD (2): in North America, substantive name of certain Icteridae, especially *Agelaius* spp. (see ORIOLE (2)).

BLACKCAP: *Sylvia atricapilla* (see WARBLER (1)).

BLACK-CAPPED DONACOBIUS: *Donacobius atricapillus* (see WREN (1)).

BLACKCOCK: special name for the male of the Black Grouse *Tetrao tetrix*, the female being called 'greyhen' (see GROUSE).

BLACKEYE: substantive name of *Chlorocharis emiliae* (see WHITE-EYE).

BLACKSTART: *Cercomela melanura*, of south-western Asia and north-eastern Africa (for subfamily see THRUSH).

BLADE: see FEATHER.

BLASTODERM; BLASTODISC: see DEVELOPMENT, EMBRYONIC; EGG; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

BLEATING: see MECHANICAL SOUNDS.

BLIND: see BIRD-WATCHING.

BLOOD: the fluid that, in all vertebrates, carries oxygen from the lungs to the tissues and returns carbon dioxide (see VASCULAR SYSTEM); carries soluble products of digestion to storage or modifying organs such as the liver and to the tissues (see ALIMENTARY SYSTEM); and carries waste substances in solution to the kidneys (see EXCRETORY SYSTEM). Antibodies produced against invading organisms are distributed; so also are hormones from the endocrine glands (such as the pituitary or thyroid) to their sites of activity, which may be further endocrine glands, the specific organs to be affected, or the tissues in general (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM). Above all, blood is the vehicle by which the 'internal environment' of the tissues is kept constant.

Blood consists of two main parts, one cellular and the other fluid. The white cells or leucocytes help to combat infections, while the erythrocytes or red cells (corpuscles) have as their main function the carriage of oxygen and carbon dioxide. The erythrocytes are, of course, too small to be visible individually and so form the red coloration. The cells are suspended in the fluid element, the plasma.

Plasma. This itself consists of two parts, water and proteins (substances of very large molecules containing nitrogen). Food and waste products are dissolved in the water, while the proteins behave usually as a colloidal suspension. Antibodies are likewise proteins and in adult animals are an appreciable fraction of those in the blood. The blood proteins may be divided into classes because their molecular sizes tend to fall into definite groups, although with no absolute divisions between them. These can be separated by techniques such as electrophoresis or chromatography, in which the molecules of different sizes move at different speeds under the influence, respectively, of an electric current or of an advancing capillary front.

Erythrocytes. In all vertebrates the erythrocytes start their development as nucleated cells, but those of mammals lose their nuclei before being pushed out into the blood stream (except in conditions of disease). In birds—as also in reptiles, amphibia, and fishes—the erythrocytes retain the nuclei; they are also oval, although flattened. (In mammals the erythrocytes are round—except in the Camel, Llama, and Vicuna, where they are again oval.) In birds they are large; thus in man there are about 5 million per mm^3, but in birds about 2 million. The smaller ones are more efficient. In a remarkable series of papers in the *Proceedings of the Zoological Society of London* round about 1850, George Gulliver recorded the measurements of the red cells of many animals, including birds. He pointed out that there was a fairly consistent average for a species but wide variations between different species. However, there was no relation between these measurements and the accepted systematic classification, e.g. in the owls (Strigiformes), of which he examined several species which would still be considered as closely related. The average life of a red cell is only a few weeks, after which it is removed from the circulation by the so-called 'reticuloendothelial system' and replaced by new cells formed in the sinusoids of the bone-marrow by a process of development strictly comparable to what is found in mammals.

Haemoglobin. It is this red pigment of the cells that is fundamentally responsible for the complex series of changes by which oxygen is absorbed or liberated by the red cells as required. Chemically it is similar in all vertebrates, a protein containing iron, and recent work by the techniques mentioned above has shown in many groups of animals that is can be divided into several slightly different substances. In birds, electrophoretic methods have as yet failed to subdivide the haemoglobin in some of the birds that have been examined, e.g. some pigeons (Columbidae) and penguins (Spheniscidae). Chromatography, however, has revealed five types, some of which appear to be similar to those of man, e.g. human Haemoglobin E, which is an inherited abnormality responsible both for the rare disease called thalassaemia and for a marked degree of resistance to infestation with malaria parasites. In birds the arrangement of the five types of haemoglobin in the species examined bears some relationship to broad systematic factors. Thus, one factor found in the older groups such as Pelecaniformes, Falconiformes, or Ciconiiformes is absent in those believed to be of intermediate antiquity, such as Cuculiformes, and yet reappears in Passeriformes.

Leucocytes. As with so much detailed work on birds, most observations have been made on such domesticated species as fowls and pigeons. Their blood contains about 5000 leucocytes per mm^3, but variations have been observed with season and with laying times. In contrast to mammals, except very young ones, the blood contains a greater proportion of lymphocytes than the granulocytes which ingest invading bacteria. The granulocytes also differ in having nuclei split into many small lobes, but otherwise the cells and their mode of development differ little from those of mammals.

Blood groups. The importance of these in human blood transfusion is well known. They depend on specific antigens present in the the plasma, red cells, and other tissues, and forming several series independent of each other and controlled by a number of genes inherited according to the established laws of genetics (see GENETICS). They form, indeed, one of the best worked-out series of inherited factors, have been correlated with liability to certain diseases, and provide very important evidence with regard to the relationship between races of mankind. In domestic fowls no less than twelve distinct series have been described using saline agglutination of cells with iso-immune sera; complement fixation techniques have not proved as satisfactory. There are some cross reactions, so some antigenic material must be common to several series, but genetically they segregate independently. The 'B' system at least seems to be related to the production of antibodies to tissue grafts from other individuals, while some heterozygotes of this system appear to confer an increased survival to the lines bearing them. In the Golden Leghorn fowl an antigen for human serum has been found in the erythrocytes. The male bird may carry the double gene of his ZZ chromosome while the female can have only one on her ZW chromosome, which has analogies with some aspects of the well-known Rhesus blood group system of man, although the arrangement of the sex chromosomes as between males and females is reversed in mammals and birds. In ducks one blood group is sex-linked, a condition only recently found in one human blood group. Serological differences between species have been investigated in the genus *Streptopelia* (Columbidae); the differences between *S. 'risoria'*, *S. chinensis*, and *S. senegalensis* have been resolved serologically into a number of specific antigens, some of which are held in common between two species.

Systematic serology. Birds certainly produce antibodies to many antigens introduced from outside, e.g. bacteria and the blood of other animals; those of the former class are presumably of use to the bird as to other animals, but the latter are of course an entirely artificial phenomenon. In mammals, the specific antibodies to the blood of different species produced in one experimental animal, e.g. the Rabbit, have been shown to be related for systematically related species; but such work on birds has so far led to equivocal results. R.E.R.

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BLOOD VESSELS: see HEART; VASCULAR SYSTEM.

BLOSSOMCROWN: *Anthocephala floriceps* (for family see HUMMINGBIRD).

BLUEBILL (1): substantive name of *Spermophaga* spp. (see ESTRILDID FINCH).

BLUEBILL (2): a name in North America for the Scaup *Aythya marila*, and in Australia for the Australian Stifftail *Oxyura australis* (see DUCK).

BLUEBIRD: substantive name of *Sialia* spp., of North and Middle America (see THRUSH).

BLUEBIRD, FAIRY-: see FAIRY-BLUEBIRD; and under LEAFBIRD.

BLUE-BONNET: substantive name sometimes used for the Australian PARROT *Psephotus haematogaster*.

BLUECREST: *Orthorhyncus cristatus* (for family see HUMMINGBIRD).

BLUETAIL: *Tarsiger cyanurus*, of the eastern Palearctic (one of the bush-robins)—for subfamily see THRUSH.

BLUETHROAT: *Luscinia svecica*, of the northern Palearctic (for subfamily see THRUSH).

BOATBILL: otherwise the Boat-billed Heron *Cochlearius cochlearius*, of the Neotropical Region (see HERON).

BOATSWAIN-BIRD: see BO'SUN-BIRD.

BOBOLINK: *Dolichonyx oryzivorus*, native to North America (see ORIOLE (2)).

BOBWHITE: *Colinus virginianus*, one of the American quails (Odontophorinae)—see under PHEASANT.

BODY: see SIZE; TOPOGRAPHY; and for care of body surface see COMFORT BEHAVIOUR.

BOG-BIRD: name sometimes applied to *Balaeniceps rex* (see SHOEBILL).

BOKMAKIERIE: well-known Afrikaans name (from the duetting call) for *Telephorus zeylonus* (see SHRIKE).

BOMBYCILLIDAE: family of PASSERIFORMES, suborder Oscines, comprising subfamilies Bombycillinae (see WAXWING) and Hypocoliinae (see HYPOCOLIUS).

BONE: see PALATE; PNEUMATIZATION OF BONE; SKELETON, POST-CRANIAL; SKULL. Also, with regard to bone formation, under ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

BONXIE: alternative name for the Great Skua *Stercorarius skua* (see SKUA).

BOOBY: substantive name of certain *Sula* spp. to which 'gannet' is sometimes alternatively applied (see GANNET). See photo RITUALIZATION.

BOOM: see BITTERN.

BOOMING GROUND: special term in North America for the social display ground of the Greater Prairie Chicken *Tympanuchus cupido* (see GROUSE; LEK).

BOOTED: otherwise 'holothecal' or 'ocreate', term applied to the horny covering of the tarsus when it, or most of it, is in an undivided piece (see LEG; compare LAMINIPLANTAR; SCUTELLATE). In poultry literature 'booted' means having a feathered tarsus; in general this is not an ornithological usage, 'rough-legged' being preferred, but the adjective has that sense in the name of the Booted Eagle *Hieraaetus pennatus*.

BOREAL: term applied to a climatic zone immediately south of the Arctic; sub-divided in North America into 'Hudsonian' and 'Canadian'.

BOREAL FOREST: see TAIGA.

BO'SUNBIRD: sailors' name for *Phaethon* spp. (see TROPICBIRD). It is said to 'carry a marlin-spike in the tail'.

BOTAURINAE: see BITTERN.

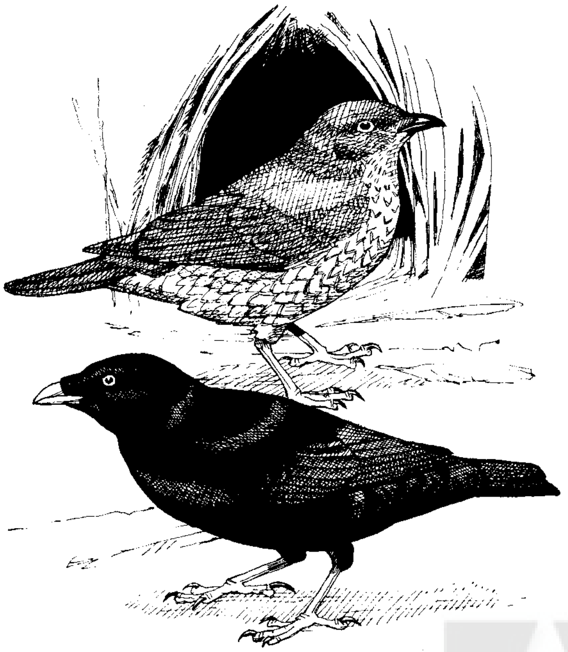
BOTULISM: see DISEASE.

BOUBOU: substantive name of some *Laniarius* spp. (see SHRIKE); to be distinguished from BRUBRU.

BOWERBIRD: name variously applied to all species of Ptilonorhynchidae (Passeriformes, suborder Oscines), or just to the polygamous species when contrasted with the monogamous ones, collectively termed catbirds (*Ailuroedus*). Bowerbirds are medium sized passerines (21–38 cm long) renowned for their arena behaviour which involves elaborate display courts and bowers made and maintained by males.

Systematics. Bock (1963) concluded from the cranial anatomy that bowerbirds and birds-of-paradise (Paradisaeidae) are closely related and descended from a common cnemophiline bird-of-paradise ancestor, but sufficiently distinct to be placed in separate families as followed here. Gilliard (1969) and Schodde (1976) combine both groups in the Paradisaeidae on zoogeographic, morphological and behavioural grounds. Other bowerbird affinities are uncertain; they have been variously allied to Sturnidae, Menuridae, Callaeidae and the 'corvine assemblage'.

Characteristics. Bowerbirds range from thrush-size almost to crow-



Satin Bowerbird *Ptilonorhynchus violaceus*, female and male (front). (*N.W.C.*).

size (*c.* 22–40 cm) and the males are usually beautiful. Most have coloured ornamental plumes of various kinds. In some almost all feathers produce brilliance by means of 'interference' effects. In others there is a brief nuchal crest, in another a ruff draping much of the back. The sexes are rarely alike. Wings and tail tend to be short, the legs short and strong; the bill is short and strong, sometimes decurved, and slightly hooked.

Distribution and habitat. Nine of the 18 species are endemic to New Guinea, 7 to Australia and 2 occur on both land masses. Distributions vary from extensive and continuous (e.g. Great Grey Bowerbird *Chlamydera nuchalis*) to very restricted (e.g. Adelbert Bowerbird *Sericulus bakeri*). Most bowerbirds inhabit wet forests, some occurring as high as 3,000–4,000 m in true cloud forest (*Amblyornis*, *Archboldia*). But *Chlamydera* species live in drier habitats such as riverine forest, open woodlands and grasslands and include the only 2 Australian species with extensive inland distributions.

Food. Bowerbirds are predominantly vegetarian and frugivorous. Present studies of 6 wet forest species in north-east New South Wales and north Queensland indicate a 9 : 1 ratio of plant to animal food in the diet. Plant foods eaten include the fruits of many tree and vine species, leaves, buds, flowers seeds and succulent stems. The serrated bill of the Tooth-billed Catbird *Scenopoeetus dentirostris* appears to be mainly an adaptation to leaf eating. Animals eaten by bowerbirds include large insects, earthworms, spiders, millipedes, frogs and small nestling birds. Bowerbirds forage at all levels in the forest vegetation from ground to canopy, but co-habiting species usually differ somewhat in their preferred feeding heights.

Mating systems. Catbirds are monogamous with biparental brood-care. Parental investment by male Green and Spotted Catbirds *Ailuroedus crassirostris* and *A. melanotis* involves defence of breeding territories, feeding the female and helping to feed young. All other bowerbirds are thought to be polygamous with brood-care provided by females. Emancipated males exhibit arena behaviour, competing to attract multiple mates by elaborate visual and vocal display at bowers or courts. Vellenga (1970) confirmed polygamy in the Satin Bowerbird *Ptilonorhynchus violaceus* and studies in north-east New South Wales show that males of this species are promiscuous (see LEK; POLYGAMY). This is likely to be true of all the polygamous species.

Most polygamous bowerbirds are sexually dimorphic in plumage (and often size), but the degree of dimorphism varies from dramatic contrast in plumage coloration in genera like *Sericulus*, *Prionodura* and *Ptilonorhynchus* to the slight differences characteristic of Archbold's Bowerbird *Archboldia papuensis* and Spotted *Chlamydera maculata* and Great Grey Bowerbirds. The monogamous catbirds and polygamous Tooth-billed Catbird, Vogelkop Gardener Bowerbird *Amblyornis inornatus*, Fawn-breasted Bowerbird *Chlamydera cerviniventris* and Lauterbach's Bowerbird *C. lauterbachi* are sexually monomorphic in plumage. In polygamous, sexually dimorphic species, males attain adult plumage later than females and are female-plumaged until mature. Thus wild male Satin Bowerbirds assume adult plumage when 7 years old (Marshall 1954) while females may breed at 2–3 years old, and male Australian Regent Bowerbirds *Sericulus chrysocephalus* acquire adult plumage at 4–6 years although females may breed when 3 years old (Disney and Lane 1971). It is not surprising that ages of 5–15 years have been recorded for *Ptilonorhynchus*.

Bowers and display. Bowers of sticks, grasses and mosses are built by polygamous males at display areas to which females are attracted to copulate. There are 4 basic bower types: court, mat, maypole and avenue. The Tooth-billed Catbird clears several square metres of forest floor and decorates this display court with fresh leaves, undersurfaces uppermost. Archbold's Bowerbird makes a simple 'mat' of mosses and dry ferns. Maypole bowers vary in complexity. The terrestrial maypole bowers of *Amblyornis* spp. range from a conical stick column surrounding a sapling emerging from a basal, saucer-shaped moss platform (*A. macgregoriae*) to elaborate roofed, stick towers based on one or more saplings (*A. subularis* and *A. inornatus*). The Golden Bowerbird *Prionodura newtoniana* builds a vast maypole bower up to 3 m high and comprising one or two stick massifs originating at arboreal sites and spreading upward and downward. The sticks are fused together with fungus. Avenue bowers comprise two vertical, parallel walls of twigs or grasses on a stick platform; Lauterbach's Bowerbird adds a short wall at each end of the avenue.

Males decorate their bowers with both natural objects such as mosses, ferns, lichens, flowers, fruits, insects, snail shells and feathers, and in the genera *Ptilonorhynchus* and *Chlamydera*, human artefacts. There are pronounced species preferences in ornament colour and Marshall (1954) suggested that these match the colours of rival, conspecific males. Avenue builders 'paint' the inside walls of their bowers with vegetable matter and saliva. The adaptive significance of this behaviour is unknown.

Gilliard (1969) showed an inverse correlation among *Amblyornis* species between the extent of male epigamic plumage coloration and bower complexity. He postulated that intense sexual selection had led to a 'transferral effect' in advanced bowerbirds in which epigamic function had been transferred from male plumage to display objects. While this is plausible, the Golden Bowerbird, in which the brilliantly coloured male builds an elaborate and huge bower, is clearly an exception.

Courtship display at the bower has been described in few species. There is a single, intriguing observation of a male *Archboldia* crawling in a fledgling-like posture over the mat bower towards a perched female. Displaying male *Amblyornis* hold objects in the bill and expose the crest where present. In *Amblyornis macgregoriae* the displaying male and visiting female maintain positions on opposite sides of the central maypole. Male Satin Bowerbirds perform strutting, bowing and wing-opening displays on the bower platform to a visiting female in the avenue. Immature males of this species display to one another and to females in rudimentary bowers as well as visiting and displaying in adult males' bowers. *Chlamydera* males execute a headturning display which exposes a pink crest on the nape in 2 species; Gilliard argued that the presence of this display in the 2 uncrested species which also build more elaborate bowers supported the 'transferral effect' hypothesis. Copulation has been observed in or near the avenue in 2 avenue builders and is probably largely restricted to the bower site in all polygamous species. Adult male bowerbirds typically build and maintain one bower per season, but *Prionodura* males 'own' more than one simultaneously. Raiding neighbours' bowers and stealing their ornaments has been noted in 3 species. Catbirds do not exhibit arena behaviour except for *A. dentirostris*.

Movements. Monogamous Green and Spotted Catbirds occupy all-purpose territories year-round. In the few polygamous species studied, females only defend the nest site and males a small area around the bower during the breeding season. The bowers of Golden, Australian Regent, Satin and Fawn-breasted Bowerbirds are evenly dispersed in suitable habitat and not clustered in dispersed leks (Gilliard). Some bowerbirds form flocks in the non-breeding season.

Voice. Bowerbirds have a wide variety of species-typical vocalizations including harsh buzzes, rattles and hisses, melodious whistles and high-pitched squeaks. Males of several polygamous species mimic cohabiting bird species and even mechanical sounds.

Breeding. The Australian species breed from September to February. Breeding seasons of New Guinea species are less well documented but probably either coincide with this timing or are at least of comparable length. Bowerbird nests are open cups built 1–30 m up in tree vegetation, except in *Prionodura* which uses crevices from 0.5 m to 15 m high. Catbird nests are bulky, those of the avenue builders shallow and frail, and the Tooth-billed Catbird constructs a tiny, cryptic cup of tendrils in a vine tangle.

Clutch size is 1–3, usually 2 eggs. The eggs of *Ailuroedus*, *Scenopoeetes*, *Amblyornis* and *Prionodura* are pale and uniform in colour but other genera have spotted and streaked eggs. Egg dimensions are 32–45 × 23–32 mm. In Green Catbirds and Satin Bowerbirds incubation takes 19–24 days and nestling development 18–21 days but there is little comparable information for other species. In north-east New South Wales Green Catbird nesting success was about 70% and Satin Bowerbird success around 20%. Females of these 2 species renest within one week of nest failure and normally rear one brood per season. The breeding biology of most other bowerbirds has been little studied.

R.H.D., C.B.F. and A.L.

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BRACE: collective noun for two birds of the same species, irrespective of sex; mainly used in the plural (unchanged) for the enumeration of dead game (e.g. 3½ brace = 7 birds of a kind)—cf. PAIR.

BRACHYPTERACIIDAE: see CORACIIFORMES; GROUND-ROLLER.

BRACHYRAMPHINI: see AUK.

BRAILING: rendering a captive bird incapable of flight by binding the manus to the forearm so that the wing so treated cannot be unfolded (compare CLIPPING; PINIONING).

BRAIN: see NERVOUS SYSTEM.

BRAIN-FEVER BIRD: name applied to the Hawk Cuckoo *Cuculus varius* of India, both representing the sound made ('brain fever, brain fever') and suggesting the wearisome effect of its loud and constant reiteration; sometimes misapplied to other species, for the second of these reasons (see CUCKOO).

BRAMBLING: *Fringilla montifringilla*, native to the northern Palearctic (see FINCH).

BRANT: North American name for the Brent Goose *Branta bernicla* (see under DUCK).

BRASSYTAIL: *Metallura aeneocauda* (for family see HUMMINGBIRD).

BREAST: see TOPOGRAPHY.

BREAST-BAND: see TOPOGRAPHY.

BREASTBONE: see SKELETON, POST-CRANIAL.

BREATHING: see RESPIRATORY SYSTEM.

BREEDING BIOLOGY: see under specialized articles e.g. BREEDING SEASON; EGG; PARENTAL CARE.

BREEDING BIRD SURVEY: see ATLAS; CENSUS.

BREEDING CYCLE: the complete sequence of reproductive activity from initial COURTSHIP and pair formation through nesting to the final independence of the young.

BREEDING DISTRIBUTION OR RANGE: see DISTRIBUTION, GEOGRAPHICAL; RANGE CHANGES.

BREEDING SEASON: the period of the year during which, in any particular area, birds mate, build their nests, lay their eggs and raise their young; by convention, the start of the breeding season of any species in any area is normally described by taking the mean date of the first eggs of first clutches in the populations concerned. The laying dates of a large number of the world's species are still poorly known or unknown. Laying dates can, however, often be extrapolated from incubation dates, from the age of young birds or even from moulting adult birds, since many birds have a post-breeding MOULT.

Ultimate and proximate factors. Two kinds of factor govern the timing of breeding seasons (Baker 1938). A factor which results in natural selection favouring a particular time of breeding is called an ultimate factor. Birds often have their young in the nest when food is most available; in such cases food may be the ultimate factor which influences the time of breeding.

The second kind or proximate factor ties in the bird's behaviour with favourable environmental conditions. Obviously, if the ultimate factor is the availability of food for the nestlings, the parents must commence their breeding cycle much earlier than the period of peak food abundance, since there is a considerable interval between the commencement of breeding and the hatching of the young. For example, in the European Robin *Erithacus rubecula* it takes a minimum of 3 weeks from ovulation to hatching (4 days from the start of rapid follicular growth to laying, 4 days to lay 5 eggs, 13 days for incubation); even this period is an underestimate since it does not take into account the time needed for the reproductive organs to come into breeding condition, which may take 5 weeks or more (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM). While many small birds are able to produce young as quickly as the Robin, many larger ones take longer, the extreme case being probably the Wandering Albatross *Diomedea exulans*, where incubation takes 11–12 weeks. Proximate factors are discussed in more detail below.

The breeding seasons of different species. There have been a great many studies of the timing of breeding in relation to the environment; a review is given in this section (see also Lack 1954). As might be expected, the breeding season varies with the geographical location, since this may have marked effects on the local climate. Most of the more obvious variations follow the general bioclimatic laws of Hopkins (1938) whereby:

(1) spring arrives about 4–5 days later for each 1° increase in latitude;

(2) spring arrives about 4–5 days later for each 125 m increase in altitude;

(3) spring arrives later the further one moves from the sea towards the centre of a continent. This effect varies markedly in relation to local winds etc. but in the western USA spring arrives about 4 days later for each 5° eastwards.

Correlations of the timing of breeding with latitude stand out. Birds breeding at high latitudes have the shortest breeding seasons and all species are closely synchronized. Towards the Equator breeding seasons become more extended and less closely synchronized (Fig. 1). At high latitudes, the breeding cycle can be regarded as a race against the clock to get the breeding over and the chicks developed sufficiently well to migrate southwards before the onset of winter. Some birds, such as the arctic-breeding geese, arrive on the breeding grounds when the area is still snow covered and there is little or no food available. But the females are able to lay and incubate their clutches from their large body reserves and are thus able to start breeding as soon as suitable nest sites are exposed. In late springs they are delayed and may use up their body reserves to such an extent before laying that they either lay small clutches, fail to lay, or are forced to desert their eggs. The season for development of the young is very short and goslings may die if the autumn freeze-up comes before they are able to fly. As a result, geese breeding at high latitudes have very variable nesting success; in some years almost all birds fail to raise any young. Other characteristics of high latitude breeding include the tendency to have no repeat or second clutches and rapid development of young. In the waders (Charadriidae), post-breeding moult, especially of the flight feathers, may be very rapid or may be deferred until the birds have moved further south; in a few passerines the moult may be brought forward to overlap with the raising of the young.

In the tropics, especially in the least seasonal habitats such as the equatorial rain-forests, birds may be found breeding at all times of the year. Nevertheless, almost every species so far studied can be said to have a breeding season. A few species, such as the Scaly-breasted Ground Dove *Columbina passerina* in semi-arid central America and the Red-footed Booby *Sula dactylatra* in the Galapagos, show no breeding season for the population as a whole and breeding may occur at any time of year. Each bird can be said to have its own, individual reproductive cycle since it breeds for part of the year and then has a rest period during which it moults: however, these individual cycles are neither synchronized, nor necessarily annual. Within any area (outside the high latitudes) there are marked variations in the breeding seasons of the different species. In general these differences reflect the ecology of the individual species and support the hypothesis that breeding seasons of birds have evolved so that the birds have their young in the nest when food is most available. For example in central Europe the small birds of prey fit such a pattern. The Kestrel *Falco tinnunculus* breeds early so as to catch its small mammal prey before vegetation becomes too thick to find them easily; the Sparrowhawk *Accipiter nisus* breeds later, feeding its young on the fledglings of small woodland birds which have only just left the nest and are vulnerable. The Hobby *F. subbuteo*, breeding later still, feeds its young on fledgling swallows and martins (Hirundinidae) and on large insects which appear later in the season. In the Mediterranean and North Africa there are two other small birds of prey, Eleonora's Falcon *F. eleonorae* and Sooty Falcon *F. concolor*, which lay their eggs at midsummer and feed their young on the hordes of small passerines which pass southwards for the winter. There are many such general observations on the timing of breeding and the food supply; for example, most insectivores which take larvae from the leaves tend to breed earlier than those which catch flying insects: again the availability of their food is parallel with variations in breeding seasons.

Compared with the temperate regions, the pattern of breeding seasons in the tropics is less well known and more variable. Many tropical areas are as highly seasonal as temperate ones although rainfall rather than temperature is the key environmental variant. Again, however, general correlations are in accord with food being the most important ultimate factor affecting the breeding cycle; for example, insectivorous birds tend to breed early in the rains, feeding their young on the flush of insects on the new vegetation; seed-eaters, in contrast, breed a good deal later, when the grasses are well-grown and the new seeds begin to ripen.

The breeding seasons of seabirds pose special problems. In temperate and colder parts of the world, they normally accord with those of other birds; they nest in the spring and raise their young before the cold weather returns; at very high latitudes it may be critical to get the young away before the sea freezes over. In the tropical seas, the seabirds have very varied breeding seasons. In some, breeding may still be annual (though not necessarily synchronized with other seabirds in the same area), but not in others. Wideawake or Sooty Terns *Sterna fuscata* return to breed on Ascension Island in the mid Atlantic very closely synchronized, about every 9.6 months. Others have both shorter and longer cycles (Bridled Tern *Sterna anaethetus*, Seychelles, Indian Ocean, about 8 months; Audubon's Shearwater *Puffinus lherminieri*, Galapagos, 9–10 months; Brown Booby *Sula leucogaster* and the Frigatebirds *Fregata*, cycles of more than one year). In these cases, it is assumed that the interval between seasons is the minimum possible in which birds can breed, moult and return to breed again, and that the food supply does not have an annual cycle. Although such non-annual cycles are known to be widespread in seabirds, they seem very rare in land-birds even in the (relatively) season-less tropical rain-forests. Cycles of about 9 months have, however, been suggested for 2 species of forest passerines in Sarawak, the Red-winged Tree Babbler *Stachyris erythroptera* and the Little Spider Hunter *Arachnothera longirostris*.

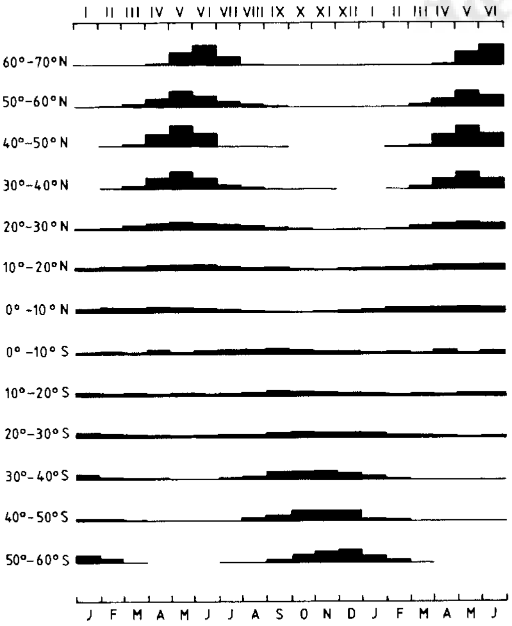

Fig. 1. Egg-laying seasons in relation to latitude (months indicated by Roman numerals and initial letters). (From Baker 1938).

A few seabirds and some large birds of prey, such as the condors and large albatrosses, take 2 years to complete a breeding cycle. In these species parental care usually takes far longer than the one year, and so the individuals breed only every other year. If, however, the birds lose their eggs or young at an early stage they will nest again the following year.

The King Penguin *Aptenodytes patagonicus* has a unique breeding cycle. In November the female lays the single egg, which becomes a large chick by the following winter. It remains dependent on its parents for food throughout the winter, but does not grow much and may even lose weight; it puts on weight and becomes independent in the following spring (December). By the time the parents have moulted, they are not ready to lay again until about January, an interval of about 14 months. The chick from this late laying is still small when winter comes and, if it survives, takes the whole of the following summer to reach independence (about March). By this time it is too late for the parents to moult and breed again before mid-winter so they do not lay until the spring (November). Hence, if successful, King Penguins raise 2 young in every 3 years. If they lose a chick they will revert to laying in November, i.e. they raise only one young every 2 years. The closely related Emperor Penguin *A. forsteri* breeds annually; the pair come on to the ice in mid-winter and the female lays the egg and leaves the male to incubate it for about 9 weeks (during which time he drops in weight from 40–20 kg). The chicks hatch at the beginning of the Antarctic spring. Although they thus have the whole of the summer period for growth, the young are not full-grown by late summer at which time they leave their parents and swim out to sea to fend for themselves and complete their growth.

Length of breeding season and number of broods. The time at which birds start breeding in each year, and the physiological and endocrinological changes involved have been the subject of much published work. Less attention, however, has been paid to the termination of breeding; in some ways it has been more difficult to study. Nevertheless in one or two species the reason for the variation in timing is fairly clear. The European Blackbird *Turdus merula* feeds its young largely on earthworms. These are easily available in midsummer if the weather has been wet and the ground is soft; Blackbirds cease breeding much earlier in a dry summer.

In many species the date at which breeding ends varies considerably between years and has a major effect on the number of broods attempted and hence the reproductive output. Many species, particularly passerines, may have a prolonged breeding season and raise several broods. The most raised in the wild seems to be about 6 consecutive broods. However, there are reports of Zebra Finches *Poephila guttata* under captive conditions raising as many as 21 consecutive broods. This species has been claimed to be an opportunistic breeder, laying in arid areas of Australia at irregular intervals after rain storms and continuing to breed until conditions deteriorate. While the laboratory breeding pattern mentioned above is consistent with such a view, more information is needed to establish this, since in at least some areas the Zebra Finch shows a more regular, seasonal pattern.

The length of the breeding season depends presumably on the relation between success of breeding and the survival of the adult birds, but this has not been studied in detail. Breeding is dangerous since it ties the parent birds to a restricted area, the nest or brood, making them more vulnerable to predation than at other times. In addition, breeding tends to defer moult and to postpone the accumulation of reserves while raising young. Hence, a further brood reduces the adults' chances of survival to the following breeding season. Whether or not they should have that brood may depend on its chances of success. In many species late broods do not produce as many surviving young as earlier ones. Natural selection has evidently favoured the tendency to have further broods up until that time at which the probable gains (in terms of surviving young) are outweighed by the reduced survival of their parents.

Although a great many passerines in the warmer parts of the world prolong their breeding season by having more than one brood, this behaviour is not common in non-passerines. One of the reasons is that non-passerines are generally larger and have a longer breeding cycle than passerines and thus less opportunity. Among the exceptions are the Barn Owl *Tyto alba* under conditions of abundant food, and some rails, notably the Moorhen *Gallinula chloropus*.

Not only do most non-passerines have only a single brood, but in some orders such as the Procellariiformes the reproductive organs start to regress soon after the egg is laid, and replacement clutches are very rare even when the egg is lost soon after laying. In the arctic geese, mentioned earlier, replacement clutches are not laid because the birds do not have the reserves nor do they have the time available to raise the young.

The breeding season, moult and migration. Although the breeding season is here considered in isolation it must be remembered that other factors, such as favourable times for MOULT and MIGRATION, may impose their own constraints on its length.

In a very few cases, the breeding seasons of individual birds may be prolonged by breeding in two different places. For example, the European Quail *Coturnix coturnix* may, on its northward migration, stop and breed in North Africa. As this area becomes more arid in late spring, the birds move on northwards and breed again in mid-Europe. Two discrete breeding areas have also been suggested for some Redpolls *Carduelis flammea*. In Africa, the Red-billed Quelea *Quelea quelea* migrates considerable distances, following the rains; it may breed in two or more different places. Other species probably have similar migration patterns, but whether they breed in more than one area is not known. Occasionally individual long distance migrants e.g. the Swallow *Hirundo rustica* have been reported breeding in their wintering range.

Ultimate factors affecting breeding seasons. Excluding the demands imposed by moult and migration (see above), the evolutionary factors which have resulted in the observed breeding seasons of birds may be divided into three. Two relate to food supply and the third to features associated with predation.

(1) Food for the chicks. It seems likely that this is an overriding factor controlling the timing of breeding in most species. Broods raised by the European Blackbird in mid-season are not only the largest, but also the young in them tend to be the heaviest; hence in this case there is good evidence that breeding may be at the best time for raising young.

It is often not known at what point in the nesting period the young need their greatest amounts of food. Indeed, in some species it may be that the fledged young are in greatest need. For example, the breeding of the East African White-backed and Rüppell's Griffon Vultures *Gyps africanus* and *G. rueppellii* may be timed so that the newly fledged young are searching for food at the time of year when the biomass of dead game is highest.

There may also be a difference between the times when food is most plentiful and the times when it is most easily caught (i.e. most available). For example, the European Kestrel and European Grey Heron *Ardea cinerea* both breed early in the year. The reason for this appears to be that their prey (small rodents and fish respectively) are easier to catch when the vegetation is not well developed. The prey species are not necessarily more common early in the season, but they are more visible and hence more easily captured.

(2) Food reserves for the laying hen. To have her young in the nest when food is most plentiful a female bird must lay her eggs very considerably before that time, when, especially in markedly seasonal areas, food may not be at all plentiful. There are a number of observations which suggest that the female may not always be able to acquire enough extra energy at this time to lay a clutch (Perrins 1970). Perhaps the most important concerns the survival of the young. In a number of species, such as the Great Tit *Parus major*, the earliest young to leave the nest may have the highest survival, all later young having progressively lower chances of survival as the season progresses (Fig. 2). By inference therefore, the later broods are not being raised at the best time of year and the breeding females would have been more successful if they had nested earlier. The male often feeds the female a considerable amount of her daily requirements at this time, again suggesting that the female needs more food than she can easily gather. Further, experiments involving the provision of extra food have resulted in the birds breeding earlier than those in adjacent areas with natural food supplies.

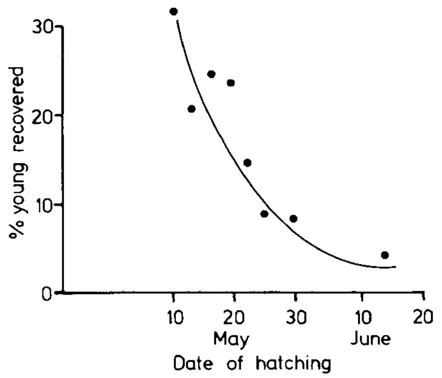

Fig. 2. Post-fledging survival of young Great Tits *Parus major* in relation to their date of hatching. Survival is measured by the percentage of the young, hatched at each point in the season, which are subsequently recaptured alive.

Many species do not seem able to build up reserves for egg-laying earlier though by no means all are likely to be prevented from breeding at the most opportune time. There are perhaps two main reasons why some birds do not lay down such reserves. Firstly the period prior to the breeding season is not a good time for finding food; secondly, in the case of small passerines laying 5 or 6 eggs or more, the amount of stored reserves would make flight difficult or impossible. The Blue Tit *Parus caeruleus*, which weighs about 10 g in winter, reaches 15 g during laying (including the weight of the enlarged reproductive organs and the egg in the oviduct) without storing food for the other eggs. It might be possible for migrants, feeding in a richer area elsewhere, to lay down reserves for breeding, but again they must lay down considerable fat for migration and the extra weight of reserves for eggs might pose a serious problem for flight.

At least two migrants are known to arrive on the breeding ground with some reserves for laying. The females of high arctic geese, e.g. the Lesser Snow Goose *Anser caerulescens caerulescens*, arrive on their nesting areas weighing about 50% more than they do at the end of incubation; this excess is sufficient to provide nutrients for egg formation and to enable the birds to survive the laying and incubation periods with little feeding. The African Red-billed Quelea also lays down reserves before laying. In their case, the clutch is small and the birds migrate only relatively short distances just before laying; even then they appear to need favourable feeding conditions at the nesting site before they start to lay.

(3) Safety from predation. There are two ways in which the timing of breeding may affect the chance of success.

(i) Safety of nest site. A number of species are reported to defer nesting until such time as the nest-site becomes safe from predation. Certain arctic species, such as the Eider *Somateria mollissima*, may defer nesting until its island sites are no longer connected to the mainland by ice. Islands, especially small ones, tend to be free of mammalian predators, so that such a delay confers obvious advantages. Similarly, the Reed Warbler *Acrocephalus scirpaceus* starts to breed only when the new reeds begin to grow up; earlier the nests would be very conspicuous and vulnerable.

(ii) Synchrony. In some species laying is closely synchronized, while in others separate pairs may not be. Close synchrony may reduce predation. For example, both early and late eggs of the Wideawake Tern suffer heavier losses than those laid in the middle of the season; then the large numbers of eggs and young 'swamp' their predators and nesting losses are relatively low. Predation may also be the underlying reason for the extremely close synchrony shown by the Quelea, which nests in colonies of enormous size and fledges its young before the predators have managed to build up locally to any great extent.

All close synchrony within colonies may not be explicable in terms of predation. Within adjacent colonies of certain seabirds, such as the Kittiwake *Rissa tridactyla*, the birds are closely synchronized but the timing of laying between such colonies may vary markedly (this phenomenon is known as the Fraser Darling effect (Darling 1952)); such intra-colony synchrony is presumably an aspect of SOCIAL FACILITATION. But the ecological reasons, if any, are far from clear, especially since the birds from the different colonies presumably mingle at sea when they are searching for food, so that supplies for different colonies are not likely to show seasonal variations to parallel the differences in laying date between the colonies. It has also been suggested that within-colony synchrony may be advantageous for food-finding since individuals can learn from one another where the best food supplies are (see FLOCKING); such information sharing could, of course, be the cause or the function of synchrony.

Proximate factors. It is of extreme importance for birds to get the timing of their breeding season right. Accordingly, there will be strong natural selection for proximate factors which give the best measure of the coming season. Since the ecology of different species varies so much, it is not surprising that different 'timing devices', often referred to as *Zeitgeber* (time-givers), are used by different species.

Birds do not slavishly follow any single proximate cue, but show considerable plasticity in the timing of breeding. Many species modify the actual time of breeding by the use of more than one cue. For example, the Great Tit may be brought into breeding condition (at least as measured by the development of gonads) by experimental increase in the daylength. Nevertheless, it does not lay at a fixed time of year; in the wild its breeding season varies by a month between years. Much of the variation can be related to spring temperatures (Marshall 1949 and see below).

The main proximate factors which have been described for birds are as follows.

(1) Exogenous factors (environmental factors).

(i) Daylength. The importance of this factor was first described by W. Rowan. The length of day varies regularly and entirely predictably throughout the world in a way that no other factor does. Given that an animal can make some measure of the daylength (see RHYTHMS AND TIME MEASUREMENT), this is an ideal marker of the seasons. This statement is less true of areas close to the Equator where changes in daylength are very small; how or whether birds breeding in such places can use daylength as a cue is a matter of dispute. But the breeding seasons of some birds are exceptionally constant, strongly suggesting that they use some such cue. For example, the mean date of laying of the Slender-billed Shearwater *Puffinus tenuirostris* in Australia varied by only a little more than a single day during a period of 7 years.

(ii) Temperature. In certain species the date of laying each spring can be closely correlated with the temperature, laying starting earlier in a warm spring than a cold one. Such a correlation has been clearly demonstrated for the Great Tit. Although, in warm springs, the individuals will need less food for body maintenance and hence have the opportunity to use more food for egg-formation earlier than in a cold spring, it seems unlikely that this is the whole reason for the correlation observed. For example, both the Pied and Collared Flycatchers *Ficedula hypoleuca* and *F. collaris* show similar correlations to that in the Great Tit between laying dates and spring temperatures, but the birds concerned are migrants and absent from the breeding grounds for most of the period concerned. Variations in temperature probably have their effect on the birds indirectly through the food supply, since insects emerge earlier in warm springs than in cold ones.

(iii) Rainfall. Birds in deserts may be stimulated to breed by heavy rain, or by the appearance of green grass. Since rainfall in deserts may not always occur at a predictable time of the year, some response directly associated with the flush of food resulting from the rainfall is of obvious advantage. Certain species come into breeding condition very quickly after it has rained. In the case of the Quelea, the sight of green grass or even the rainfall itself may stimulate nest-building. The Black-faced Wood-swallow *Artamus cinereus* of central Australia starts courtship within minutes, and copulates within 2 hours of the first rains after a prolonged drought. Local observers even claim that the birds start nest-building behaviour if a cloud crosses the sky!

(iv) Food supply. In some species food supply is likely to affect the timing of laying. However, most evidence on this point is circumstantial and few experiments have been conducted. In an experiment in which Great Tits were fed liberal supplies of food, the birds bred about a week earlier than birds in the control area; in a similar experiment with the American Red-winged Blackbird *Agelaius phoeniceus* the laying date was advanced by more than 3 weeks. Food supply in an earlier part of the year may have an important influence on the breeding season. In the Kestrel oocytes developed much faster in well-fed than poorly-fed birds, suggesting that the nutritional state of birds in spring may affect their laying dates.

(v) Presence of mate. The presence of a mate may be an essential element triggering the onset of development of the reproductive organs. For example, in the Canary *Serinus canarius* the presence of a mate in a nearby cage, or even just its song, may be sufficient to cause the female to ovulate.

(2) Intrinsic factors.

(i) Internal rhythms. In addition to being able to use external cues, birds have an internal clock which gives them a strong indication of the time at which they should undertake certain aspects of their annual cycle, such as moult, migration and breeding (see RHYTHMS AND TIME MEASUREMENT).

Birds such as Willow Warbler *Phylloscopus trochilus*, Chaffinch *Fringilla coelebs* and Short-tailed Shearwater *Puffinus tenuirostris* kept under constant conditions in the laboratory will come into breeding condition at about the correct time each year (though on average a little earlier than wild birds would normally breed). Hence each individual bird (at least in these species) has an internal clock which, in conjunction with external cues, results in the bird breeding when it does.

(ii) Age of bird. In a large number of species, birds breeding for the first time tend to lay later than older birds. In some species there is a progressive advance in laying dates with increasing age over several years. The differences are usually small though in the Song Sparrow *Zonotrichia melodia* it may be as much as 2 weeks. In the Yellow-eyed Penguin *Megadyptes antipodes* 2-year-old birds had a mean laying date of 24th September, while 3-year-olds were on average over 2 days earlier.

Evolution and inheritance. It is of such critical advantage to birds to get their timing right that it is not suprising to find that it is under tight evolutionary control. Little work has been done on this subject, but the laying date must be fairly plastic. For example, the laying dates of most North Temperate species must be very recent attributes of these birds because of the ecological changes since the last Ice Age. Most habitats were undergoing great changes during a period from about 12,000 BC to 5,000 BC and the birds moving into these habitats must have been undergoing considerable changes also.

The great selective advantage of getting the timing of breeding right may mean that change can be fast enough to observe. The laying date of the Great Tit is an inherited characteristic demonstrating that timing of laying is a character susceptible to evolutionary change (van Noordwijk *et al* 1980). In Holland there is evidence for recent changes in laying dates of a number of species. In particular, the laying date of the Black-tailed Godwit *Limosa limosa* has changed by about 2 weeks during the last 50 years, probably in response to changes in farming practice where progressively earlier hay-cutting has selected increasingly against birds which lay late in the season. C.M.P.

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BRIDLING (1): a facial plumage marking that resembles a bridle, e.g. in the Bridled Tern *Sterna anaethetus*, in a 'morph' of the Guillemot (or Murre) *Uria aalge* (see POLYMORPHISM), and in some ducks Anatidae (see PLUMAGE).

BRIDLING (2): a behaviour term applied to a form of display in the Black Noddy *Anous tenuirostris* (see TERN).

BRILLIANT: substantive name of *Heliodoxa* spp. (for family see HUMMINGBIRD).

BRISTLE: a modified feather, consisting of a shaft with usually little or no vane and resembling a stiff hair (see FEATHER; PLUMAGE).

BRISTLE-BILL: used as a substantive name of *Bleda* spp., of tropical Africa (see BULBUL).

BRISTLE-BIRD: substantive name of *Dasyornis* spp., of Australia (see WREN (2)).

BRISTLE-FRONT: substantive name of 2 species of TAPACULO of the genus *Merulaxis*.

BRISTLEHEAD, BORNEAN: *Pityriasis gymnocephala* (Passeriformes, suborder Oscines), a bird of the lowland forests of Borneo, of uncertain affinities. About 25 cm long, it is a heavily built bird with a massive hooked bill. The top and sides of the head are devoid of normal feathers, the crown being covered with short straw-coloured bristles and the auricular region with dense blackish bristles. The rest of the head and neck are red, the feathers of the lower throat with blackish bristle-like tips. The rest of the plumage is dark slate-grey, except for red thighs and, in the female only, red spots on the flanks.

The Bristlehead is insectivorous and arboreal. It is known to utter harsh notes, considered corvine by some, and a high-pitched whining note, sometimes given in chorus with others. It is highly social, and regularly joins mixed-species foraging parties; its nesting is unknown.

Its systematic position has been debated. It has been variously placed with the shrikes (Laniidae), helmet-shrikes (Prionopidae), starlings (Sturnidae), or in a family of its own, Pityriasididae (Voous). Recent evidence from DNA–DNA hybridization indicates that it is most closely related to the Australian family Cracticidae (Ahlquist *et al* 1984).

(D.W.S. (1))

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BRISTLE-TYRANT: substantive name of a group of tyrant-flycatchers of the genus *Pogonotriccus* (see FLYCATCHER (2)).

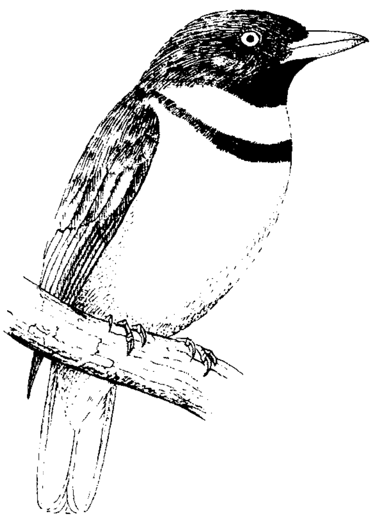
BROADBILL (1): substantive name of the species of Eurylaimidae (Passeriformes, suborder Deutero-Oscines, infraorder Eurylaimi); in the plural a term for the family.

Characteristics. Eight genera of small to medium, dumpy-shaped birds 12.7–28 cm long and in the weight range 20.5–160 g, with strong feet, rounded wings, short to graduated tail and, in most genera, a wide laterally inflated and colourful bill. Most have strikingly coloured plumage in which reds to pinks and greens and blues predominate, and black-and-light contrast-patterns are frequent. All except the monotypic *Cymbirhynchus*, *Psarisomus*, *Corydon* and *Pseudocalyptomena* are sexually dichromatic. The Philippine Broadbill *Eurylaimus steerii* has a sky-blue periocular wattle.

Electrophoretic analysis of egg-white proteins indicates a more direct relationship with cotingids and tyrannids than with pittas, from which broadbills also differ in the anatomy of the syrinx. Linked deep plantar tendons, hindering independent movement of the hallux, provide the only distinctive anatomical character not shared with some representative of these Neotropical families. Broadbill nests likewise resemble those of some cotingids.

The Sundaic green broadbills *Calyptomena* spp. have been reserved to a subfamily Calyptomeninae. A distinctive tuft of feathers covers the nostrils and in males most of the rest of the bill, which lacks lateral inflation. The gape is nevertheless relatively wider than in any eurylaimine species. Central African *Pseudocalyptomena* possesses calyptomenine colours and shape. It lacks a frontal tuft but is the only other broadbill with an uninflated bill and is probably closer to *Calyptomena* than to African eurylaimine broadbills. A gape-width/bill-length ratio places it neatly with this genus.

Distribution. Fourteen species are distributed across the humid Paleotropics from West Africa to the Philippines, 4–5 occurring together in lowland dipterocarp forest of the Sunda subregion. The family may be relict but for palaeoclimatic reasons a fossil occurrence in lower Miocene Europe is no particular evidence of later retreat before more advanced passerines. Most near competitors now are non-passerine.



Black and Yellow Broadbill *Eurylaimus ochromalus*. (*K.J.W.*).

Habitat. African *Smithornis capensis* and Asian *Cymbirhynchus* inhabit scrub and forest-edge thickets, *Cymbirhynchus* usually near water and to the landward edge of mangroves. Other broadbills are birds of the interior of inland forest, lowland or, as in *Pseudocalyptomena* and Bornean *Calyptomena whiteheadi*, exclusively montane. Several inhabit hill-slopes and *Psarisomus* retreats upward into montane moss-forest in the equatorial part of its range.

Movements. Presumed sedentary, except for *Calyptomena viridis* which wanders according to fruit supply. In Malaya it has twice been mist-netted with nocturnal migrants beyond its normal habitat and altitude range.

Food and feeding. The eurylaimine broadbills with inflated and decurved to hooked bills feed mainly on arthropods, especially large orthopterans. *Eurylaimus javanicus* is recorded taking a small lizard.

Most species forage at mid-levels of the forest profile though South-east Asian *Corydon* is strictly a canopy bird. Modes include flutter-snatching from the foliage, and searching along branches and on occasional trunks and trailing creepers (up which *Psarisomus* can climb). Many also snatch aerially for flying prey, and the 2 forest-edge species sometimes go to ground, *Cymbirhynchus* taking, besides insects, small aquatic organisms such as crabs and molluscs; even fish.

While some carnivores take occasional fruit, soft fruit and buds form most of the diet of *Calyptomena* species. *Pseudocalyptomena* also appears to eat a higher proportion of plant than animal material. Some of its behaviour has been interpreted as aerial insectivory, but *Calyptomena viridis* will also sometimes snatch flying termites. Both range widely over the forest profile.

Sluggish movements may keep broadbills from regularly joining mixed species gatherings.

Behaviour. Sundaic *Eurylaimus* species occur mainly alone or in pairs. Both members loudly advertise their position and are answered by neighbours, who remain spaced. *Cymbirhynchus*, *Smithornis* species and the calyptomenines are also usually solitary. *Calyptomena viridis* and *C. hosei* advertise their presence vocally and *viridis* pairs will repeatedly drive conspecifics off defensible fruit sources. At times they gather in small groups but, when not breeding, some other broadbills associate in considerable foraging flocks, of up to 20 in *Serilophus* and over 30 in *Psarisomus*. *Corydon*, the Dusky Broadbill, is the only species known to be permanently gregarious, in noisy groups of up to 10 individuals with a collective home range.

Voice. *Eurylaimus ochromalus* and *E. javanicus* utter an explosive, churring trill on a rising scale (preceded in *javanicus* by a sharp whistle). It is often uttered in response to thunder and neighbours invariably reply. No comparable call is recorded from the less known Philippine *E. steerii*. *Cymbirhynchus* gives a briefer but similar call, though rarely. Jerky, screaming whistles on a rising scale advertise the group position of *Corydon* and soft but carrying cooing rattles given by the green broadbills *Calyptomena viridis* and *hosei* probably also have a spacing function.

All broadbills otherwise produce whistling, popping or churring notes and a particular shrill dissyllable, possibly with short range contact function, is widely recognizable among eurylaimines: *twee-uu* in *Smithornis capensis*; *pree-u* or *wee-uk* in Sundaic *Eurylaimus* species; *wee-ark* in

Cymbirhynchus; *pee-u* in *Serilophus*; *pee-u* or *tsee-u* in *Corydon*; and *tseeay* in *Psarisomus*. *Smithornis* species also produce an apparently non-vocal throbbing croak, likened in *S. rufolateralis* to a klaxon horn, during short, circular flights on vibrating wings. In *S. capensis* it is audible at 60 m and could have territorial significance. The white back of males is exposed simultaneously. Some Asian broadbills have a whirring flight, notably *Eurylaimus steerii*, which also bill-snaps.

Breeding. All known broadbill nests are large, conspicuous pear-shaped bags with a porched entrance in the lower half, thickly built of fibre, twigs, tendrils, rootlets, leaves and grass, which hang below in a ragged beard. Several are lined internally with green leaves. They are decorated externally with cobweb, living creeper, lichen, green bryophytes or frass and slung via a long suspensor of nest-material from an inaccessible bough, liane, or the pendant tip of a bamboo or palm frond (commonly a rattan). Most are found in mid-profile positions typically over a clear space but *Calyptomena viridis*, whose nest is strapped over its support like that of a sunbird, rarely builds above 2 m from the ground. *Smithornis* species also tend to build low. *Cymbirhynchus* often uses an exposed snag isolated in water and may adopt service-wires through its habitat. All members of the *Corydon* group help to nest-build but kinship and subsequent co-operation have not been investigated (see CO-OPERATIVE BREEDING).

Broadbill eggs are white, cream or pinkish, speckled and spotted purple or reddish, sometimes sparsely, sometimes almost hiding the ground-colour. *Calyptomena* and *Smithornis* eggs are unmarked, respectively cream and white. Clutch-size varies with latitude. *Serilophus* and *Psarisomus* lay 4–5 and 4–8 eggs in the outer Himalayas, 2 and 3 in the Sunda Subregion. All Sundaic species have clutches of 2 or 3 and African *Smithornis* 1–3. *Eurylaimus ochromalus* fosters the cuckoo *Cuculus micropterus*. (C.W.M.-P.) D.R.W.

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BROADBILL (2): substantive name sometimes used for some MONARCH FLYCATCHERS of the genus *Myiagra*.

BROAD-FRONT MIGRATION: see MIGRATION (under Flight performance).

BROKEN-WING TRICK: see DISTRACTION BEHAVIOUR.

BROLGA: *Grus rubicunda* the Australian CRANE.

BRONCHUS: see RESPIRATORY SYSTEM; and under SYRINX.

BRONZEWING: sometimes used alone as substantive name of various Australian 'bronzewing pigeons', in several genera (see PIGEON).

BROOD: collectively, the young hatched from a single clutch of eggs.

BROODING: sitting on the young, usually in the nest and mainly to keep them warm (although also as protection against hot sun, rain or predators) (see PARENTAL CARE); sometimes also used of sitting on eggs (see INCUBATION).

BROOD NEST: a resting place for young birds built by one or both of the parents. It may or may not be the nest in which the brood was hatched.

BROOD-PARASITISM: the exploitation by one species (the brood-parasite or nest-parasite) of the parental behaviour of another species (the host). Some bird species occasionally deposit their eggs in nests of other species, or other individuals of their own species. This quite often occurs in colonial breeders, but it is also recorded for solitary breeders with combinations such as Lapwing *Vanellus vanellus*/Ruff *Philomachus pugnax*, Kentish Plover *Charadrius alexandrinus*/Little Ringed Plover *C. dubius*, Bearded Tit *Panurus biarmicus*/Savi's Warbler *Locustella luscinioides*. In its usual sense, however, brood-parasitism refers to cases where birds lay their eggs regularly or normally in the nests of other birds, and these act as hosts by incubating the eggs and rearing the young. Brood-parasitism is not unique to birds, since parallels are found among many social insects and certain freshwater fishes. Among birds the Common Cuckoo *Cuculus canorus* and related species (see CUCKOO) are the exemplars, and insects such as bees, wasps and ants which foist their broods upon the care of others are often called cuckoo-bees, and so on.

Jay *Garrulus glandarius* female, with crest erected and abdominal feathers fluffed, about to brood her nestlings. (*Photo: P.O. Swanberg*).

Incidence of brood-parasitism. Brood-parasitism is relatively rare among birds, occurring in only about 1% of all bird species. The habit is developed to various degrees in unrelated groups. In the Anatidae, the Black-headed Duck *Heteronetta atricapilla* of South America lays in the nests of other ducks such as the Rosy-billed Pochard *Netta peposaca*, and also in the nests of coots and rails, ibises, herons, and even in the nest of a carrion-eating hawk (*Polyborus* sp., Falconidae). It may be a recent and almost accidental change of habits. This form of brood-parasitism involves no special adaptation to the host, since the parasitic duck eggs receive only protection and warmth from the host and the ducklings leave the nest and feed and care for themselves shortly after hatching. In this respect, it has a negligible effect on the breeding success of the host. Interspecific brood-parasitism also occurs in other ducks. For instance, Redheads *Aythya americana* lay eggs in the nests of other duck species, in particular of Canvasbacks *A. valisineria*. Similarly, Ruddy Ducks *Oxyura jamaicensis* parasitize nests of the Cinnamon Teal *Anas cyanoptera*, and the Palearctic Shelduck *Tadorna tadorna* regularly parasitizes the nests of Red-breasted Mergansers *Mergus serrator*. This kind of parasitism influences the breeding success of the host, because for both Canvasback and Cinnamon Teal the number of eggs found in parasitized nests is inversely related to the number of parasite's eggs. In the Shelduck the parasitic habit may be a very recent acquisition, since it is often deleterious to the parasite's ducklings. Merganser adults usually take their offspring to deeper water soon after hatching, where the Shelduck ducklings perish as they are not adapted to deep diving for food.

In the weavers (Ploceidae) and allies (Viduine finches, Estrildidae) several species, all African, are brood-parasites. The Parasitic Weaver or Cuckoo Finch *Anomalospiza imberbis* mainly parasitizes small warblers of the genera *Prinia* and *Cisticola* (see WEAVER). Often two parasite chicks are found in the same nest and the young of the host usually disappear. The whydahs and indigo-birds (*Vidua* spp., of uncertain systematic position but certainly related to the Ploceidae—see WHYDAH (1)), of which there are some 14 species, parasitize estrildid finches. This parasitism is host-specific; the young mimic their hosts in their begging calls and mouth colour and markings, and the adult parasites show song mimicry. The young parasites and hosts are usually reared together with little effect on the breeding success of the hosts.

In the Icteridae, a small group of species—the cowbirds (*Molothrus*, *Tangavius*, *Scaphidura*)—are brood-parasitic. *Molothrus* shows an interesting gradation in the elaboration of parasitic habits as one species is non-parasitic, the Bay-winged Cowbird *M. badius* of South America,

Crowned Willow Warbler *Phylloscopus coronatus* feeding young Oriental Cuckoo *Cuculus saturatus*. (*Photo: A. Knystautas, Y. Shibnev*).

which either appropriates occupied or abandoned nests of other species or, occasionally, builds a nest of its own (see ORIOLE (2)). The parasitic cowbirds are the most important brood-parasites of the New World; the Common Cowbird *M. ater* is extremely successful, parasitizing a wide range of passerines (more than 100 species). Cowbirds usually have little impact on the breeding success of the host species as parasite and host young are reared together. In the Giant Cowbird *Scaphidura oryzivora* a beneficial effect has been claimed, because the parasite young may reduce the mortality of the host young by removing botfly larvae from them (Smith 1980). The beneficial effect applies only to nests which are not placed near wasp or bee colonies. Botflies are deterred by the presence of wasps and bees; nests thus protected may suffer from parasitism by the Giant Cowbird, whose young outcompete the host young. Apparently as a consequence, hosts nesting near wasp or bee colonies reject cowbird eggs, whereas those nesting away from wasps and bees accept them (see NESTING ASSOCIATIONS).

Among the cuckoos (Cuculidae) the whole of one subfamily (Cuculinae) and some species in a second subfamily (Neomorphinae) are brood-parasitic. Altogether nearly half of the 130 species in the family are brood-parasites (see CUCKOO). Specializations connected with parasitism have reached a high level among cuckoos, and the habit is probably a very old one. Parasitic cuckoos reduce the breeding success of the host as usually only the young cuckoo survives. Nestlings of the genera *Cuculus*, *Cacomantis* and *Chrysococcyx* evict the host's eggs and young from the nest at a very early stage. They are structurally adapted to doing so, having a hollow back. In the Koel *Eudynamys scolopaceus* (and probably also *Scythops* spp.), which mainly parasitizes crows, the chicks do not show this morphological feature and they do not evict nest-mates. The parasite or parasites (since very often more than one egg is deposited in the same nest—up to 13 are recorded in one nest) are reared together with the host young. The chicks of *Clamator* spp. also do not have a hollow back and do not evict nest-mates, and often more than one egg is found in a host nest. As regards the Pied Crested Cuckoo *Clamator jacobinus*, in Africa 22% of parasitized nests of the bulbul *Pycnonotus capensis* contained more than one cuckoo egg, and for the same species in India, 39% of the nests of the babbler *Turdoides striatus* were parasitized. Often only the cuckoo nestling survives by monopolizing the food, but in some cases, especially when the cuckoo's egg is laid in a nest containing incubated eggs, thus giving the host nestlings a start, both the young cuckoo and some foster nestlings are successfully raised. In *C. jacobinus* (in India) and *C. levaillantii* (in Africa), which parasitize mainly babblers of the *Turdoides* group, the young of both host and parasite have the advantage of being fed by a group of adults, which reduces the chance of being under-nourished.

Lastly, there are the honeyguides (Indicatoridae), of which all whose breeding is known are brood-parasitic (see HONEYGUIDE). Further research will probably reveal that the remainder (including the Asian species) are brood-parasitic also, so that this may be the only bird family totally dedicated to the habit.

Restrictions on brood-parasitism. Various behavioural and structural adaptations have been evolved for the furtherance of brood-parasitism, but certain general conditions restrict the spread of the habit. It is not worthwhile to parasitize scarce species, or those whose nests are hard to find or enter. A parasite obviously cannot use host species which feed on entirely different food or are unable to bring enough to the nest. In some cases food dissimilarity is not detrimental, e.g. in the Black-headed Duck, because the duckling feeds itself; but most parasitic bird species are altricial. Most finches feed seeds to their young, therefore in such cases a young cuckoo fails to survive. Hence seed-eating cardueline finches are rarely parasitized, whereas emberizine finches, which feed insects to their young, are often parasitized. In the New World few carduelines are parasitized by cowbirds, although more than 100 species of fosterers are known and apparently some seed-eaters can rear a cowbird to fledging. Fruit-eaters among the passerines are generally avoided by cuckoos, except for some tropical and subtropical *Pycnonotus* species that feed insects to their young.

Territorial behaviour and mating system. A population of Common Cuckoos parasitizing Reed Warblers *Acrocephalus scirpaceus* in an area of about 150 ha in England was studied by Wyllie (1981). There were 6 female Cuckoos (as judged from egg-type) and at least 2 males. One female laid in almost identical sites and with the same hosts as a year previously. One female was apparently dominant and prevented the others so far as possible from laying in suitable nests in her territory. By the end of the season this dominant female had laid a minimum of 12 eggs, another female 6, a third 4, and three others 1 or 2 eggs each. There were 54 pairs of Reed Warblers and 136 of their nests were located, of which 25 (18%) were parasitized. The known outcome of 95 unparasitized nests revealed that 25 (26%) were deserted, 60 (63%) were robbed, and only 10 (11%) produced fledged young. Egg-stealing seems to be a common habit of cuckoos and apparently restricted to females, as shown by Löhrl (1979) in aviary experiments. He observed that one female swallowed 65 eggs in one breeding season. The eggs are swallowed whole and must be a substantial protein, lipid and calcium source in the diet of the female.

In the Amur region (USSR) it has been observed that at the height of the breeding season females of *Cuculus micropterus* are often accompanied by 1 or 2, sometimes 3, males, but only one male is believed to mate with the female. Similar behaviour has been observed in the sedentary race in Java, *C. micropterus concretus*. For a large number of cuckoos, especially in the tropics, nothing is known about the mating system; but at least in *Cuculus* and *Clamator* it seems that there must be a temporary pair-bond, as there is some co-operative strategy in egg-laying (see below).

In the honeyguide *Indicator xanthonotus* the males are polygynous. One marked male was observed to mate with 18 different marked females. Male Indigobirds *Vidua chalybeata* are also polygynous, sometimes mating with 3 or 4 females in a day. In both of these groups, the mating system resembles that of birds such as grouse or manakins in which males occupy fixed sites (LEKS) and display to females, which visit these places to mate. Also in cowbirds males may mate with one or more females.

In his pioneer work on Common Cuckoos parasitizing Meadow Pipits *Anthus pratensis*, Chance (1940) found no evidence of co-operation between male and female in egg-laying, but Wyllie (1981), studying cuckoos parasitizing Reed Warblers, observed that the male sometimes accompanies the female when egg-laying. This behaviour probably serves to lure the fosterer away from the nest. For the African Cuckoo *Cuculus gularis*, it was observed that the male (perhaps because of his hawk-like appearance) attracted the attention of drongos *Dicrurus adsimilis* and lured them away from the nest (drongos are particularly aggressive birds), while the female approached the nest silently and inconspicuously. Pairs of *Clamator jacobinus* in southern Africa work in close co-ordination when an egg is to be laid and the male, by provocative behaviour, deliberately draws the attention of the hosts to himself. Similar behaviour can be inferred from observations of *Clamator jacobinus* in India parasitizing nests of the babbler *Turdoides striatus*. A pair of Great Spotted Cuckoos *C. glandarius* were kept in an aviary together with a pair of Rollers *Coracias garrulus*; the male cuckoo normally showed no special interest in the rollers but, as soon as the female was ready to lay, he diverted the rollers' attention by persistently chasing them round the cage and so making it possible for the female to slip into the rollers' nest-hole. Similarly for some honeyguide species, there may be a struggle lasting a day or more before the male can lure the hosts away so that the female can get into the nest-hole.

Host selection. Other things being equal, it should be easier for a brood-parasite to exploit related species, because their incubation and fledging periods, the food requirements of the young etc., should be similar. This is the case for the viduine finches, which parasitize species of Estrildidae. Their hosts feed their young almost exclusively on grass seeds, and this is apparently a suitable diet for young viduines as they have been reared successfully in captivity on a seed diet. Exploitation of closely related species is not, however, the rule for other nest-parasites. Cowbirds may parasitize the non-parasitic cowbird *Molothrus badius*, but more regularly parasitize other passerines. The honeyguides predominantly parasitize woodpeckers, barbets and bee-eaters. This is of particular significance, because all of these, and honeyguides, have much longer fledging periods than most birds of their size.

The cuckoos, which parasitize passerines, are taxonomically the most remote from their hosts. In this group, which has a wide size range, the size of the parasite's egg is adapted to that of the host. For example the Common Cuckoo and Himalayan Cuckoo *Cuculus saturatus*, which parasitize relatively small passerines, lay relatively small eggs (2.8–3.2% of body weight), whereas in the Little Cuckoo *C. poliocephalus*, the Drongo-cuckoo *Surniculus lugubris*, and the Fan-tailed Cuckoo *Cacomantis variolosus*, which have relatively large host species, the relative egg weight is rather high (7.0–7.3%) (Becking 1975).

Host-nest selection is made solely by the female cuckoo, usually by watching from a vantage point or by intensive searching for nests in the process of construction or before the host eggs are laid. Observation of the host's nest-building activities probably controls the time of ovulation of the cuckoo egg. The egg may be retained in the oviduct for a day, so that when laid it is one day ahead in development compared with a fresh host egg. In some cuckoo species (e.g. *C. canorus*) birds of open woodland are parasitized more often than birds of dense forest or birds in treeless grasslands, perhaps because the female cuckoo can find nests more easily when perched on an observation point in the open. But some other species, such as *Cuculus saturatus*, *C. fugax* and *C. sparverioides*, are primary forest birds cuckolding forest species.

Sympatric cuckoo species usually parasitize different fosterers, but there are exceptions. In India some hosts are shared by 2 or more cuckoos, and 6 cuckoo species parasitize one Australian host. A honeyguide and a cuckoo parasitize *Spreo bicolor* in South Africa. Some cuckoos have a rather broad host range, e.g. the Common Cuckoo and Fan-tailed Cuckoo, whereas others have a very narrow host range and even species-specific host relations; for instance the Himalayan Cuckoo parasitizes small *Phylloscopus* and *Seicercus* warblers (but recently with another egg colour also found with *Cettia* (Higuchi and Sato 1984)) and the Little Cuckoo selects mainly *Cettia* warblers, and *Chrysococcyx malayanus* only the gnateater *Gerygone sulphurea*. Relationships may vary locally; for instance the sedentary race of *Cuculus micropterus* in Java parasitizes drongos and the same host is reported for India, but it parasitizes mainly shrikes in the Amur region of the USSR and Azure-winged Magpies *Cyanopica cyana* in northern China.

Egg-laying. The egg must be laid quickly to avoid unduly disturbing the host. From Chance's observations on Cuckoos parasitizing Meadow Pipits it was evident that individual females laid at two-day intervals, usually in the afternoon. When visiting a nest to lay, the females spent not more than a minute in its immediate vicinity and on average only about 9 seconds depositing the egg. All eggs were laid directly in the nest. At a Reed Warbler's nest Wyllie (1981) saw a female Cuckoo scramble through the reeds, remove the Reed Warbler's single egg and lay her own directly in the host's nest, the whole operation taking only 11 seconds. With regard to the Pied Crested Cuckoo parasitizing the Jungle Babbler, Gaston (1976) observed that a female cuckoo perched about 5 seconds *c.* 15 cm above the babbler's nest and this was sufficient for her to drop an egg into the nest. On examination it was found that one babbler egg had a circular depression on the upper side, probably caused by the impact of the cuckoo egg falling on it. In babblers' nests containing cuckoo eggs, damaged or 'slightly dented' babbler eggs were often found.

Cuckoo eggs are laid on alternate days, and each egg is probably held for a day in the oviduct, so that the embryo develops for a day before the egg is laid. This was originally observed in the Jacobin (or Pied Crested) Cuckoo (R. Liversidge), but holds also for the Common Cuckoo in Europe, as Cuckoo eggs 1–2 days incubated have been found in host nests containing incomplete clutches which have not been incubated (C.M. Perrins). Some other cuckoo species lay at intervals of 2 or 3 days, and it is not known whether their eggs are likewise developed at laying time.

The number of eggs laid in a season in a particular area by one female Cuckoo was determined by differences in colour pattern and size and estimated to be at least 12 (Wyllie); others have reported smaller numbers. In field experiments in which the host nests were collected as soon as the Cuckoo egg was laid, causing the host to nest again and to be parasitized repeatedly, individual Cuckoos laid 18–25 eggs in one season. Examination of the ovaries of several species of African cuckoos has shown that these lay *c.* 16–25 eggs in a season. The cuckoos ovulate on alternate days, and 3–6 eggs make up a series or 'clutch'.

The number of eggs laid in a season by cowbirds *Molothrus ater*, estimated by searching for parasitized nests, ranges from 7–25. Captive cowbirds lay more eggs in a series than is known for cuckoos; H. Friedmann reported a female laying 13 eggs in 14 days in nests with candy eggs. However, ovary histories of wild females show that they normally lay in series of 2–5 eggs.

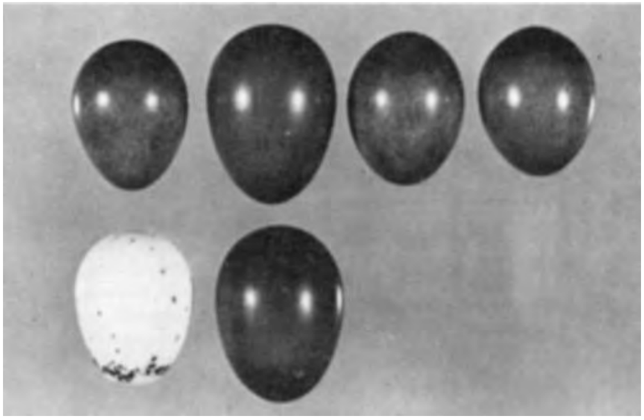
If the parasites do not find enough fosterers in a certain area, they may dump their eggs in old and deserted nests. This has been regularly observed in the Common Cuckoo, also for *Cacomantis* species (*C. variolosus* and *C. merulinus*), *Clamator jacobinus*, and even for the parasitic duck *Heteronetta atricapilla*.

Multiple laying, i.e. 2 or more parasite eggs in the same nest, has been recorded occasionally for *Cuculus*, *Cacomantis* and *Chrysococcyx* species. It is, however, far more common in *Clamator* and *Eudynamis*. In the Koel 3 eggs in the same nest are regular, 7–9 have sometimes been found, and once 13.

Egg mimicry. One of the most striking adaptations for brood-parasitism, found only in the cuckoos, is the matching of egg colour and pattern to the eggs of the host. Close matching increases the likelihood of the alien egg being accepted by the host. Classic (Leverkühn 1891) and more recent work on the introduction of alien eggs into the nests of passerines showed frequent rejection of the alien egg or desertion of the nest. Some hosts are rather discriminating, others not so. Among the most undiscriminating are some South African bulbuls (*Pycnonotus* spp.) which appear never to reject either natural or experimental parasitism by the Pied Crested Cuckoo, whose large plain white eggs are very unlike the red, heavily spotted bulbul eggs. At the other extreme the Common Iora *Aegithina tiphia* often deserts its nest if parasitized by the Banded Bay Cuckoo *Cacomantis sonneratii*. Here the egg shows such a high degree of adaptation that it can be distinguished only by microscopical examination of the eggshell surface (see EGGSHELL, ULTRASTRUCTURE OF). Cuckoo eggs are adapted to certain hosts and, among European passerines, rejection of Cuckoo eggs seems to be most pronounced among species that are only infrequently parasitized.

Some cuckoos show mimetic egg polymorphism, with egg-races or 'gentes' adapted to particular hosts. The best example is the Eurasian Common Cuckoo, which produces two main types of eggs, one spotted and the other immaculate, plain blue. The plain blue egg-type is rather common in northern and central Europe and is adapted to the Redstart *Phoenicurus phoenicurus*, chats *Saxicola* spp., and the Dunnock *Prunella modularis* (in Britain, however, this egg-type is unknown although Dunnocks are frequently parasitized, usually successfully). The spotted egg-type is variable, with different varieties adapted to pipits *Anthus* spp., wagtails *Motacilla* spp., shrikes *Lanius* spp., and Robins *Erithacus rubecula*. Another example is the South-east Asian Plaintive Cuckoo *Cacomantis merulinus*, which has a white, red-spotted egg-type matching the eggs of tailorbirds *Orthotomus* spp. and a uniform brick-red or chestnut egg-type matching the eggs of the Ashy Wren-warbler *Prinia socialis* in India or the Yellow-bellied Wren-warbler *P. flaviventris* in Java. Only very rarely are these egg-types found in a nest of the wrong host. Similarly the Koel lays a green egg-type mimicking the eggs of crows, the main fosterers in the western part of its range, and a red egg-type associated with magpie-larks, honeyeaters and orioles in Australia. Sometimes there is some ecological separation between birds laying eggs of different types. For instances, in Hyderabad City in India the Plaintive Cuckoo habitually parasitizes the locally abundant Ashy Wren-warbler (brick-red egg-type), but in the surrounding country its principal host is the Indian Tailorbird *Orthotomus sutorius* (white, brown-spotted egg-type). In Java the situation is reversed: in open scrub country it parasitizes *Prinia flaviventris*, and in villages *Orthotomus* spp.

A main problem is to explain why the egg mimicry and polymorphism do not break down in areas where more than one kind of egg-type occurs. Cuckoos laying different egg-types show no difference in voice or behaviour and live in mixed populations. It has been suggested that egg mimicry is maintained by a sex-linked gene complex on the W chromosome in the heterogametic female sex. A female would thus transmit to all her daughters the same gene complex determining egg colour that she herself has. The daughters, as a result of IMPRINTING on the foster-parent



Red egg-morph of Plaintive Cuckoo *Cacomantis merulinus*; *Above*: with eggs of Yellow-bellied Wren Warbler *Prinia flaviventris*, showing egg mimicry; *Below*: with egg of Ashy Tailorbird *Orthotomus ruficeps* (actual size). (*Photo: J.H. Becking*).

species in whose nests they hatch, would then continue to lay host-matching eggs in nests of the same species. Occasional deviations from this pattern could be explained by (1) chromosomal crossing-over (or translocation) between Z and W (see GENETICS for terminology of avian sex chromosomes); (2) breakdown of imprinting; or (3) lack of proper host nests, and other accidental situations.

Structural egg adaptations. Cuckoo eggs also show structural specializations. They tend to have thicker calcified shells than passerine eggs. For instance, *Cuculus canorus* has an eggshell thickness of 85–90 μm compared to its fosterers' 50–54 μm. This is also evident from the so-called Rey's index (egg length × width in mm, divided by eggshell weight in mg), which is 1.5–1.6 for cuckoo eggs and 2.0–2.5 for fosterers' eggs. Eggshell thickness reaches an extreme in the eggs of *Clamator* species, which are dropped from some distance into the open cup-shaped nests of the host. In *C. coromandus* the calcified shell measures 200–204 μm and in *C. jacobinus* 140–160 μm, whereas their fosterers, *Garrulax* and *Turdoides* spp., have eggshells with a thickness of 103 and 101 μm, respectively. Moreover, cuckoo eggs gain extra strength from their shape. The eggs of *Clamator* species are nearly spherical, as is evident from their shape index (egg length : maximal width) of 1.17–1.28. The eggs of other cuckoos, e.g. *Cuculus* and *Cacomantis* spp., are characterised by very rounded ends, much rounder than those of their hosts. Finally, cuckoo eggs are adapted to adverse circumstances by their rather special pore structure, showing pores with plugs of organic matter (see EGGSHELL, ULTRASTRUCTURE OF). This is presumably an adaptation against water loss, as the eggs are liable to lie for some time unattended in host nests.

Adaptations of young. Brood-parasites usually develop faster than their hosts, and early hatching gives them a head start on the host young in the nest. Incubation periods of parasitic cuckoos are usually 11–14 days, often 2–4 days shorter than their hosts. The honeyguide *Indicator minor* has an incubation period of 12 days, which is short compared to its barbet hosts. The cowbird *Molothrus ater* hatches in 11–13 days, often a day or two before its hosts. The finch *Vidua chalybeata* hatches in 10–11 days, usually 1–3 days before its host.

Nestling periods of cuckoos which evict nest-mates are relatively long, for instance 20–21 days in *Cuculus* and *Chrysococcyx*. Cuckoos which are reared with nest-mates have growth rates and nestling periods like those of their hosts, e.g. 11–15 days in *Clamator jacobinus*. Nestling periods of non-parasitic cuckoos range from 15–20 days for large terrestrial species (*Geococcyx* and *Centropus*) to 6–10 days for smaller arboreal or terrestrial ones (*Coccyzus* and *Crotophaga*). Both parasitic and non-parasitic cuckoos fledge upon reaching 50–60% of adult body weight.

Young cuckoos of the genera *Cuculus*, *Cacomantis* and *Chrysococcyx* kill their nest-mates. Upon hatching they manoeuvre an egg or nestling onto their concave back, then rear back to the rim of the nest until the egg or young bird drops over the edge. In Australia the Koel, parasitizing Magpie Larks *Grallina cyanoleuca*, is reported to evict the host nestlings, but this behaviour has never been observed in other populations of the Koel or in *Clamator* species. Young honeyguides (*Indicator* spp.) have sharp hooked bills at hatching, and kill their nest-mates by biting and stabbing.

Parasitic cuckoos which evict nest-mates are born naked and usually differ form their nest-mates by a darker slate-black skin (mainly dull brown in the host young) and a huge mouth with an orange-red palate and gape. The mouth of the young cuckoo and its persistent screaming, begging calls probably function as a 'feeding releaser' eliciting prolonged feeding by the foster parents. When handled, young cuckoos often produce a hissing sound and, with their gaping response and jerking movements, have a snake-like appearance which may deter potential predators. Some (e.g. *Clamator levaillantii*) evacuate a vile-smelling brown fluid from the cloaca as a defence mechanism.

In nest-parasites which are reared together with their nest-mates there is a tendency to mimic the host's young, both in appearance and in their calls. Morphological differences between nestling cuckoos of the genera *Clamator* and *Eudynamis* and their hosts' young are slight. Viduine young differ only slightly from their estrildid hosts, and in particular their mouth colour and markings closely match those of their nest-mates. Nestling cowbirds resemble the young of some of the species in whose nests they are raised. Vocal mimicry has been reported in nestlings of the Great Spotted Cuckoo parasitizing the Pied Crow *Corvus albus*, and the nestling Striped Cuckoo mimics the call of the chicks of its principal fosterer, the Arrow-marked Babbler *Turdoides jardineii*. Vocal mimicry has also been reported in the young of one parasitic species which kills its nest-mates, the Greater Honeyguide parasitizing the Red-throated Bee-eater *Merops bulocki*. J.H.B. and D.W.S.(1)

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BROOD-PATCH: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; INCUBATION.

BROOD REDUCTION: a process of selective feeding of the largest members of a brood when food is short, so that only a few large but relatively well-nourished young fledge. Were food to be shared evenly amongst the brood none would be adequately fed and all might die. When food is plentiful, however, the full brood can be fed and reared successfully, so the parents are then more productive than they would have been starting with a smaller clutch. The phenomenon is most frequent amongst (both aerial and marine) plankton-feeders and amongst birds of prey. In the latter group fighting between siblings (so-called 'CAIN AND ABEL strife') is frequently observed. An initial size gradient within the brood is usually brought about by differences in egg size and by starting incubation before laying is complete.

BROWNBUL: used as a substantive name for some African species of Pycnonotidae (see BULBUL).

BRUBRU: *Nilaus afer* (see SHRIKE)—to be distinguished from BOUBOU.

BRUSH-BIRD: earlier substantive name of *Atrichornis* spp. (see SCRUB-BIRD).

BRUSH-FINCH: substantive name of *Atlapetes* spp., of the Neotropical Region (see BUNTING).

BRUSH-RUNNER: substantive name of the South American furnariid *Coryphistera alaudina* (see OVENBIRD (1)).

BRUSH-TURKEY: name used in Australia for *Alectura lathami*; in the plural, serves as a general term for this and allied genera (see MEGAPODE).

BUBALORNITHINAE: see WEAVER.

BUCCAL: pertaining to the mouth (buccal cavity)—see TONGUE.

BUCCONIDAE: see under PICIFORMES; PUFFBIRD.

BUCEROTES; BUCEROTIDAE: see CORACIIFORMES; HORNBILL.

BUCORACINAE: see HORNBILL.

BUDGERIGAR: *Melopsittacus undulatus*; also 'betcheryygah' and other transliterations of the aboriginal name (see AVICULTURE; PARROT).

BUFFALO-WEAVER: see WEAVER.

BUFFLEHEAD: *Bucephala albeola* (see DUCK).

BULBUL: substantive name of most species of Pycnonotidae (Passeriformes, suborder Oscines), in the plural general term for the family. Other substantive names used are greenbul (several genera), brownbul, leaflove and bristlebill. The bulbuls are an Old World and largely tropical group of birds of moderate size varying in length from 13–23 cm.

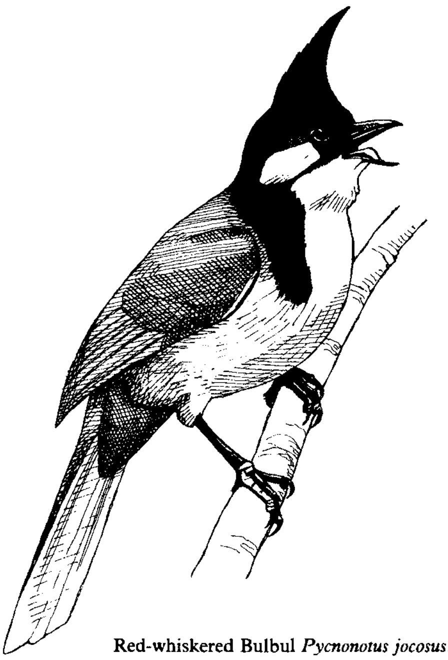
Virtually all authors have stated or implied a relationship between bulbuls and cuckoo-shrikes Campephagidae but the egg-white protein evidence does not support this. Rather the evidence suggests a relationship to the Dicruridae and possibly with the Sturnidae and Oriolidae. Over 120 species in 15 genera have been recognized. Of these, 10 genera (about 50 species) are confined to Africa and Madagascar (or to one or other), 2 (*Spizixos*, *Setornis*) are confined to southern Asia, 2 (*Pycnonotus*, *Criniger*) are found in both Africa and Asia, and *Hypsipetes* extends from Madagascar and the Mascarene Islands to eastern Asia. Hall and Moreau (1970) placed 8 species of *Pycnonotus* (some from Africa and Asia) into a superspecies and some Asian species in *Criniger* have been considered to be conspecific with certain African species.

Characteristics. Bulbuls have rather short concave wings and comparatively long tails (12 feathers) that are graduated in some species (e.g. in *Thescelocichla*), but more often either square (e.g. in *Baeopogon*) or rounded. Their bills are never large, but slender (except those in the genus *Spizixos*), notched, and usually have well developed, stiff rictal bristles near the gape. The nostrils are long or oval, more or less operculated. The tarsi and toes are always rather weak, usually small and often very short. In *Bleda* the middle and outer toe are fused to the first joint. The body feathers are long, soft and fluffy, particularly on the lower back. On the nape of some species (e.g. in *Criniger*) are long hair-like feathers which fall on to the mantle. Some bulbuls are noted for their well developed crests.

Bulbuls are not brightly coloured. Some have yellow underparts but the majority have dull colours such as olive green, brown and grey. The upperparts are usually uniform in colour, but in several species the tail is coloured rust-red or reddish brown in marked contrast to the rest of the upper parts. Any bright colours (crimson, yellow, rufous) are confined either to the throat, undertail coverts or to streaks on the head or ear coverts. The sexes are alike in colour and size and the immatures are very similar to adults and unspotted.

Field characteristics, habitat and distribution. The majority of bulbuls are found in forests of one type or other which offer a diversity of habitat allowing wide sympatry. No less than 35 of the 50 or so African species occur either in the lowland forest block of Zaire or in the montane forests of eastern Zaire. In the lowland forests of north-east Gabon 22 species occur (Brosset 1971). Other bulbuls inhabit sparsely wooded areas and quite a number, particularly in *Pycnonotus*, are found in cultivations and gardens in towns and villages.

The most widely distributed and common species in Africa is the African Bulbul *Pycnonotus barbatus*. It has numerous races and is closely related to several Asian species. They are all dusky coloured with bright under tail coverts, and inhabit open country and cultivations avoiding true forest although not the forest edge. One of these, the Red-whiskered Bulbul *Pycnonotus jocosus*, has been successfully introduced to Fiji, Australia (Sydney and Melbourne, since the 1880s) and Florida (Miami, since 1960).



Red-whiskered Bulbul *Pycnonotus jocosus*. (*N.W.C.*).

The Striated Bulbul *Pycnonotus striatus*, a common montane forest species from Nepal to Burma, is olive but its upper and underparts are striped with white. In the same area is found the Finch-billed Bulbul *Spizixos canifrons* which has a short thick finch-like bill distinctively coloured pale yellow, looking almost white in the field. It is also unusual in having a forward pointing crest. The other member of the genus is found in eastern and central parts of China and on Taiwan.

Five species in *Hypsipetes*, usually regarded as a superspecies, occur on islands in the Indian Ocean. One of these, the Black Bulbul *Hypsipetes (Microscelis) madagascariensis*, also occurs in Asia. There are numerous black, black and white, and grey forms which all have a bright red bill, legs and feet as do other species in *Hypsipetes*. A close relative, the Brown-eared Bulbul *H. amaurotis*, inhabits islands and coasts of eastern Asia from the Philippines to Hokkaido.

The Asian species (5) in *Criniger* show a wide variation in colour, pattern, and size and shape of tail, but all have a conspicuously coloured throat. The African members (4 species) are a much more uniform group. They all inhabit forests, are often crested, and coloured either olive, yellow or brown. Some are found as high as 1,500–3,000 m.

Movements. The majority of forest bulbuls are suspected to be sedentary but some are nomadic. Ringing studies in Gabon and in Asia have shown that both the Green-tailed Bristle-bill *Bleda eximia* and the Large Olive Bulbul *Pycnonotus plumosus* are remarkably sedentary (Brosset 1981a, McClure 1974). Brosset also showed, in contrast, that the Yellow-whiskered Bulbul *Andropadus latirostris* was nomadic. Ringing studies have shown that the Brown-eared Bulbul migrates within the Japanese islands and some forms of the Black Bulbul migrate to winter in considerable numbers in north-east Burma.

Food. Small fruits and berries form the bulk of the food of many bulbuls (e.g. the African species in *Andropadus*, *Thescelocichla*, *Chlorocichla* and *Ixonotus*). Some feed on buds and the nectar of flowers and several genera are strictly insectivorous (e.g. *Bleda*, *Criniger*, *Phyllastrephus*, *Baeopogon*, *Nicator* in Africa). Insectivores usually search the foliage for their food but may catch flying insects in the manner of flycatchers (e.g. Finch-billed Bulbul). In the Gabon Brosset (1981b) found the Yellow-whiskered Bulbul omnivorous, although fruits were its staple diet, and feeding at all levels of the vegetation. In contrast, the sympatric Green-tailed Bristle-bill was a specialized insectivore only feeding in a narrow horizontal layer of the forest vegetation.

Behaviour. Forest bulbuls are characteristically secretive and skulking whereas those found in gardens and parklands are much more bold and conspicuous. Many species are gregarious and noisy, especially when feeding, but are territorial in the breeding season. Recent studies have revealed interesting exceptions and there may be others. In the Gabon, Brosset (1981c) found that the Green-tailed Bristle-bill lived in family units made up of a pair and yearlings of the previous breeding season. These family units associated daily with mixed parties of insectivorous birds. He found that they had two periods of feeding activity during the day, were long lived (often for more than 10 years) and that their populations were stable. In marked contrast the sympatric Yellow-whiskered Bulbul, an apparent aberrant case, was solitary outside the breeding season and gregarious during the breeding season when males formed leks (see LEK), the females alone brooding and feeding young. There was no defended territory even by the breeding females which often occupied nests close to each other. The life expectancy of this bulbul was small and the population showed considerable fluctuations during the 10 year period of the study. Feeding at fruiting trees took place several times throughout the day.

In at least 2 African species (the Spotted Greenbul *Ixonotus guttatus* and the White-tailed Greenbul *Thescelocichla leucopleura*) several helpers contribute to the nest construction and/or feeding of nestlings.

Voice. The chances that a chattering noise, throaty babbling or melodious whistle heard in the tropical forests is due to a bulbul are high. Although these calls are very varied they are an important means of field identification, although initially difficult to learn. Apart from calls several bulbuls have extremely beautiful songs which are rich in quality and powerful, for example in Africa the West African Nicator *Nicator chloris* and in Borneo the Yellow-crowned Bulbul *Pycnonotus zeylanicus*. Brosset found males of the Yellow-whiskered Bulbul singing only at leks during their restricted mating season.

Breeding. Brosset studied the breeding of 11 species of bulbul from 8 genera and found that their nests were not concealed but rather placed in open situations at heights less than 6 m above ground. Bulbul nests are not substantial structures and their loose texture allows the tropical rains to drain quickly through them. They are cup shaped, made of twigs, stems and dead leaves and lined with grasses and fungi (*Marasmius*), the mycelium of which serves to consolidate the structure. Some species of *Hypsipetes* place their nests 8–15 m above the ground.

Most species of bulbuls have a clutch size of 2 but it is 3 for the Yellow-whiskered Bulbul and 1 for the West African Nicator. Some Asian species have clutches of 4 or 5. The ground colour of the eggs ranges from white, pinkish white or cream coloured, to brown or green. They are heavily marked and blotched with various shades of brown, dark olive and purple. Incubation for those species studied is in the range 12–14 days and nestling period 13–14 days but 11 or 12 days in the Lesser Icterine Greenbul *Phyllastrephus icterinus*.

White-cheeked Bulbul *Pycnonotus leucogenys*. (*M.W.*).

The breeding seasons of some bulbuls are restricted to a short period (e.g. Yellow-whiskered Bulbul) during which clutches that fail are quickly replaced and fledged young are quickly abandoned. In some years Brosset found that the Yellow-whiskered Bulbul did not breed. Other species of bulbul (e.g. Green-tailed Bristle-bill) have a prolonged breeding season, do not replace clutches that are lost, and family units stay together for several months. A.I.I. and L.G.G.

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BULLA: see SYRINX.

BULLFINCH: substantive name of *Pyrrhula* spp. used without qualification, in Britain, for *P. pyrrhula*; applied in the West Indies to species of *Loxigilla* and *Melopyrrha* (see FINCH; AVICULTURE).

BUNTING: substantive name of Old World species of Emberizinae, a subfamily of the Emberizidae (Passeriformes, suborder Oscines); in the plural, general term for the subfamily. In North America, most of these birds have the substantive name 'sparrow' or 'finch', the name bunting being used mainly for brightly coloured species of the subfamily Cardinalinae (see CARDINAL-GROSBEAK).

Systematic characteristics. The Emberizinae are frequently grouped together with the Carduelinae (see FINCH) into a single expanded family Fringillidae. The cardueline finches, however, are clearly of Old World origin, whereas the Emberizinae are a New World group that has spread via one or a few colonizations to the Old World where adaptive radiation has proceeded almost entirely within the confines of the single genus *Emberiza*; the 3 other Old World genera, *Miliaria*, *Melophus* and *Latoucheornis*, are all monotypic. Two further genera, *Calcarius* (the longspurs) and the monotypic *Plectrophenax*, are circumpolar and, properly speaking, not typical elements of either the New or Old World avifauna. The situation among the New World Emberizinae is far more complex, and despite the modern tendency towards the recognition of broadened genera within the subfamily, as many as 60 genera can reasonably be distinguished on present evidence. Of these, 4 genera restricted to the Galapagos Archipelago and Cocos Island are treated in a separate article (see DARWIN'S FINCHES), and many other Neotropical genera have been little studied and are only uncertainly placed within the Emberizinae.

The buntings of the Old World form a group which is clearly distinct from ecologically similar, sympatric species such as finches (Fringillidae), sparrows (Passeridae) and weaverbirds (Ploceidae). They number 42 species: the circumpolar Snow Bunting *Plectrophenax nivalis* and Lapland Longspur *Calcarius lapponicus*, the typical buntings *Emberiza* spp., the Corn Bunting *Miliaria calandra*, the Crested Bunting *Melophus lathami* and, finally, the rare and enigmatic *Latoucheornis siemsseni* from China. The large genus *Emberiza* is best represented in the Palearctic Region, which has 28 breeding species; an additional one, the House Bunting *E. striolata*, is shared by the Palearctic and Afro-tropical Regions, and the other 8 are Afro-tropical. The most familiar is probably the Yellowhammer *E. citrinella*, which inhabits western Eurasia to Iran and central Siberia. The Corn Bunting is a Palearctic species closely allied to the genus *Emberiza*, but is differentiated on account of its large size, bill structure, moult pattern (complete post-juvenile) and certain aspects of its behaviour. The Crested Bunting inhabits northern India and the Indo-Chinese countries, and is the only member of the subfamily in tropical and subtropical Asia. The male differs from all other buntings by having a long, pointed crest, and also has an unusual plumage for a bunting, being glossy blue-black, unstreaked and unspotted, with chestnut wings and tail; the female is streaked, however, has no crest, and resembles many other buntings.

The systematic position of some New World groups is so uncertain that it is very difficult to compare the Emberizinae of the Old World with those of the New, but the species are certainly far more numerous and diverse in the Western Hemisphere. Most closely related and physically similar to the Old World forms are principally Nearctic genera such as the juncos *Junco* spp. and the many streaky-brown plumaged sparrows of *Zonotrichia* and *Ammodramus*. Three species in *Zonotrichia* deserve special mention: firstly, the Song Sparrow *Z. melodia*, whose life history and behaviour were the subject of the seminal field study conducted by Mrs M.M. Nice in the late 1920s and 1930s, and whose population biology has since been studied both widely and in great detail; secondly, the White-crowned Sparrow *Z. leucophrys*, which has been a key species for studies focusing on the physiological ecology of birds; and thirdly, the Rufous-collared Sparrow *Z. capensis*, which is found over a huge geographical range from Mexico southwards, and which is possibly the best-studied of any predominantly Neotropical emberizine. The largest and most colourful emberizines of the New World are the ground-feeding towhees *Pipilo* spp., and among the smallest are the tiny grassquits *Tiaris* spp. which can frequently be seen clinging to seeding grass-stems along the roadsides of Caribbean islands. One of the most numerous genera in terms of species is *Altapetes*, the stout and predominantly olivaceous brush-finches which, as their name indicates, inhabit brushy areas from Mexico south to the Guianas and Brazil in the east, and to Peru, Bolivia, and north-western Argentina in the west.

Characteristics. In physical characteristics the emberizines are rather homogeneous, being small birds with legs of medium length and big feet equipped for scratching. Their size averages about 15 cm, but some species are a good deal smaller and others attain around 20 cm. Some are attractively coloured and patterned but the plumage is rarely brilliant, being brownish, greyish or olivaceous as a rule, streaked or disruptive in pattern, and sometimes including various combinations of other colours. Certain species have a short crest, the Crested Bunting alone has a long, pointed one. The tail is fairly long in many species, sometimes graduated or slightly forked. The wing, which has 9 obvious primaries (although a vestigial and hidden 10th, outer primary may be present), is long and pointed in most migratory species, rounded and short in most sedentary species. The bill is short, or relatively so, conical and attenuated, and some typical *Emberiza* spp. are provided with a hump in the roof of the mouth for crushing seeds. In the Reed Bunting *E. schoeniclus* the shape of the bill varies geographically to a remarkable extent, from very small, slight and attenuated to globular, massive and parrot-like in shape, these variations being correlated to the type of reed bed that the bird inhabits. Among small, omnivorous passerines, larger beak size is frequently held to be correlated with the inclusion of larger and/or harder seeds in the diet, but in the case of the Reed Bunting it is the smaller-beaked races that feed on seeds in winter whereas the larger-beaked forms subsist at this time on insect prey which they obtain by crushing reed stems.

Habitat, distribution and populations. The emberizines are predominantly terrestrial, or dwell in bushes and thickets, but their habitat preferences vary greatly. Many species inhabit grasslands or weedy and bushy areas in open or fairly open regions; some, especially Neotropical species, frequent open woodlands or the edges of forest, usually avoiding the denser and higher growth. With these few restrictions, buntings can be found anywhere and in all sorts of climates, from the hottest or most arid to the coldest and most humid, from the seashore to the very high and barren plateaux of the Andes, and from virtually one end of the earth to the other. Some American species inhabit Tierra del Fuego or the high Arctic; the Snow Bunting breeds at the tip of northern Greenland, farther north than any other land bird. In suitable habitats populations of particular species can reach extremely high densities. Thus among sedentary populations of Song Sparrows which have been studied on the salt marshes of San Francisco Bay, California, and on small Mandarte Island off the British Columbia coast, 20 or more breeding pairs may be present on every hectare of favoured habitat.

Food. The great majority of emberizines can be classified as omnivorous. During much of the year most species subsist predominantly on seeds, mainly secured by foraging on the ground. But during the breeding season many buntings rear their young largely or entirely on arthropod prey.

Behaviour. In many aspects of their behaviour, there is enormous specific variation. Many species collect together in large flocks outside the breeding season, but others are rarely seen in groups of more than 2 or 3. The Snow Bunting and the House Bunting are so confiding that they nest by preference in occupied dwellings when available, whereas other buntings are amongst the most wary and furtive of birds. In a majority of species, at least among the better studied Holarctic forms, males defend territories against conspecifics during the breeding season, and, indeed, the role of territorial behaviour in the life of birds was first elucidated largely through studies on the Reed Bunting and Song Sparrow. In the Sharp-tailed Sparrow *Ammodramus caudacutus*, however, territorial behaviour may be absent and males overlap greatly in their home ranges. Mating systems vary from the monogamy and occasional bigamy of most species studied, through the highly polygamous behaviour of some populations of Corn Buntings, to the apparent complete promiscuity recorded for the Sharp-tailed Sparrow in which relations between the sexes are limited to copulation alone.

Yellowhammer *Emberiza citrinella*. (*D.A.T.*).

Voice. The song can be loud, rich and musical, or so feeble as to be scarcely audible to man, being very high pitched and similar to the buzz of an insect.

Breeding. The nest of typical buntings and New World sparrows is cup-shaped, but is domed in many Neotropical members of the group, e.g. the grassquits *Tiaris* and the bullfinches *Loxigilla*. Grasses, fine roots and sometimes moss and lichens are normally the chief material; a few hairs and sometimes feathers are added to the lining where they can be found. The nest may be in a bush or tree, usually not high above ground; or it may be built on the ground. The choice of site seems to be less important than secure support and concealment. The Reed Bunting may build among reeds and sedges in shallow water; some species nest in holes in trees or on the ground or in crevices among boulders. The eggs may be immaculate or marked with blotches and scribbles, and clutch sizes vary from 2–7 or rarely more. The larger clutches tend to be found among species and populations inhabiting higher latitudes, and the smallest clutches in tropical forms. Incubation, from 11–14 days, may be either by the female alone or shared by both sexes, whereas care of the young is normally carried out by both parents, being restricted to the hen alone in only a few species. The young may leave the nest in as little as 8 days and fledge at 12–14 days. Among the typical buntings of the Holarctic Region which have cup-shaped nests frequently situated on the ground, nest predation may be high, but this is offset by the willingness of most to replace lost clutches. Adult mortality of these species normally lies within the range 35%–55% per annum.

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BUPHAGINAE: see OXPECKER.

BURGOMASTER: sailors' name for the Glaucous Gull *Larus hyperboreus* (see GULL).

BURHINIDAE: see under CHARADRIIFORMES; THICKKNEE.

BUSH-BIRD: substantive name of *Thamnistes* spp. (see ANTBIRD).

BUSH-CREEPER: substantive name, in Africa, of *Macrosphenus* spp. (for subfamily see BABBLER).

BUSH-CROW: substantive name sometimes used for *Zavattariornis stresemanni*, a crow-like African bird of uncertain affinities (see under CROW (1)).

BUSH-HEN: name used in Australia for *Amaurornis ruficrissus* (see RAIL).

BUSH-QUAIL: substantive name sometimes used for the Indian gamebirds of the genus *Perdicula* (see PHEASANT).

BUSH-SHRIKE: substantive name of some species of Malaconotinae; in the plural, general term for the subfamily (see SHRIKE).

BUSH-SKULKER: *Turdoides fulvus* of Africa (for subfamily see BABBLER).

BUSH-TANAGER: substantive name of *Chlorospingus* spp. (see TANAGER).

BUSHTIT: substantive name of *Psaltriparus* spp., of the New World (see TIT).

BUSH-TYRANT: substantive name of the tyrant-flycatchers of the genus *Myiotheretes* (see FLYCATCHER (2)).

BUSKING: the aggressive display of the male Mute Swan *Cygnus olor* in which he advances across the water towards an intruder with his neck drawn back and his wings arched, proceeding with a jerky movement because during this display, as opposed to normal practice, he paddles with both feet in unison.

BUSTARD: the most usual substantive name of species of Otididae (Gruiformes, suborder Otides); in the plural, general term for the family. This is a phylogenetically independent, relatively homogeneous Old World family of medium-sized to large terrestrial birds (*c*. 40–130 cm). There are 22 clear species, but 3 of these (see below) are divisible to comprise up to 5 further species; the number of genera (treated here as 8) is also debatable.

Characteristics. All species are rather long-legged and long-necked, with stout (but often tapering) bodies, rather flattened heads and straight, short bills. Flight is powerful and sustained, the wings are broad and long, the tail broad and fairly short. The tarsi are covered in hexagonal scales and the feet have 3 short, broad toes with flattened nails (hallux absent). The back plumage of all species is essentially cryptic, but the sexes are usually strikingly dimorphic, either in size (males much bigger) or in (breeding) plumage (males more boldly marked, chiefly on head, neck and belly). Certain species have ornamental plumes (crests, moustachial bristles, ruffs, etc.), exaggerated or exposed in display; often also swollen subcutaneous tissue in the neck, and inflatable gular sacs or distensible oesophagi in the larger species. Females and young remain cryptic in both colour and behaviour. Bustards lack a uropygial gland, but have dense, friable powder-down, tinged pink in the absence of light; they frequently dust themselves but never bathe in water.

Habitat. They are typically birds of warm, dry, open landscapes, occupying habitats that range from semi-desert (1–3 species) through arid scrub, rolling grassland and savanna (most species) to quite dense bush with scattered clearings (2–3 species). Despite the use of farmland by some Palearctic species (though more readily outside the breeding season), birds are sensitive to disturbance and deterioration of habitat, and generally disappear in the face of expanding agriculture.

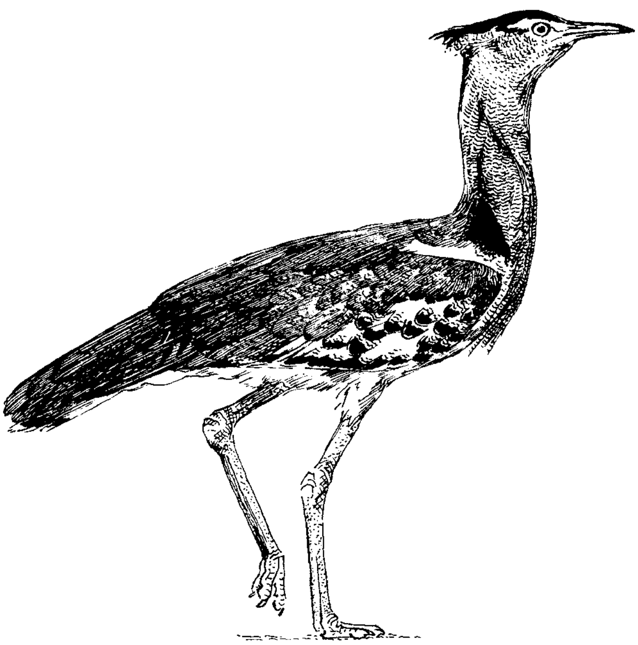
Distribution. The family belongs principally to the Afrotropical Region, within which there are 2 main areas of speciation: southern Africa below the Zambesi, and eastern Africa in the triangle formed by the Horn and the Nile above Lake Victoria. In the former area there occur exclusively the Blue Korhaan *Eupodotis caerulescens*, Karroo Korhaan *E. vigorsi*, Rüppell's Korhaan *E. rueppellii*, Black Korhaan *E. (Afrotis) afra*, and Ludwig's Bustard *Neotis ludwigi*; in the latter, Little Brown Bustard *E. humilis*, Hartlaub's Bustard *E. (Lissotis) hartlaubi* and Heuglin's Bustard *N. heuglini*. The Kori Bustard *Ardeotis kori* occurs in both, but nowhere else; the Red-crested Bustard *E. (Lophotis) ruficrista* (here including '*E. savilei*' and '*E. gindiana*') occurs in both, with a third population straggling across the Sahel; the White-bellied Bustard *E. senegalensis* (here including '*E. cafra*') has a distribution similar to *E. ruficrista* but with a fourth, scattered population in central Africa. Two species, the Black-bellied Bustard *E. (Lissotis) melanogaster* and Denham's Bustard *N. denhami* (here including '*N. cafra*' and '*N. burchelli*') are widely distributed across the Afrotropical Region, and 2 more, the Arabian Bustard *A. arabs* and Nubian Bustard *N. nuba*, are largely restricted to the Sahel region alone, although the former also has small populations in the south of the Arabian peninsula and (possibly still) in north-west Africa.

Not counting this small overlap by *A. arabs*, the Palearctic and Oriental regions hold 3 species each, Australasia one. The Great Bustard *Otis tarda* has a highly fragmented distribution extending from Portugal to Manchuria; that of the Little Bustard *Tetrax tetrax* is largely similar, but stops west of the Tien Shan range. The Houbara *Chlamydotis undulata* occurs sparingly throughout the arid zones of the region (Canary Islands, North Africa, the Middle East, and the cold deserts of the USSR). The Bengal Florican *Houbaropsis bengalensis* is confined to the extreme north-east of the Indian subcontinent, also Cambodia; the Lesser Florican *Sypheotides indica* is very thinly distributed across India into Nepal; and the Great Indian Bustard *A. nigriceps* is now largely confined to western India. Its closest relative, the Australian Bustard *A. australis*, occurs in the remoter parts of Australia, and also southern New Guinea.

Populations. All bustards are long-lived with slow reproductive rates, and therefore cannot rapidly recolonize landscapes from which they have been exterminated. Most Afrotropical species probably maintain their populations, but those with restricted ranges may be at risk; *A. kori* has declined sharply in southern Africa. All non-Afrotropical species are subject to serious and chronic depletion. The most endangered is probably *A. nigriceps*, with reputedly far fewer than 1,000 birds remaining; the floricans, which are now reduced to tiny pockets of habitat; and *T. tetrax* is dying out in all parts of its range save Iberia. In many of the countries where it occurs *O. tarda* is also on the brink of extinction: its long-term survival depends on the conservation policies of a handful of nations. This may also ultimately be true of *C. undulata*, which in recent years has been massively persecuted by hunters throughout its range. Reckless shooting, habitat destruction and introduced animals are blamed for the disappearance of *A. australis* from areas where it was once abundant.

Movements. Most Palearctic populations are at least locally migratory (but highly site-faithful as breeders), with the most pronounced and regular movements occurring in (to and from) the USSR. The Oriental and Australasian species are resident or seasonally nomadic, though *S. indica* may also undertake regular local migrations. Some Afrotropical species show fairly distinct but vaguely understood seasonal movements, notably for example *A. arabs* and *N. denhami* in West Africa, but patterns possibly vary not only between years and species but between localities and geographical regions as well as within species.

Food. Bustards feed opportunistically on a wide range of food items, varying with the season and local conditions. Vegetable food includes green shoots, leaves, flower-heads, seeds, pods, berries and, for Afrotropical species, *Acacia* gum. The chief animal prey is insects (Orthoptera, Coleoptera, mantids, termites, larvae, etc.) but also (e.g.) molluscs,



Kori Bustard *Ardeotis kori*. (*C.J.F.C.*).

arachnids and myriapods. Vertebrate prey consists of small reptiles, frogs, small mammals and the eggs and nestlings of ground-nesting birds. Bustards forage in a cautious, attentive walk through the vegetation, with frequent pauses not only to seek or take food items but to lift head to observe surrounding landscape; the bill is also used to probe and dig for food. Drinking occurs occasionally, but generally appears unnecessary.

Behaviour. Where persecuted, bustards can be wary and retiring; where not, they are often easily approached, especially on horseback or in a vehicle. Many species are gregarious, some even while breeding. The mating systems are barely studied, but probably often complex. *A. nigriceps* is considered polygynous, one male consorting with 3–5 hens; congeners seem likely to behave similarly. In *O. tarda* a non-territorial lek system seems to prevail, in which an elite of males establishes the right to display freely and copulate promiscuously with any females within the general lek area. Males of both floricans, who advertise their presence by leaping several metres into the air, calling, and parachuting down, appear to be promiscuous; this is probably also true of the 3 savanna-dwelling korhaans in southern Africa (*E. ruficrista*, *E. melanogaster* and *E. afra*), which like the floricans all have extensive black on their underparts, give spectacular aerial displays, and live solitarily; by contrast, the open-country species (*E. vigorsi*, *E. rueppellii*, *E. caerulescens* and *E. senegalensis*) lack black underparts and aerial displays, live gregariously, and appear to breed in group territories. The terrestrial self-advertising displays of the larger species are striking and unusual: *Ardeotis* and *Otis* both cock their tails forward and inflate highly distensible gular sacs, the latter also contorting its wings to make huge white rosettes; *Chlamydotis* puffs its long white ruff over its head, and struts in circles and long runs as if decapitated. In these 3 genera, copulations appear to involve lengthy and complex preceding rituals.

Voice. *Otis* and *Chlamydotis* are largely silent at all times, but *Ardeotis* species may emit deep booming sounds during display. Males of *T. tetrax* have a short rasping snort in the breeding season, and their wings produce a powerful sibilance. The floricans and small Afrotropical species have penetrating, repetitive calls consisting of froglike croaks, belches, clicks, whistles, etc.

Breeding. Breeding seasons (sometimes governed by rains) may be relatively protracted, except in *O. tarda* and *T. tetrax*. The female scrapes a shallow depression on bare ground, and (in most if not all species) assumes sole responsibility for incubation and care of the young. The smooth, subelliptical, usually dull-coloured but (in some species) glossy eggs number 2–6 in Palearctic species and *S. indica*, 1–2 in the others; incubation generally lasts 3–4 weeks. The young are precocial and nidifugous, and fed initially bill-to-bill; they fledge at *c.* 5 weeks. Sexual bimaturism probably occurs in all species that are sexually dimorphic in size. N.J.C.

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BUSTARD-QUAIL: synonymous with BUTTONQUAIL.

BUTCHER-BIRD (1): popular name in Britain and North America for *Lanius* spp. (see SHRIKE). The name relates to the habit of forming a 'larder' of the prey.

BUTCHER-BIRD (2): substantive name of members of the genus *Cracticus* of the Cracticidae (Passeriformes, suborder Oscines).

Characteristics. The 6 (sometimes 7) species, ranging from 20–40 cm in length, are smaller than the other members of the family. All are rather large song-birds, with stocky bodies and large heads supporting a heavy bill, hooked at the tip. Their plumage is sombre, black, grey and white with a tendency for browns to occur in the plumage of juveniles; a recognizable brown variant *rufescens* of the Black Butcher-bird *Cracticus quoyi* occurs in Queensland.

Habitat. Butcher-birds are most widespread in woodlands, but some of the tropical species also live in rain-forest and mangrove fringes. The 2 southern forms, the Pied *C. nigrogularis* and the Grey *C. torquatus*, adapt well to farmland clearing and are common around Australian homesteads. They do less well in urban areas.

Distribution. The genus is confined to Australia and New Guinea. In most of Australia the Pied Butcher-bird occupies the inland and the Grey, including the race *argenteus* (Ford 1979), the wetter coastal areas, with substantial overlap of range. Clearing has favoured the spread of the Pied towards the coast. Two species, the Black-headed *C. cassicus* and the White-rumped *C. louisiadensis*, are confined to New Guinea. Two mangrove/rain-forest species, the Black and the Black-backed *C. mentalis* occur in both Australia and New Guinea.

Populations. Little is known about the density of the northern species. The Grey Butcher-bird in Western Australia holds a breeding territory of 30–40 ha but the density may be greater in eastern Australia.

Movements. There is no evidence of movement by any butcher-bird.

Food. Butcher-birds feed on large insects, crustacea, reptiles, small mammals and young birds. They are not related to the true shrikes (Laniidae) but have the shrike-like habit of impaling prey on thorns or wedging it in tree forks. The birds seek food by perching a few metres above the ground and pouncing on small animals when they see them.

Behaviour. In some species the breeding group contains more than 2 birds but detailed studies are lacking. At many nests a simple pair is found. The nests of the Black Butcher-bird are often close to those of the Trumpet Manucode *Manucodia keraudrenii*. Apparently the manucode chooses this arrangement and may gain protection from the aggressive nature of the butcher-bird.

Voice. All butcher-birds have loud songs, with which they proclaim the possession of their territory throughout the year. The song of the Pied Butcher-bird contains many almost pure tones, and is considered by Australians to be one of the most beautiful in the country. The only blemish on this reputation is that singing begins at dawn and the species is often known as the 'Bushman's Clock'.

Breeding. Butcher-birds build large cup-shaped nests of sticks lined with grass in tree forks up to 15 m or higher. Clutches range in size from 2–5 eggs, the southern species laying slightly larger clutches than the northern ones. The incubation period is 20–23 days and the nestling period 28-31 days. Breeding butcher-birds are very pugnacious and sometimes attack humans. S.J.J.F.D.

Ford, J. 1979. A new subspecies of Grey Butcherbird from the Kimberley, Western Australia. Emu 79: 191–194.

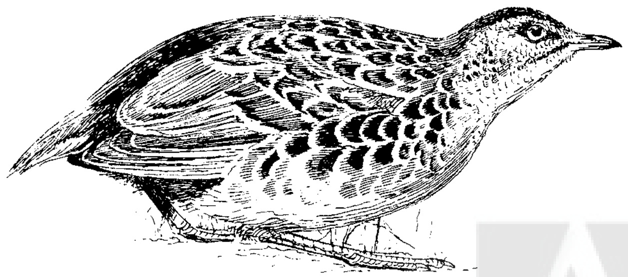
BUTEO: sometimes used in North America as a vernacular term for *Buteo* spp., there included under the general term 'hawk' although in Britain called 'buzzards' (see HAWK).

BUTEONINAE: subfamily, used by some authors for the larger members (buzzards and eagles) of the family Accipitridae (see ACCIPITRIFORMES; HAWK).

BUTT: an earthwork—usually one of a series in line—erected for the concealment of persons waiting to shoot driven birds, notably Red Grouse *Lagopus lagopus scoticus*.

BUTTERBALL: a name applied in North America both to the Bufflehead *Bucephala albeola* and to the Ruddy Duck *Oxyura jamaicensis* (see DUCK).

BUTTERFLY FLIGHT: a slow flapping flight used in aerial display by many birds.



Little Buttonquail *Turnix sylvatica*. (*C.J.F.C.*).

BUTTONQUAIL: substantive name, alternatively 'hemipode', of species of Turnicidae (Gruiformes, suborder Turnices); often used without qualification for the sole European species; in the plural (alternatively 'hemipodes'), general term for the family. The latter and the Australian monotypic family Pedionomidae (see PLAINS-WANDERER) together form the suborder. This small Old World group of only some 15 species is also considered to be allied to the sandgrouse and the pigeons.

Characteristics, habitat and distribution. The buttonquails or hemipodes are terrestrial grassland birds inhabiting mainly the tropics and subtropics, and remarkably resembling true quails *Coturnix* spp. (Phasianidae) in general appearance, plumage pattern, habitat preference, and mode of life. They are 11–18 cm in length. The family is characterized by having only 3 toes on the foot, a hind toe being absent. In flight the wings appear much rounded and the short tail is barely visible. The bill is like that of a quail but generally rather small and slender. A crop is missing. The oil gland is feathered; the feathers have an aftershaft.

Buttonquails live very secretively in arid or marshy grass and brush country, savannas, and more open woodland. When disturbed, they prefer to run for cover, but, if forced to take wing, they fly straight and fast, with whirring wings for 150 m or more before dropping back to the ground and disappearing into cover.

The typical genus of the family includes 13 species, 6 of which inhabit the Australasian Region. The other *Turnix* species are found in Africa, Madagascar, and the warmer countries of Asia, only one extending to Europe (in its extreme south-western part). This widely distributed (mainly Indo-African) Buttonquail (also called Striped or Little Buttonquail or Andalusian Hemipode) *Turnix sylvatica* is a bird with greyish-rufous, variably blotched and streaked upper parts, and pale below except for the rufous breast flanked with dark spots; its Philippine race is the smallest representative of the genus. In this species the sexual dimorphism in coloration is much less conspicuous than in the Barred (or Common) Bustard-quail *T. suscitator* of India and eastern Asia, in which the female acquires a black throat and chest in nuptial plumage. Many females of this species are trapped by the use of female decoy birds and then kept to be pitted against each other.

Several species have similar black markings below, e.g. the Madagascar Buttonquail *T. nigricollis* and the Black-breasted Buttonquail *T. melanogaster*, a very rare bird of the rain-forest scrubs of Queensland. One of the finest and largest species is the brightly coloured Ocellated (or Spotted) Buttonquail *T. ocellata* of Luzon (Philippines). In the Yellow-legged (or Indian) Buttonquail *T. tanki* the hen is distinguished by a broad orange-rufous nuchal collar; it has a breeding distribution from India to Manchuria and is migratory in the northern part of its range. The similar Spotted (or Red-backed) Buttonquail *T. maculosa*, ranging from Australia, New Guinea, and Melanesia to the Lesser Sunda Islands and Mindanao, seems to be its eastern counterpart. Some of the smaller Australian species are remarkable for their stout bill, e.g. the Redchested Buttonquail *T. pyrrhothorax*, which, like *T. maculosa*, has spread northwards, leaving two small island populations on Sumba and Luzon.

The second, and quite different, genus is monotypic. The little Lark-quail (often misnamed Quail-plover) *Ortyxelos meiffrenii* inhabits very dry sandy scrub country in the tropical grassland belt from Senegal to East Africa. It has sandy-rufous upper parts, rather long black and white wings, and strong jerky flight; it resembles a tiny courser *Cursorius* on the ground and a bushlark *Mirafra* on the wing.

Movements. According to local climatic conditions, buttonquails are sedentary, nomadic or migratory.

Food. The food consists of small invertebrates (termites, ants and other insects, spiders, snails), grass-seeds, grain and green shoots. The birds pick off items from the surface of the ground as well as scratching with feet alternately. Water is taken with a 'bibbling' action of the mandibles, similar to sandgrouse, without raising the head at each mouthful as do most birds.

Behaviour. Little information is available in regard to behavioural characters, but dusting and sunning are recorded regularly in captivity. Buttonquails are usually seen singly, in pairs or in small family parties, but some species tend to keep together in coveys of 15–30 birds.

The female is larger and more brightly coloured than the male, is extremely pugnacious against rivals of the same sex, and takes the leading part in courtship.

Voice. In the breeding season the female utters a loud drumming or booming call, only the hen being provided with a specialized vocal organ—an inflatable bulb of the oesophagus and an enlargement of the trachea.

Breeding. The nest is placed on the ground in a shallow depression scratched among grass, in a tussock, or beneath the shelter of a low bush or herbage. It is built of dry grasses and dead leaves, and varies from a more or less well-made cup to a substantial domed structure with a side entrance, sometimes with a short covered runway leading to it. In some species both sexes bring material, which they jerk in plover-like manner over their shoulders towards the nesting place, and work in turn from inside. The eggs are commonly 4 in number (in *Ortyxelos* only 2), short ovate to pyriform, rather glossy, pale greyish to buffish in ground colour and profusely freckled, dotted, and blotched with chestnut, dark brown, slaty-grey, or other shades. In captivity some females lay each day until a clutch is completed and then can start a new clutch within a couple of days. The male performs the duties of incubation and later of rearing the young, although the female may occasionally assist during a few days after laying. The behaviour of birds breeding in captivity and evidence from field observations strongly suggest that the hen lays several sets of eggs to be attended by different males.

Besides these and other peculiarities in the breeding behaviour, the buttonquails show a rather special kind of nidifugous development. Their incubation period of only 12–13 days is by far the shortest among birds with young hatching in a similarly advanced state, and even ranks near the lower limit known in the nidicolous group. The downy chicks leave the nest soon after hatching, are very agile and follow the male parent, by whom they are brooded and fed, the food being presented in the tip of the bill. When being hand reared, chicks must be hand fed for at least 7–10 days even though they begin feeding on their own on the second or third day. Presumably the male feeds the chicks for the same period of time. They begin to flutter when about 1 week old, and after another week they can fly and look after themselves, although the family keeps together for 1 or 2 more weeks, and finally at the age of 6–7 weeks they attain the size and weight of adults.

During this short growing period, characterized by a steady gain in weight, two moults are accomplished. At the end of the second week most of the natal down is replaced by juvenile feathers, and at the same time, when the bird is scarcely half-grown, a complete moult of the juvenile plumage begins. This is completed at the age of about 10 weeks, and results either in the adult postnuptial plumage or directly in the nuptial one. In the rapid succession of plumages and in many other features the buttonquails present a remarkable convergence towards the gallinaceous type of development, which implies a very early ability to fly. They differ, however, in that the adaptation of the growing wing to continuous use is attained in a less specialized manner; all the juvenile quills grow out nearly together, the only important modification being that the inner primaries are considerably reduced in size, particularly the innermost one, which remains almost vestigial. This primary is the first to be shed, the process taking place before the outer juvenile quills are fully grown. Sexual maturity too is reached early, at least in birds reared in confinement; these may begin to lay in the third to fifth month of life. The breeding season is prolonged and some species nest opportunistically in all months. These birds seem to be very short lived. Captive records of several species would indicate normal life span of only 2 to 3 years.

(E.S.) D.B.

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Trollope, J. 1970. Behaviour notes on the Barred and Andalusian Hemipodes *Turnix suscitator* and *Turnix sylvatica*. Avicult. Mag. 76: 219–227.

BUZZARD: substantive name of *Buteo* spp. (Accipitrinae); also used, in combination, for the honey-buzzards *Pernis* spp. (Perninae)—for both these subfamilies of the Accipitridae see HAWK. In America, where true buzzards are named 'hawks' (which they of course are), 'buzzard' is a popular misnomer for members of the Cathartidae (see VULTURE (2)), and is sometimes also applied to the Caracara *Caracara cheriway* (see under FALCON).

C

CACATUINAE: see PARROT.

CACHALOTE: substantive name of *Pseudoseisura* spp. (see OVENBIRD (1)).

CACIQUE: substantive name of species in 4 tropical genera (*Cacicus*, etc.) of the Icteridae (see ORIOLE (2)).

CADGE: term used in FALCONRY.

CAECUM: a blind tube branching from the junction of the small intestine and large intestine, usually paired ('caeca') but in some taxonomic groups single or absent (see ALIMENTARY SYSTEM).

CAGE BIRD: term applied to a variety of smaller birds (mostly psittacine and passerine) commonly kept in captivity, especially those which are totally domesticated, such as the Budgerigar and the Canary. The Budgerigar *Melopsittacus undulatus*, first brought alive from its native Australia by John Gould in 1840, has become the most popular of all pet birds, on account of its friendly and affectionate personality, bright colours and ability to mimic the human voice. An immense variety of colour mutations has been established.

A close second in popularity is the Canary *Serinus canaria*, from the Azores, Madeira and Canary Islands. First imported into Europe during the 16th century, it now exists in a diversity of varieties, colours and plumage patterns. In the UK the most popular breeds are the Border, Gloster, Norwich and Yorkshire Canaries (bred for their 'type') and the Roller which is bred solely for its exquisite song. Hybrids between the Canary and British finches such as the Goldfinch *Carduelis carduelis* and the Greenfinch *C. chloris*, are known as mules and are bred for song and exhibition.

Two small finches which are totally domesticated are the Bengalese, whose origin lies with one of the mannikins *Lonchura striata*, and the Zebra Finch *Poephila guttata* from Australia. Both these birds, which are bred in a variety of colour mutations, are ESTRILDID FINCHES (Estrildidae) while the Canary is one of the true finches (Fringillidae).

Another Australian species, more recently domesticated, is the Cockatiel *Nymphicus hollandicus*. Increasingly popular as a cage pet in the UK, this little cockatoo has long been cherished in the USA. A handsome long-tailed bird, it is grey with striking orange cheeks. It is being bred in a variety of mutations, such as White (Lutino), Pied and Pearl. It breeds freely in cage or aviary and young birds make affectionate pets, quickly becoming tame and learning to mimic.

In the 19th and early 20th centuries many British species were kept as cage birds, especially for their song. Legislation has now restricted the species which can be kept in captivity, and these are all aviary-bred (and closed-ringed, as proof of captive breeding). Mainly finches are kept (e.g. Goldfinch, Greenfinch and Bullfinch *Pyrrhula pyrrhula*) and these have been bred in captivity for a number of generations. A few mutations have been established, such as the Lutino Greenfinch.

There are several hundred cage bird societies in the UK, all of which stage at least 2 shows a year, the main show season being from October until December. The majority of exhibits are Budgerigars and Canaries, Zebra and Bengalese Finches and the species of British birds permitted under the Wildlife and Countryside Act (mainly finches); exotic birds, including parrots, are also exhibited. The majority of members of cage bird societies keep domesticated species but keepers of exotic birds are also catered for. In the USA the situation is different; societies are less local and more specialized, generally catering for breeders of budgerigars, canaries, parrots or finches rather than for the whole range of cage birds. See also AVICULTURE. R.L.

CAHOW: name for a species of petrel *Pterodroma cahow* breeding in small numbers on Bermuda, where it was rediscovered in recent years after having been thought to have become extinct (see PETREL).

CAIN AND ABEL SYNDROME: 'Cain and Abel' strife describes the sibling aggression frequently found in broods of owls and raptors, herons and various seabirds. The aggression is associated with food shortage and often results in a smaller sibling being killed and in some cases eaten (see CRONISM) by older chicks (see BROOD REDUCTION).

CAIQUE: substantive name of the Neotropical *Pionites* spp. (Arini) see PARROT.

CAIRININI: see DUCK.

CALAMUS: the hollow proximal portion of the shaft of a feather, below the vane (see FEATHER).

CALCIUM METABOLISM: see ENERGETICS; METABOLISM; NUTRITION.

CALFBIRD: one name for *Perissocephalus tricolor* (also 'Capuchinbird')—for family see COTINGA.

CALIDRITINAE: see SANDPIPER.

CALLAEIDAE: a family of the PASSERIFORMES, suborder Oscines; WATTLEBIRD (2). The editors of the *Check-list of Birds of the World*, vol. 15, have deliberately retained this traditional spelling, although a purist would prefer 'Callaeatidae', or possibly 'Callaeadidae'.

CALL-NOTE: see VOCALIZATION.

CALYPTOMENINAE: see BROADBILL.

CALYPTURA: substantive name now commonly used for *Calyptura cristata*, the smallest (and probably the rarest) of the COTINGAS, known only from a restricted area in south-eastern Brazil.

CAMAROPTERA: substantive name used for some members of the African warbler genus *Camaroptera* (see WARBLER (1)).

CAMOUFLAGE: see COLORATION, ADAPTIVE.

CAMPEPHAGIDAE: a family of the PASSERIFORMES, suborder Oscines; CUCKOO-SHRIKE.

CAMPO: term used in South America for a habitat consisting of grassy plains with scattered bushes and low trees.

CANARY: *Serinus canaria* (see AVICULTURE; CAGE BIRD; FINCH; VOCALIZATION).

CANASTERO: substantive name now regularly used for the species of the furnariid genus *Asthenes*, small birds with long, pointed and markedly graduated tail-feathers (see OVENBIRD (1)).

CANCELLATE: marked with cross lines, as on the webs between the toes of some water birds (see LEG).

CANNON-NETS: see TRAPPING.

CANOPY: the branching parts of trees, forming the tree layer in woodland. Where the canopy is continuous, the trees being close together, it is said to be 'closed', while an 'open' canopy is found where the trees do not touch each other.

CANOPY FEEDING: term used to describe hunting method of the Black Heron *Egretta ardesiaca* in which the wings are held forward over the head (see HERON). Also used to describe feeding in the canopy or upper layer or a forest, usually by itinerant parties of birds.

CANVASBACK: *Aythya valisineria*, a North American species of pochard (see DUCK).

CAP: an area of distinctive colour, in some plumage patterns, covering part of the top of the head, and sometimes down to the nape (see TOPOGRAPHY).

CAPERCAILLIE: name (of Gaelic origin, and sometimes spelt 'capercailzie') of *Tetrao urogallus*, and can be applied also to *T. parvirostris* (see GROUSE).

CAPITONIDAE: see under PICIFORMES; BARBET.

CAPITONOIDEA: see under PICIFORMES.

CAPON: a castrated domestic fowl.

CAPRIMULGI; CAPRIMULGIDAE: see below.

CAPRIMULGIFORMES: an order, alternatively 'Caprimulgi', comprising 2 suborders: Steatornithes and Caprimulgi, and 5 families: Steatornithidae (OILBIRD), Podargidae (FROGMOUTH), Aegothelidae (OWLET-FROGMOUTH), Nyctibiidae (POTOO), Caprimulgidae (NIGHTJAR). The nightjars are known in America as 'night-hawks' and 'goatsuckers'. The owlet-frogmouths are sometimes called 'owlet-nightjars', and the potoos 'tree-nightjars'. They are all cryptically plumaged and nocturnal.

CAPUCHINBIRD: one name for *Perissocephalus tricolor* (also 'Calfbird')—for family see COTINGA.

CARACARA: substantive name of most species of Daptriinae; used without qualification, in the USA, for *Caracara plancus*; in the plural, general term for the subfamily (see FALCON).

CARBOHYDRATE METABOLISM: see ENERGETICS; METABOLISM; NUTRITION.

CARDINAL: substantive name best restricted to *Cardinalis cardinalis* Northern Cardinal, and *Cardinalis phoeniceus* Vermilion Cardinal; used without qualification in the USA for the former species (also known locally as 'Cardinal Redbird', etc) (see CARDINAL-GROSBEAK). The name is misapplied to some other reddish birds, e.g. certain South American tanagers (Thraupinae); and it is used in the Old World for *Foudia madagascariensis* (for family see WEAVER).

The Northern Cardinal *Cardinalis cardinalis* occurs naturally from parts of temperate North America south into Middle America and on certain adjacent islands; it has been introduced successfully into the Bermudas and south-western California—also Hawaii, where it breeds all the year round and has become a pest to fruit-growers. It is about 15–20 cm long, varying somewhat geographically, and weighs 35–50 g. The bill is large and stout, nearly conical. Males are mainly some variant of conspicuous scarlet-orange to deep scarlet. Females have more muted coloration, the reds being mixed with browns and buff. Numerous subspecies have been named, mainly on the basis of geographical variation in depth of coloration.

Habitat. Woodland edges and gardens with a mixture of clearings and young trees, bushes or vines.

Movements. It is usually sedentary, but some individuals are highly migratory.

Food. Like the subfamily, it is mainly vegetarian, feeding on seeds and berries, but some insects are taken seasonally.

Voice. The song, which may be heard throughout the year, is a series of melodious frequently repeated whistles, varying in pitch. The female has also a song, which is a subdued version of that of the male.

Behaviour. The male Cardinal elongates his body in courtship song and may slip sideways along a branch until he reaches the female, the performance ending in copulation.

Breeding. Nest sites vary from on the ground to high in a tree, but are typically about 1–5 m from the ground. The nest is in a shady situation such as within a young evergreen, a hedge, or a tangle of vines. It varies from flimsy to compact, and is quite large for the size of the bird. There are usually 3 eggs, very pale blue, finely spotted with browns and lavender. Only the female incubates (12–13 days) and broods; the male feeds her, usually away from the nest. The young leave the nest in 9–10 days, and for some time thereafter the male tends and feeds them while the female may begin building a new nest. The pair-bond is maintained for successive broods through the season and, in some known instances, has persisted for as long as 3 years. R.S.P.

For references see CARDINAL-GROSBEAK.

CARDINAL-GROSBEAK: in the plural, general term for the subfamily Cardinalinae (Emberizidae; Passeriformes, suborder Oscines). The subfamily was known formerly as 'Richmondeninae' and 'Pyrrhuloxiinae'. There is still some doubt about the position of some genera within it and difference of opinion about generic limits, but a tentative list of those that should be included is: *Spiza* (1 species), *Pheucticus* (4, including '*Hedymeles*'), *Cardinalis* (3, formerly *Pyrrhuloxia*), *Caryothraustes* (2), *Rhodothraupis* (1), *Periporphyrus* (1), *Pitylus* (1), *Saltator* (12), *Guiraca* (5, sometimes included in next genus), *Passerina* (7). In English terminology, the commonest substantive name is 'grosbeak', but others are 'cardinal' (see above), 'bunting', 'saltator' and 'dickcissel'. See also GROSBEAK; FINCH; and for American usage, see BUNTING.

Cardinalinae are thick-billed 'seed-crunchers'; they differ in structure of palate, tongue and jaw musculature from the more slender-billed Emberizinae, which are 'seed-peelers' (Ziswiler 1965). The Dickcissel *Spiza americana* takes an intermediate position between this group and the American 'sparrows' (Emberizinae) and icterids (Icteridae). Typically cardinal-grosbeaks are 'buntings' of medium to large size (lengths 15–20 cm); and the males are usually brightly coloured. The group is confined to the New World and is predominantly tropical in distribution—but with 5 genera represented among birds breeding north of the Mexican border. Apart from the Cardinal (see above) the North American members of the subfamily include the Dickcissel (the male a brownish bird with yellow breast and black bib), the Rose-breasted Grosbeak *Pheucticus ludovicianus* (the male mainly black and white, apart from the rosy-red breast patch), the Blue Grosbeak *Guiraca caerulea* (the male dark blue all over, except for tan wing-bars), the Indigo Bunting *Passerina cyanea* (the male all blue) and the Painted Bunting *Passerina ciris* described as 'the most gaudily coloured American bird'; the male has red underparts and rump, green on the back, and blue on the head and wings; the female is green above and yellowish-green below. The remaining genera are represented only in the Neotropical Region, but—except for *Periporphyrus*—as far north as Middle America and the West Indies (Streaked Saltator *Saltator albicollis* on some of the Lesser Antilles). R.S.P.

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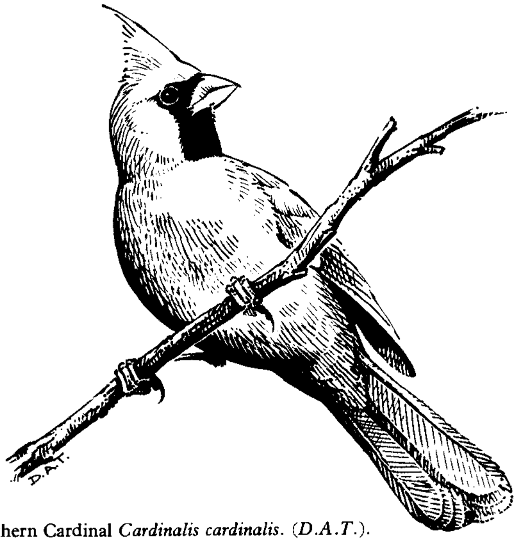

Northern Cardinal *Cardinalis cardinalis*. (*D.A.T.*).

CARDINALINAE: see CARDINAL-GROSBEAK; EMBERIZIDAE; FINCH.

CARDIOVASCULAR SYSTEM: see BLOOD; HEART; VASCULAR SYSTEM.

CARDUELINAE: see FRINGILLIDAE; FINCH.

CARE OF SICK, INJURED OR ORPHANED BIRDS: wild birds are frequently found in need of care as a result of accidental damage caused typically by collision with road vehicles, flying into overhead power cables or uncovered surfaces of glass, or after attack by cats or other predators. Less often they are discovered in poor condition through sickness. Seasonally, orphaned young, which have lost one or both parents, must either be fostered or allowed to die. For the special problem caused by oil at sea, see OIL-POLLUTION.

Sickness. (See DISEASE; ECTOPARASITE; ENDOPARASITE) Reasons for sickness can be varied and include bacterial and fungal infection, infestation by parasites, poisoning and nutritional diseases. Many drugs are available for treatment; the majority, however, are specific and early diagnosis of the cause of illness by a veterinary surgeon is therefore essential. Broad spectrum antibiotics (such as terramycin) will control most harmful bacteria and can be used as a precautionary treatment. As a counter to dehydration, initial fluid replacement can be effected by administering a glucose/saline solution orally, or by subcutaneous injection, at about 4% body weight twice during the first 12 hours.

Most importantly, the bird should be placed in a clean cardboard box (roughly 3–4 times its length) and made comfortable if necessary in a 'nest' of replaceable soft tissue. The top of the box should be covered with lightweight cotton material (or similar), secured around the top with clothes pegs and placed somewhere uniformly warm, so that the interior temperature attains about 25–30°C. If suitable food and water is within easy reach, the bird will feel secure and the relatively high body temperature of about 41°C will be more easily maintained.

Force feeding will often be necessary in the early stages of confinement and can either take the form of small, easily digested meals at regular intervals until an improvement in the condition occurs or, in cases where difficulty in accepting solid food is experienced, liquid, or liquidized solids, can be gently pumped directly into the crop using a soft polyvinyl chloride or rubber tube connected to a suitable syringe. Care must be taken to avoid the glottis (the opening to the trachea at the base of the tongue) and a suitable lubricant, such as liquid paraffin, will ease the passage of the tube into the oesophagus.

Jackdaw *Corvus monedula* with anchor strap in place and wing 'splint' about to be applied to immobilize broken left wing. (*Photo: I. Buchanan*).

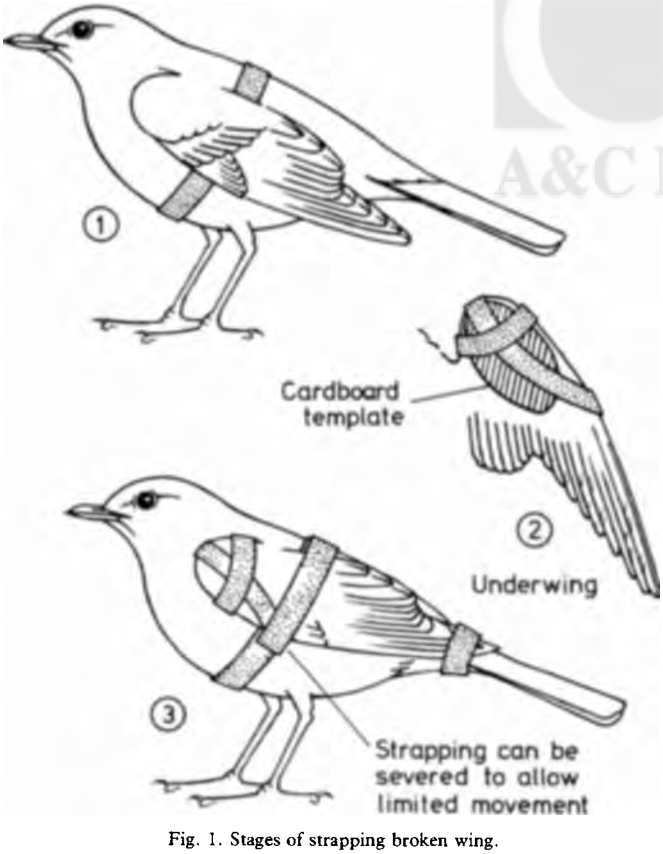

Fig. 1. Stages of strapping broken wing.

Regular removal of soiled material from beneath birds which are unable to stand is essential and their legs, feet and anal region must be bathed as required.

The presence of ectoparasites, many of which are very sensitive to temperature change, may be more obvious on sick birds and, in fact, numbers of lice may increase. Insecticides should be applied cautiously but pyrethrum, derived from the natural plant, is usually quite safe.

Injury. Most serious injury involves structural damage to wings and legs, and only experience will determine when treatment will be effective. Generally, however, simple fractures on small and medium-sized birds can be successfully repaired by immobilizing the damaged member in its correct position for 2–3 weeks whilst natural healing occurs. Personal experience has led to a system of treating wing damage which allows total, or partial, immobility in stages. This is obtained by first placing a strip of adhesive tape 1 cm wide completely around the body of the bird, in front of the thighs and behind the shoulder joints: this to be used as a basis for further attachment. Next, using the undamaged wing as a pattern, a stiff, cardboard template, cut to the shape of the forward part of the wing, is made. Small quantities of cotton wool padding attached to the card with adhesive tape will allow the true contours of the damaged wing to be followed accurately and this can then be fixed in position. Finally, a further strapping across the face of the wing and another securing the wing tips to the base of the tail will complete the operation (see Fig. 1). After 2 weeks, the outer strapping can be cut through below the wing to allow limited movement from the shoulder for a few days before total removal.

To limit unnecessary movement and to facilitate healing, a cardboard box of suitable size can be used for housing the patient as described above, and low perches, from which the bird can easily jump, will enable it to keep clean. Fresh water and food should be supplied in small, heavy, earthenware or similar dishes. Broken legs can be splinted in a variety of ways. For birds of Starling *Sturnus* size (20–25 cm) and above, a plaster of Paris cast can be formed, using specially prepared bandages, moistened and formed to the contours of the leg; these rapidly dry to form a rigid cast. Care must be taken not to apply more than necessary or the limb will become very cumbersome. Splints made from plastic tube, split longitudinally, or carefully rolled cylinders of light cardboard, suitably padded and attached with adhesive tape, are usually very effective alternatives. More complicated fractures can be dealt with successfully but involve the special expertise of a qualified veterinary surgeon.

Orphaned young. Genuinely orphaned young birds (as opposed to those regularly 'rescued' just after leaving the nest when they appear naive and helpless) require regular attention, and both adequate food and suitable accommodation are important. Three distinct phases should be considered: the period which would naturally be spent in the nest (particularly nidicolous species), the subsequent period of learning from the parents (e.g. birds of prey), and the final release to the wild.

Warmth and a feeling of security are of paramount importance, and most small young will readily settle in a nest of soft tissues, covered lightly with a dark, heavy linen cloth as a false brooder. The inevitable cardboard box will add shelter and security. Heat from an overhead lamp or, preferably, controlled bottom heat to maintain 25–30°C will reduce the amount of energy expended in keeping warm. Food should be provided at least hourly, roughly throughout the daylight period, and as a crude guide the following items can be used effectively. Small, insectivorous birds will readily accept tiny snippets of lean, raw beef, supplemented when possible with small mealworms and freshly killed winged insects. For those species which add fruit to an insect diet (e.g. white-eyes *Zosterops*), small pieces of strawberry, banana or other soft fruit should be offered. A mixture of finely crushed, dry brown bread, raw egg yolk, cod liver oil, abidec and grated apple, made to form a moist yet crumbly mixture, offers an invaluable addition to the basic diet for most insectivorous/vegetarian species, covering a range as diverse as Skylarks *Alauda arvensis*, Jackdaws *Corvus monedula*, thrushes *Turdus* and sparrows *Passer*. Where available, pro-nutro, manufactured by Hind Bros in South Africa, mixed to a cream, can be used almost universally for small birds and that or similar products are very useful for the pigeon family Columbidae. Special blends of food can be readily obtained for raising most young birds (Sluis mixtures from Royal Sluis, Holland, are ideal) but short term, in an emergency, a mixture of finely chopped hard boiled egg yolk and lean beef, moistened with glucose solution will feed almost everything.

To encourage young birds to feed themselves, food can be left with them in the box for a few days prior to fledging. If this is offered to them at the regular feed times, making obvious movements when selecting items from the dish, they will soon explore for themselves. In general, it is not necessary to give young birds water, as sufficient moisture will be contained in the food, but many welcome a few spots at feed times and pigeons will regularly drink heartily.

Release. A period spent after 'leaving the nest' in an outside aviary, where natural food can be obtained by the patient, either in competition with or at least in close proximity to similar species, will greatly assist a successful release. Earthworms, beetles, mealworms, soft fruits, seed mixtures, even live fish and naturally occurring insects can all be offered where appropriate so that skills can be acquired. Release is generally best effected in a suitable area where food and cover are available and, where post-breeding flocks aggregate, such areas should be chosen.

Although an emotive subject, euthanasia is sometimes inevitable and can be achieved by administering drugs, always under the control of a veterinary surgeon, but often it is more humane to use immediate, physical means. Small birds, thrown hard against a pavement or wall, will die instantaneously; and for larger birds, a blow at the base of the skull with a suitable length of metal or hard wood will be equally effective. It must be stressed that any such action should only be used to prevent further suffering and must be carried out with conviction: a half-hearted attempt may prolong suffering. C.A.J.C.

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CARIAMAE; CARIAMIDAE: see under GRUIFORMES; SERIEMA.

CARIB: substantive name of *Eulampis jugularis* and *Sericotes holosericeus* (for family see HUMMINGBIRD).

CARINA: see below.

CARINATE: having a keel (carina) on the sternum, the converse of RATITE (see also SKELETON, POST-CRANIAL).

CAROTENOID PIGMENTS: see COLOUR.

CAROTID ARTERIES: the main vessels passing up the neck to the head; the various different arrangements have been used as taxonomic characters (see VASCULAR SYSTEM).

CARPAL: name of small bones of the 'wrist', the carpal joint being the articulation of the manus with the radius and ulna and forming the forward pointing prominence of the folded wing (see SKELETON, POST-CRANIAL; WING).

CARPOMETACARPUS: the main bony structure of the 'hand' in birds, formed by the fusion of carpal and metacarpal elements (see SKELETON, POST-CRANIAL; WING).

CARRYING: transportation of various objects by birds. These are principally: (*a*) items of food for the bird's own consumption at another spot or to give to its mate (during courtship or on the nest) or young (see COURTSHIP FEEDING; FEEDING HABITS; PARENTAL CARE); (*b*) nesting materials (see NEST BUILDING); (*c*) nest refuse, including the shells of hatched eggs and the faeces of the nestlings (see PARENTAL CARE). There are also a few known instances in which birds transport their eggs or young.

Most birds carry objects grasped in the bill. Food is often carried inside the mouth, or farther down the alimentary canal and regurgitated. Only some raptorial birds carry prey or other objects in their talons (and not to the exclusion of use of the bill for lighter weights). Lovebirds *Agapornis* spp. carry nest material among the feathers on the rump. The larger penguins *Aptenodytes* spp. waddle about with the single egg or small chick resting on the tarsi, the position in which it is incubated or brooded. The Black Vulture *Coragyps atratus* sometimes moves its eggs about the laying area. Some aquatic birds habitually carry their young on their backs when swimming, e.g. swans *Cygnus* spp. and grebes (Podicipedidae). A few birds with nidifugous young occasionally transport their young in flight; for example, the Woodcock *Scolopax rusticola* does so, holding the small chick between its legs; other species in which the same behaviour has been recorded include the American Woodcock *S. minor*, the Common Sandpiper *Actitis hypoleucos*, and the White-browed Coucal *Centropus superciliosus* of Africa.

There is also the incidental transportation of, notably, plant pollen and

Swift *Apus apus* carrying food-ball for its young. (*Photo: H. Schouten*).

seeds (see POLLINATORS; SEED DISPERSAL); and the role of vector of parasites and infective organisms (see DISEASE; ECTOPARASITE; ENDOPARASITE; VECTOR). See photo PARENTAL CARE.

CARTILAGE: see SKELETON, POST-CRANIAL.

CARUNCLE: see INTEGUMENTARY STRUCTURES.

CASIORNIS: substantive name now regularly used for the 2 species of tyrant-flycatchers of the genus *Casiornis* (see FLYCATCHER (2)).

CASQUE: an enlargement on the upper surface of the bill, in front of the head, as in most species of hornbills (Bucerotidae)—or on top of the head, as in cassowaries (Casuariidae). Compare HELMET; SHIELD, FRONTAL; and see BILL; HORNBILL.

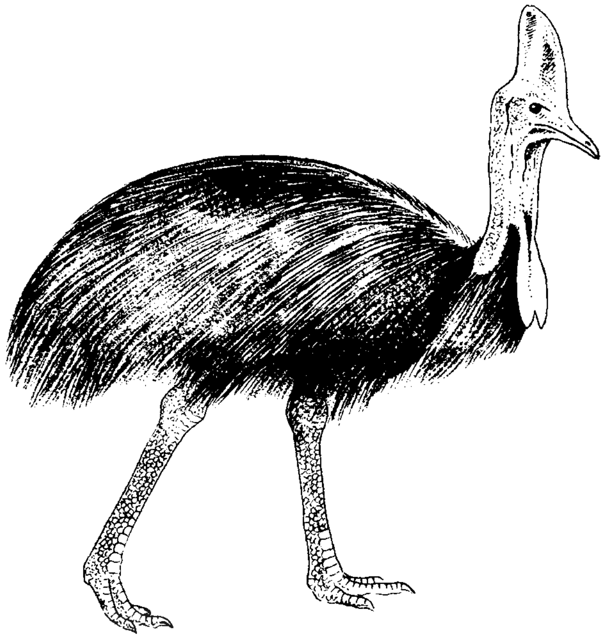
CASSOWARY: substantive name of the 3 species of the Casuariidae (Casuariiformes); in the plural, general term for the family. Cassowaries are large, heavy-bodied 'ratites' whose closest relatives are the emus (Dromaiidae) of Australia, the 2 families together composing the order Casuariiformes (see also EMU; RATITES). A cassowary is known from the Pliocene of Australia (Rich 1976). Three species are clearly recognizable, *Casuarius casuarius*, *C. unappendiculatus* and *C. bennetti*, and numerous subspecies have been described.

Characteristics. Cassowaries have coarse, bristle-like, drooping plumage, black in colour in the adult. The featherless head and neck are surmounted by a pronounced bony helmet, or 'casque', that rises from the top of the skull. Observations have recently been made on captive *casuarius* by P.J. Curry showing that the bird uses its casque as a shovel, turning over loose sand and debris. The casque's use in this way for finding fallen fruit and other food items in the litter on the forest floor seems a more plausible interpretation of its function than the traditional view that it is used to force a path through the dense forest. A conspicuous feature is the presence of wattles of coloured flesh hanging from the bare, or partly bare, neck; but they are lacking in the smallest species *bennetti*. The bill is short, strong, and laterally compressed. In the very reduced wings the remiges are reduced to bare shafts; the tail lacks characteristic rectrices. The legs are stout and powerful, the innermost of the 3 toes (numbers 2, 3, and 4 in the fundamental digital series) being armed with a long, sharp claw—a deadly weapon in combat, when the bird leaps feet first at its adversary. There have been various human fatalities among New Guinea natives as a result of an encounter with a cornered cassowary, and one case of a European boy similarly killed in Queensland. The body length of *unappendiculatus* of New Guinea ranges between 132 and 165 cm and the weight of an adult female while laying was 58 kg. The Australian form of *casuarius* stands about 150 cm high. Females are larger than males.

Distribution and habitat. Cassowaries have a restricted range in the Australo-Papuan area (New Guinea, Aru Island, Ceram, New Britain, Jobi and the eastern seaboard of north-eastern Australia from Cape York south to about Cardwell). The habitat occupied by each species appears to depend upon which other cassowary is sympatric with it (Davies 1976), but the scanty literature suggests that typically *bennetti* is a high altitude bird, *casuarius* a bird of medium altitudes and savanna woodland and *unappendiculatus* a bird of lowland rain-forests. White (1975, 1976) discusses the probable exotic status of *casuarius* on Ceram and *bennetti* on New Britain. It is clear that an extensive export trade in cassowaries has operated from New Guinea for at least 500 years, and the present distribution of the 3 species cannot be accepted as a natural phenomenon.

Food. Crome (1976) gave a detailed account of the food of North Queensland birds. They ate the fruits of 75 species of forest plant, those of the Myrtaceae and Lauraceae being most frequent. The main breeding period coincided with the peak availability of fruits of the Lauraceae. In New Guinea insects and plant tissues are also consumed.

Behaviour. Studies of the biology and breeding habits of the Australian Cassowary *C. c. johnsonii* have been made by Crome and by White (1913). The birds were found to occur largely singly or in pairs, but on occasion as many as 6 were seen together. Territories were found to be occupied during the laying season, apparently varying in extent from 1–5 km^2 (Rockingham Bay district of Queensland). During this time the birds were quite aggressive. Cassowaries were found to rest, from about noon to 4 p.m., in regular sunny spots, and to have fixed runs or tracks through the undergrowth. From time to time they were seen crossing creeks at regular points; they swim readily. Eggs were found in the nest from the middle of June until about the end of August, with a record for as late as the middle of September. Sightings of young chicks in June indicate that breeding may sometimes begin early in the dry season. The broods of 3–4 young birds, brown and initially striped, remained in company with the adult for about a year.



Cassowary *Casuarius casuarius*. (*K.J.W.*).

Voice. The call-notes—deep booming or croaking sounds—are more often heard than the birds are seen. Their wary habits and tendency to remain in cover provide abundant protection for such otherwise conspicuous birds.

Breeding. The egg sizes of *C. c. johnsonii*, perhaps the largest form, are given by White (1913); the averages of 5 separate clutches varied from 12.4 × 9.3 to 14.2 × 9.6 cm. The eggs vary in colour from pale to dark green, and are said to be darker in fresh than in incubated specimens. The shell texture may be smooth or rough, depending on the individual bird. As in the other ratites, incubation (for *c.* 30 days) of the eggs, which are laid in a clearing on the forest floor, is the province of the male, as is the care of the young, lasting *c.* 4 months.

Young cassowaries are frequently kept by the natives of New Guinea, being reared in enclosures until large enough to be eaten.

(A.K.) S.J.J.F.D.

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White, H.L. 1913. Notes on the cassowary (*Casuarius australis*, Wall). Emu 12: 172–178.

CAST; CASTING: same as PELLET.

CASTLE-BUILDER: name sometimes applied to species of spinetails (Synallaxinae)—see OVENBIRD (1)).

CASUAL (SPECIES): see VAGRANT.

CASUARII; CASUARIIDAE: see under STRUTHIONIFORMES; CASSOWARY.

CATACROMYODIAN: see SYRINX.

CATAMBLYRHYNCHINAE: FINCH, PLUSHCAPPED.

CATBIRD (1): substantive name, in North America, of *Dumetella carolinensis* and *Melanoptila glabrirostris* (see MOCKING-THRUSH).

CATBIRD (2): substantive name, in Australia, of *Ailuroedus* spp. and *Scenopoeetes dentirostris* (see BOWERBIRD).

CATBIRD (3): substantive name of the Abyssinian Catbird *Parophasma galinieri*, variously regarded as a flycatcher or a babbler (for family see MUSCICAPIDAE).

CATERPILLAR-BIRD; CATERPILLAR-SHRIKE: names sometimes applied to species of Campephagidae or, in the plural, used generally for the family (see CUCKOO-SHRIKE).

CATHARTIDAE: see CATHARTIFORMES; VULTURE (2).

CATHARTIFORMES: an order, comprising the sole Recent family Cathartidae (see VULTURE (2)). In Wetmore's system treated as a suborder Cathartae of the order Falconiformes, but as a suborder of the order Ciconiiformes by Ligon and König.

König, C. 1982. Zur systematischen Stellung der Neuweltgeier (Carthartidae). J. Orn. 123: 259–267.

CAUDAL: pertaining to the tail, or the region of the tail; or (relatively) nearer the tail.

CELL: in its special sense, a unit mass of living matter. Except in the simplest (unicellular) forms of animal life, a very large number of cells make up an organism, constituting its various tissues (see TISSUE). A cell usually has a nucleus, in which are found the chromosomes carrying the genes for the different heritable characters (see GENETICS). Cells multiply by a process of division (mitosis) in which every chromosome is split into two, one half going with each daughter nucleus. The final division leading to the formation of a germ-cell or gamete (whether spermatozoon or ovum) is a reduction-division (meiosis), in which the number of chromosomes is halved in each resulting 'pronucleus' (yielding the 'haploid' instead of the usual 'diploid' number). See also BLOOD.

CENSUS: term usually restricted to estimates of territory-holding populations. Non-territory-holding populations are often more mobile and visible, and their numbers are best estimated by a direct COUNT; this is particularly so in gregarious species.

There are several census methods currently in use e.g. mapping, transects, point counts. The choice of the most appropriate method depends on the nature of the species, its habitat and the information required. A mapping census is appropriate for an accurate census of a defined area, but a transect or point count may be sufficient to discover the approximate relative abundances of the species.

Mapping censuses. The first known mapping census was carried out in Kent, England, by the Alexander brothers in 1909. They marked the positions of summer visitors on a 6 inch map (1 : 10560) and repeated the census a second year to compare results. Few other workers used this rather laborious census technique, one exception being A.B. Williams (quoted in Kendeigh 1944) who mapped separately the birds seen on each visit to his study area and then made a composite map incorporating the data recorded on all his visits. The need to know absolute densities of breeding birds was not acute at that time and it was another 15 years before Enemar (1959) published his detailed account of mapping censuses of birds in a Swedish wood.

After further tests, this technique was adopted by the British Trust for Ornithology between 1962–1964 for their long term National Common Birds Census. This monitors year to year changes and trends in the breeding population levels of certain common birds. The rules for mapping censuses were later standardized internationally by the International Bird Census Committee (1969).

The mapping method requires a series of visits to be made to a defined study plot. On each visit, using a series of symbols, the position and activity of each bird is recorded on a large scale map (usually 1 : 2500). Each visit requires a separate map. The registrations for each species are then transferred to species maps, ideally one map for each of the common species. The resulting series of registrations often cluster into groups, each one indicating the approximate location of a bird's territory. These are delimited using a set of rules of analysis. Figure 1 illustrates a visit and species map. This method can only detect individuals which are holding territory; in some bird populations a non-breeding element may be present.

The symbols or registrations on the visit sheet (Fig. 1) indicate the locations of birds detected on that census. The letters refer to different species, e.g. WR = Wren *Troglodytes troglodytes*, R = Robin *Erithacus rubecula*, CH = Chaffinch *Fringilla coelebs*. Letters in circles are song registrations. Two song registrations joined by a dotted line indicate that both birds were seen or heard singing at the same time, while a continuous line means the same bird recorded in two different places. An underlined registration means that the bird was calling, not singing. An asterisk indicates a nest and BB indicates a fight. The registrations for each species on the species sheet are given a letter referring to the visit on which they were recorded.

Recent work has shown that intensive surveys over a few weeks in the main period of territorial establishment are quite comparable to the normal extended census (O'Connor 1980). The influence of weather factors has also been shown to be too weak to bias a season's results, although observations made on very cold or very wet days are certainly inadequate (O'Connor and Hicks 1980).

Other methods. Mapping censuses are most efficient for certain territorial non-colonial species. Nest counts, brood counts or direct counts of individuals or pairs, without delimiting into territories, are

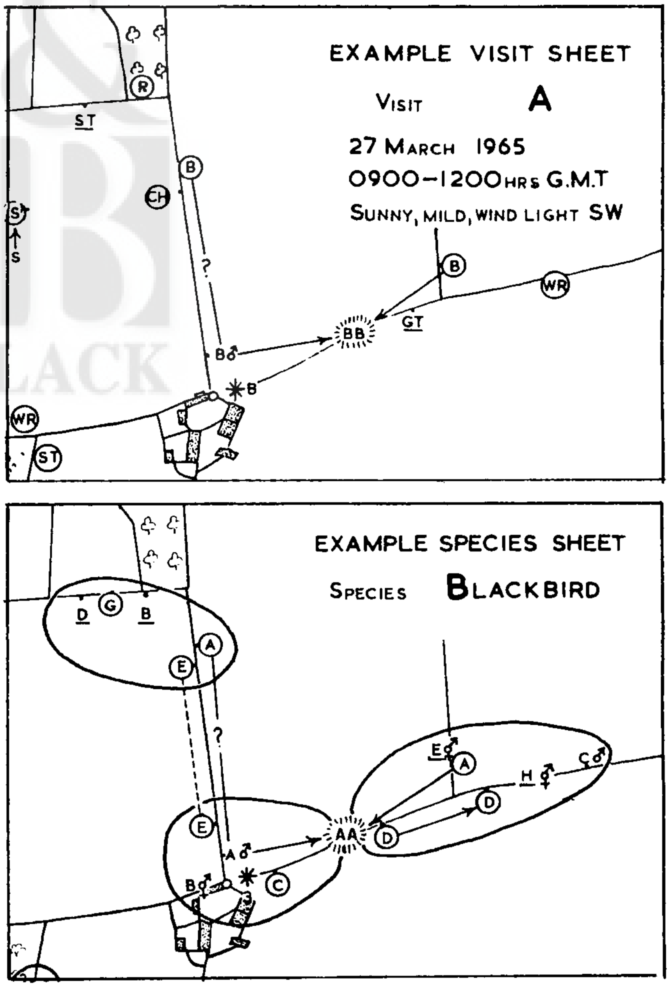

Fig. 1. Sections of visit map (*above*) and species map (scales 1 : 2,500) from a Common Birds Census plot. (Courtesy British Trust for Ornithology).

necessary for herons, ducks, geese and some waders. As an example, the national Heronry census in Britain, which started in 1928, relies on occupied nest counts made ideally in the second half of April. There are considerable problems still associated with censusing certain species, particularly seabirds, because of the difficulty of distinguishing between breeding and non-breeding individuals, the huge numbers involved and the likelihood that the whole population is not present in the breeding colony at any one time. Assessment of the size of seabird and flamingo colonies has been attempted by photography. This works best with colonies of conspicuous birds like Gannets *Sula bassana* on flat, rocky ledges and for species building relatively large nests like the Kittiwake *Rissa tridactyla*. Counts made from photographs of auk colonies may be up to 20% lower than direct counts, due to birds being obscured by rocky outcrops and by other birds. Photographs taken periodically of ranges of cliff may show up gross changes in the extent of seabird colonies.

Transects. For the first 60 years of the present century the transect type of census was usually employed. Finland, for example, has a history of line transect censuses dating back to 1916. They involve recording the numbers of birds of each species encountered along a length of habitat. The results, however, may be biased by inconsistencies in speed of walking, weather, type of habitat and conspicuousness of the species, as well as seasonal differences in the activities of different species. Therefore standardization is important. For valid comparisons, the transects need to be carried out at similar times of day, at the same time of the year and in similar weather conditions.

Some workers have used the line transect system to work out relative densities of breeding birds, e.g. Järvinen and Väisänen (1975). This method is sometimes called the complex line transect. It consists of dividing the birds recorded into those seen within 25 m on each side of the observer and those outside that distance. Densities obtained by this method are likely to be underestimates.

The advantage of the transect over the mapping census is that it enables workers to cover much larger areas of homogeneous habitat. This is particularly relevant in northern regions where the breeding season is also much shorter than further south. Enemar and Sjostrand (1967) showed that line transects increased the chances of detecting the scarce species which made up less than 10% of the populations detected on the mapping census, thus enabling a better measure of population trends and fluctuations to be obtained. There was however no advantage to be gained for commoner species.

Point counts. These may be considered a modification of the line transect technique. The birds are counted from a certain number of spots in a studied habitat in a constant time interval. Yapp (1962) called these 'time quadrats' and used them in conjunction with line transects as a check on his measures of relative abundance.

The method has since been developed in France by Blondel *et al* (1970). The observer visits spots twice in a season, in conditions good for bird song. One visit is made before the main arrival of summer visitors and one after. The higher of the two counts for each species is retained as the IPA (Indice Ponctuel d'Abondance) for a particular species in that spot in one breeding season. The observer stops at each spot for 20 minutes and then moves to another spot, ensuring that there is no chance of hearing the same birds. By noting habitat features, an analysis of the habitat preferences of birds is also possible. The rules for this and the transect method have been standardized by the International Bird Census Committee (1977). Densities have been arrived at by comparing the results with densities derived from a mapping census of the same area to obtain correction factors. There is however much variation and the results have to be treated with caution. The Point Count is most useful in habitats of limited extent such as broad-leaved trees in conifer forests. See also BIOSTATISTICS; ECOLOGY; NUMBERS. L.A.B.

Blondel, J., Ferry, C. & Frochot, B. 1970. La méthode des indices ponctuels d'abondance (IPA) ou des relèves d'avifaune par stations d'écoute. Alauda 38: 55–71.

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CENTROPODINAE: see CUCKOO.

CEPPHINI: see AUK.

CERE: the fleshy covering of the proximal portion of the upper mandible in some orders of birds (see BILL).

CEREBELLUM: part of the hindbrain (see NERVOUS SYSTEM).

CEREBRAL HEMISPHERES: parts of the forebrain (see NERVOUS SYSTEM).

CEREOPSIS: generic name sometimes used as English name of *C. novaehollandiae*, otherwise the Cape Barren Goose (see under DUCK).

CEROPHAGY: eating wax (see HONEYGUIDE).

CERTHIIDAE: a family of the PASSERIFORMES, suborder Oscines; TREECREEPER (1).

CERVICAL: pertaining to the neck.

CERYLINAE: see KINGFISHER.

CHACHALACA: substantive name of some species of Cracidae (see CURASSOW).

CHAETURINAE: see SWIFT.

CHAFFINCH: substantive name of 2 species of *Fringilla*; used without qualification for *F. coelebs* (see FINCH).

CHAJA: name commonly used in parts of South America for the Crested Screamer *Chauna torquata* (see SCREAMER).

CHALAZA: the pair of twisted strings of albumen suspending the yolk of an egg along its long axis (see EGG).

CHAMAEINI: see BABBLER.

CHAPARRAL: an environment, consisting of dense shrubs and stunted trees, characteristic of parts of North America.

CHAPARRAL-COCK: name applied to the Greater Roadrunner *Geococcyx californianus* (see CUCKOO).

CHARACTER DISPLACEMENT: divergence of the characters of closely related species in an area of geographical overlap. The probable existence of this phenomenon was first brought to light by Vaurie (1951) from a study of 2 overlapping nuthatches *Sitta tephronota* and *S. neumayer* in south-western Asia. It appeared that where they overlap they differ more in wing-length, bill-size and in the prominence of a black post-ocular stripe than they do in the areas where they are separate, and it was a reasonable explanation that competition between them had intensified their differences in the area of overlap thereby facilitating their coexistence. The theory has been applied to other cases, including some involving song differences, for instance between the Chiffchaff *Phylloscopus collybita* and Willow Warbler *P. trochilus*; but more detailed research into particular cases has tended to throw doubt on any such simple explanation of the interspecific differences in question. For instance, in some cases climatically related trends of variation may tend to produce results similar to those to be expected from character displacement. Each supposed case needs very careful examination. D.W.S. (1).

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Vaurie, C. 1951. Adaptive differences between two sympatric species of nuthatches (*Sitta*). Proc. X Int. Orn. Congr.: 163–166.

CHARADRII; CHARADRIIDAE: see CHARADRIIFORMES; PLOVER (1).

CHARADRIIFORMES: an order, comprising 3 suborders: Charadrii, Lari, Alcae; 18 families: Jacanidae (JACANA), Rostratulidae (PAINTED SNIPE), Haematopodidae (OYSTER-CATCHER), Ibidorhynchidae (IBISBILL), Recurvirostridae (AVOCET), Dromadidae (CRAB-PLOVER), Burhinidae (THICKKNEE), Glareolidae (COURSER, PRATINCOLE), Charadriidae (PLOVER (1)), Scolopacidae (SANDPIPER, PHALAROPE), Pluvianellidae (MAGELLANIC PLOVER), Thinocoridae (SEEDSNIPE), Chionidae (SHEATHBILL), Stercorariidae (SKUA), Laridae (GULL), Sternidae (TERN), Rynchopidae (SKIMMER), Alcidae (AUK).

The Charadrii are equivalent to the former order Limicolae—the 'waders' of British and 'shore-birds' of American usage. They are birds of from small to moderate size, ground-living and usually ground-nesting; they mostly frequent the vicinity of water, either inland or on the sea coast. Most of them prefer open situations, relying for safety on cryptic coloration, wariness, and mobility; some live in marshes, and a few in woodland. They can run swiftly for short distances and fly strongly; the phalaropes habitually swim. Their bills show a variety of specialized forms adapted to probing in soft ground and so on. A long bill is often correlated with long legs. In some the front toes are more or less webbed; the hind toe is small or absent except in the specialized 'lily-trotting' foot of jacanas. Most of them are markedly gregarious except when breeding; and many perform long migrations. The great majority of the species are comprised in 2 large cosmopolitan families, Charadriidae (plovers) and Scolopacidae (sandpipers, snipe etc.). Some of the smaller groups are also worldwide in distribution, while others are more restricted—sometimes to the tropics or some part thereof, the phalaropes to the far north (except as migrants), and the sheathbills to the far south.

The Lari comprise the gulls and allied groups, birds of from fairly small to rather large size, web-footed and often with predominantly white plumage. They frequent sea coasts, inland waters, and marshes. They are highly gregarious and breed colonially, using a variety of nesting sites. The skuas are parasitic in their feeding habits. The suborder is cosmopolitan in distribution and some species are notable migrants. The Alcae are highly specialized for swimming under water; they are exclusively marine and restricted to the Northern Hemisphere.

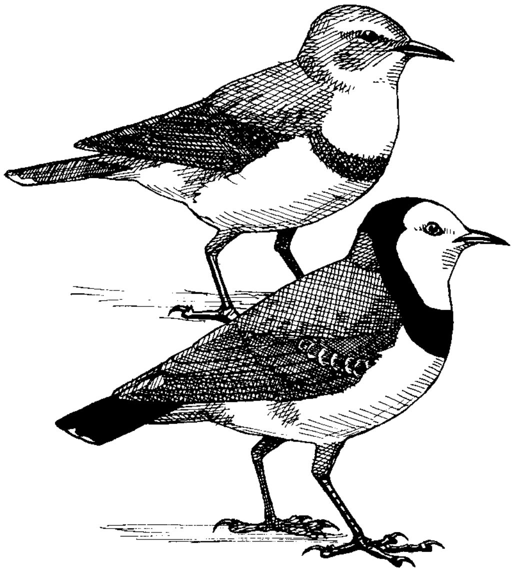
CHARDONNERET TRAP: see MARKING.

CHARM: see ASSEMBLY, NOUN OF.

CHAT (1): substantive name, in whole or part, of some species of Turdinae (see THRUSH); in the plural, general term for a subgroup ('chat-thrushes') of this subfamily, and more particularly for some of the genera, e.g. stonechats and whinchats *Saxicola* spp., wheatears *Oenanthe* spp., redstarts *Phoenicurus* spp., robin-chats *Cossypha* spp., cliff-chats *Thamnolea* spp., sooty chats or ant-chats *Myrmecocichla* spp. The name refers to the harsh 'chacking' notes of many of these birds.

CHAT (2): substantive name, in America, of certain species of Parulidae, e.g. *Icteria virens* and *Granatellus* spp., likewise 'Ground-chat' for *Chamaethlypis poliocephala* (see WARBLER (2)).

CHAT, AUSTRALIAN: substantive name for a small family, Ephthianuridae (Passeriformes, suborder Oscines), confined to Australia and Tasmania, consisting of 2 genera, *Ephthianura* (4 species) and *Ashbyia* (1 species); formerly included in the 'Australian wren-warblers' Malurinae (see WREN (2)). The possibility that the Ephthianuridae are actually more closely related to the Meliphagidae (honeyeaters) is currently being investigated with the use of biochemical techniques.



White-fronted Chat *Ephthianura albifrons*, female and male (front). (*N.W.C.*).

Characteristics. The 5 species are small (10.5–13.0 cm) songbirds with relatively long wings and short tails, and fine, slightly decurved bills. Sexual dimorphism is pronounced in *Ephthianura*, slight in *Ashbyia*. The adult males of the former are strikingly coloured and patterned: black, white and grey in the White-fronted Chat *E. albifrons*; black, white and red in the Crimson Chat *E. tricolor*; black, orange and yellow in the Orange Chat *E. aurifrons*; black and yellow in the Yellow Chat *E. crocea*. The adult male Gibberbird *Ashbyia lovensis* is greyish-brown above and dull yellow beneath with a buff breast-band. In all species the females and immatures are duller. There are indications that the adult male Crimson Chat goes into an eclipse plumage after the breeding season. The family has yet to be defined in anatomical terms; it is known, however, that all species have a brush-tipped tongue as in the HONEYEATERS.

Habitat. The typical habitat of each of the 5 species differs markedly, though there may be some overlap in this respect, particularly during eruptive movements. The Crimson Chat prefers shrub- and tree-savanna of the arid and semi-arid interior. The Orange Chat also lives chiefly in the arid zone, but favours samphire around saltlakes, and saltbush and cottonbush on stony plains. The Yellow Chat inhabits grassy swamps in northern and north-eastern Australia, and has recently been discovered well inland, in reedy swamps in the Great Artesian Basin. The Gibberbird, the most arid-living of the 5 species, frequents the sparsely-vegetated stony gibber plains of the Lake Eyre and associated drainages. The White-fronted Chat occurs mainly in southern districts, where it is found in wetter habitats than those of the other species, such as estuarine and lacustrine marshes and swamps, and damp pasture.

Movements. All species show some degree of seasonal movement. In the White-fronted Chat, the Tasmanian populations are more or less sedentary, whereas those of the mainland are partly migratory, some individuals moving north (inland) in the winter. The Yellow Chat was once thought to be sedentary and confined to certain subcoastal districts. The recently-discovered populations of the interior, however, appear to move from one artesian swamp to another, across many kilometres of open gibbers. The Crimson Chat and Orange Chat are strongly nomadic in the arid and semi-arid zones, moving and breeding opportunistically in response to good seasons and occasionally erupting towards the periphery of the continent in large numbers. The Gibberbird undertakes limited NOMADISM within the limits of its gibber habitat, exceptionally wandering southwards into wetter districts in very small numbers.

Food. Mainly small insects (including ants, wasps, bees, beetles, bugs, grasshoppers, caterpillars) and spiders are taken; less often, seeds. In addition, the Crimson Chat has been reported as taking nectar from flowers; indeed, its ability to cross deserts containing very little insect life may be attributable to its ability to use nectar as a source of energy. It has recently been suggested, however, that the brush-tongue of the Ephthianuridae is an adaptation for drinking dew and other tiny sources of water.

Behaviour. Generally gregarious, travelling and breeding in flocks of varying density. This tendency is not always obvious in the Gibberbird, because of the often well-dispersed nature of the groups. On the other hand, the Crimson Chat and Orange Chat, during periods of eruption, may occur locally in their hundreds.

Whereas the Gibberbird is almost entirely terrestrial, the other 4 species are less so, feeding largely on the ground but perching regularly in bushes or reeds. Most species are tame, often absurdly so. The Orange Chat, however, tends to be extremely wary, allowing no close approach, and it is usual to see, far off, a brightly-coloured male keeping watch from the top of a bush while the rest of the flock is feeding out of sight on the ground.

Voice. None of the Ephthianuridae is a noted songster. Their limited repertoires include a series of silvery notes (Crimson), a *tang* like a plucked violin string (White-fronted), a metallic *tang* and a mellow *cheek cheek* (Orange), an attractive descending trisyllabic call (Yellow) and an alarm of 5–6 high piercing notes (Gibberbird).

Breeding. Loosely colonial, and territorial insofar as the male protects the receptive female, eggs and fledglings but not the resources of the territory. The nest is cup-shaped, of dry grass, plant stalks and twigs; in the Gibberbird placed on the ground, in the other species low in shrubs or herbage. The eggs of all species are similar, having a whitish ground with spots of black, reds, browns and greys, reminiscent of the eggs of many honeyeaters. Clutch size is usually 3, less often 4. Incubation lasts 12–14 days, and the young are in the nest 14–15 days. In the Crimson Chat, the female builds the nest, and both sexes incubate and care for the young. All species except the Yellow Chat have been recorded putting on the 'broken wing' display to lure intruders away from nest and fledglings (see DISTRACTION BEHAVIOUR). In the breeding season, male Crimson Chats indulge in a diving display-flight from a perch, while male Gibberbirds perform a song-flight, mounting in steps to more than 30 m above the gibbers, then falling directly to earth. S.A.P.

Goodwin, D. 1967. Notes on behaviour of some Australian birds. Emu 66: 237–251.

Keast, A. 1958. The relationship between seasonal movements and the development of geographic variation in the Australian chats (*Ephthianura* Gould and *Ashbyia* North (Passeres: Malurinae)). Aust. J. Zool. 6: 53–58.

Miller, R. 1971. Nesting behaviour of the Gibber Bird (*Ashbyia lovensis*). Birds (N.S.W. Field Orn. Club) 6: 27–28.

Parker, S.A. 1973. The tongues of *Ephthianura* and *Ashbyia*. Emu 73: 19–20.

Parker, S.A. 1977. Australian chats. *In* Frith, H.J. (ed.), Complete Book of Australian Birds: 510–513. Sydney.

Williams, C.K. 1979. Ecology of Australian chats (*Ephthianura* Gould): reproduction in aridity. Aust. J. Zool. 27: 213–229.

CHAT, PALM: see PALMCHAT.

CHATTERER: substantive name formerly used for some medium-sized species of COTINGAS, and sometimes for the family as a whole; and now used for some African BABBLERS of the genus *Turdoides*.

CHAT-TYRANT: substantive name now regularly used for the chat-like tyrant-flycatchers of the genus *Ochthoeca* (see FLYCATCHER (2)).

CHECKLIST: a systematic and comprehensive list of the species (and, frequently, subspecies) occurring in a certain geographical area; less usually, a list of the species in a family or order. Checklists usually summarize available information on the status and distribution of all the forms dealt with, but do not include biological data such as behaviour, ecology etc.

CHEEK: see TOPOGRAPHY.

CHEER: *Catreus wallichi* (see PHEASANT).

CHEMICAL REPELLENTS: see REPELLENTS, CHEMICAL.

CHEST: the THORAX; if used to designate a surface area, practically synonymous with breast (see TOPOGRAPHY).

CHEWINK: alternative name for the Rufous-sided Towhee *Pipilo erythrophthalmus* (see BUNTING).

CHICK: see under YOUNG BIRD.

CHICKADEE: substantive name, in North America, of some *Parus* spp. (see TIT).

CHIFFCHAFF: *Phylloscopus collybita*, a well-known Palearctic warbler, so named from its simple repetitive song (see WARBLER (1)).

CHILIA: substantive name sometimes used for the South American furnariid *Chilia melanura* (see OVENBIRD (1)).

CHIN: see TOPOGRAPHY.

CHIONIDAE: see CHARADRIIFORMES; SHEATHBILL.

CHIPPING: see HATCHING.

CHI-SQUARE TEST: see BIOSTATISTICS; STATISTICAL SIGNIFICANCE.

CHITINOUS: made of the hard horny substance ('chitin') of which the external skeletons of insects are composed (see PELLET).

CHLOROPHONIA: generic name used as substantive name of *Chlorophonia* spp. (see TANAGER).

CHLOROPSEIDAE: name used by Wetmore for a family equivalent to the Irenidae less *Irena* (see LEAFBIRD).

CHOANA: a funnel-shaped passage; especially one of the interior nares (see NARIS; SMELL).

CHORD: see MEASUREMENT.

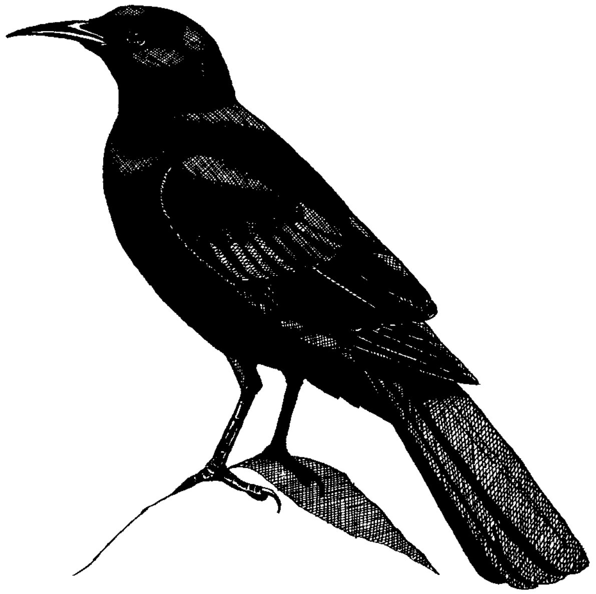
CHORDATES: see ANIMAL KINGDOM.

CHORDEILINAE: see NIGHTJAR.

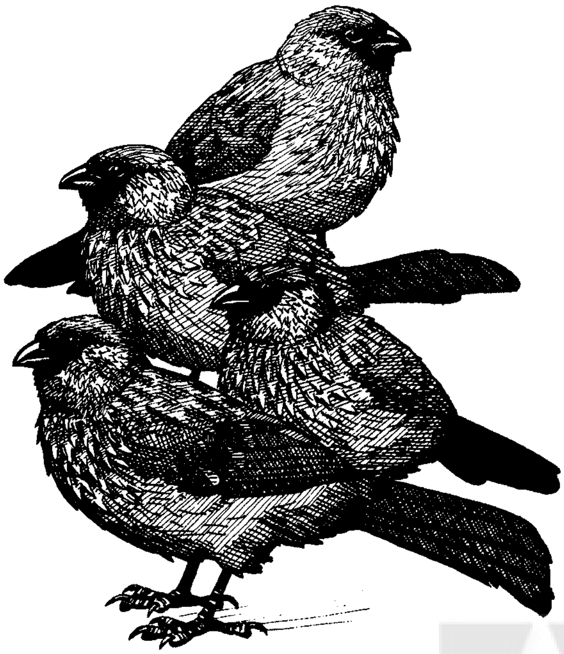
CHOUGH (1): substantive name of *Pyrrhocorax* spp., used without qualification, in Britain (but sometimes 'Cornish Chough'), for *P. pyrrhocorax* (see CROW).

CHOUGH (2): substantive name, as White-winged Chough *Corcorax melanorhamphos*, of one of the 2 members of the endemic Australian family Corcoracidae (Passeriformes, suborder Oscines), the other being the Apostlebird *Struthidea cinerea*. Until recently both were regarded as forming the subfamily Corcoracinae in the family Grallinidae, now restricted to the MAGPIE-LARK and one other species (Schodde 1975).

Characteristics. The White-winged Chough is 47 cm long, sooty black with a conspicuous white wing patch on the primaries that shows clearly in flight, a long curved bill like its namesake *Pyrrhocorax* (CHOUGH (1))



White-winged Chough *Corcorax melanorhamphos*. (*N.W.C.*).



Apostlebird *Struthidea cinerea*. (*N.W.C.*).

and long strong legs. The Apostlebird (28.5–35 cm long) is basically grey coloured with brown wings and a black tail. The strong bill is reminiscent of a sparrow's *Passer* but much larger. The eye colour changes with age in both species.

Habitat and distribution. Both *Corcorax* and *Struthidea* are confined to the eastern half of the Australian continent, neither of them reaching Western Australia or Cape York peninsula. *Corcorax* is common in the dry sclerophyll woodlands of the tablelands along the Great Dividing Range and inland to the Darling River; but is less frequent near the coast. *Struthidea* largely overlaps *Corcorax* but is found further inland and reaches the Northern Territory; it is less frequent on the tablelands or near the eastern seaboard than *Corcorax*. Both species seem to have adapted well to agricultural settlement and *Corcorax* has colonized the numerous large plantations of exotic pines planted commercially in southern Australia.

Throughout the breeding season *Corcorax* and *Struthidea* confine their activities to an area of some 20 ha surrounding the nest, which is defended against trespass by conspecifics and can therefore be regarded as a territory. For the rest of the year the birds forage over an area of several km^2; large aggregations form where food is locally abundant as on a cereal stubble after harvest. Both species are more at home on the ground than in the air and most of their travelling is done on foot. They tend to ascend trees by a series of leaps.

Food. *Corcorax* spends much of the day searching under branches, leaves, cowpats and tussocks for insects which form the major part of its diet, with seeds important in the winter. This search is accomplished by a sideways sweeping of the bill: the feet are never used for raking. *Struthidea* with its dumpy strong bill is pre-eminently a seed-eater although insects are also an important part of its diet.

Behaviour. Groups of *Corcorax* average 6 (2–20) whilst those of *Struthidea* average 9 (3–19) members, though its English name suggests the 12 Apostles. Many aspects of the group life of both species are similar. The units generally grow by the retention of offspring although fragmentation of a group after the death of the dominant male may result in the formation of a new unit by unrelated individuals. All members of the group may help to build the nest, to incubate the eggs and to feed and care for the nestlings and fledglings. No correlation between feeding rate and group size was found in *Corcorax* (Rowley, 1978a). Groups of from 4–8 birds reared similar numbers of nestlings (1.0–1.3 p.a.) whilst smaller groups were very unsuccessful and groups larger than 8 fledged most young. Only half of the young that left the nest lived to become a year old; during that time survival was better in groups of more than 6 birds than in smaller groups. Another apparent advantage of living in a large group is that after one brood has left the nest it may be cared for by part of the group whilst the others produce a second brood, reuniting later.

Display. *Corcorax* displays by waving its part-opened wings and spread tail, alternately. *Struthidea* lacks any wing marking and displays by bobbing its head up and down and waving its tail.

Voice. *Corcorax* has a series of single and double pipes and whistles which are quite unlike anything uttered by *Struthidea*, but both species have a similar creaky or rasping alarm call; *Struthidea* utters a series of calls rendered as *ch-kew, ch-kew, creechew creechew* . . .

Breeding. Both species build very similar nests of mud (as do MAGPIE-LARKS) 2–15 m above the ground on horizontal branches. These open bowls appear to be solid mud but contain up to 7% by weight of fibre. A piece of fibre (grass-stem or bark) is selected by the builder and taken to a mud source where it is dabbled until coated thoroughly; this is carried to the nest where it is trowelled into place with the bill and then settled by a rapid scissoring action of the mandibles. The side walls are seldom raised more than 2 cm per session since they need to harden before being added to. Such nests may last for years and are often reused (Rowley, 1978b). The 2 species usually nest from spring into the early summer but have been recorded responding to rainfall at other times by nest building and breeding. The normal clutch size is 2–5 but occasional multiple clutches (up to 10 eggs) have been recorded. Incubation lasts 19 days and the nestlings fledge when 23 (*Struthidea*) or 23–28 (*Corcorax*) days old. Fledglings are dependent on the adult group for food for several months. I.R.

Rowley, I. 1970. The use of mud in nest-building—a review of the incidence and taxonomic importance. Ostrich Sup. 8: 139–148.

Rowley, I. 1978a Communal activities among White-winged Choughs *Corcorax melanorhamphus*. Ibis 120: 178–197.

Rowley, I. 1978b. Apostlebirds gathering material for their mud-nest. Austr. Bird Watcher 7: 166–168.

Schodde, R. 1975. Interim List of Australian Songbirds, Passerines. R.A.O.U. Melbourne.

CHRISTMAS BIRD COUNT: see BIRD-WATCHING.

CHROMATOGRAPHY: see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA.

CHROMOSOME: see CELL; GENETICS.

CHRONOCLINE: term introduced by G.G. Simpson for the gradation of a form in time, going back towards an ancestral type.

CHRONOMETER, BIOLOGICAL: see RHYTHMS AND TIME MEASUREMENT.

CHUCK-WILL'S-WIDOW: *Caprimulgus carolinensis* (see NIGHTJAR).

CHUKAR: *Alectoris graeca* (see under PHEASANT).

CHURRING: sustained low trill or reel, e.g. Nightjar's.

CHYME: the semi-fluid partly digested food leaving the gizzard for the duodenum (see ALIMENTARY SYSTEM).

CICADA-BIRD: Australian name of *Coracina* (*'Edolisoma'*) *tenuirostris* (see CUCKOO-SHRIKE).

CICONIAE; CICONIIDAE: see below.

CICONIIFORMES: an order, alternatively 'Gressores', and formerly also 'Herodiones', comprising 3 suborders: Ardeae, Scopi, Ciconiae; 5 families: Ardeidae (HERON, BITTERN), Scopidae (HAMERKOP), Ciconiidae (STORK), Balaenicipitidae (SHOEBILL), Threskiornithidae (IBIS, SPOONBILL).

The Ciconiiformes are mainly large birds, characteristically with long legs and long bills, adapted for wading in shallow water or marshes and mostly living on fish or other animal prey.

CINCLIDAE: a family of the PASSERIFORMES, suborder Oscines; DIPPER.

CINCLODES: substantive name now regularly used for the ground-living furnariids of the genus *Cinclodes* (see OVENBIRD (1)).

CINCLOSOMATINAE: see TIMALIIDAE; RAIL-BABBLER.

CIRCADIAN: term applied to a biological rhythm of about a day, i.e. *circa* 24 hours (see RHYTHMS AND TIME MEASUREMENT).

CIRCAETINAE: see HAWK.

CIRCANNUAL (CIRCENNIAL) RHYTHMS: endogenous annual rhythms persisting under seasonally constant environmental conditions with a period of approximately (*circa*) one year (*annus*).

CIRCINAE: see HAWK.

CIRCULATION: see HEART; VASCULAR SYSTEM.

CISTICOLA: substantive name often used for some members of the large genus *Cisticola* (see WARBLER (1)).

CLADE: see CLADISTICS.

CLADISTICS: Method of biological classification, also applicable in biogeography. The basic principles of cladistics were set out by Willi Hennig (1966). The keys are his definition of relationship (Fig. 1) and his discussion of how relationship is recognized. Relationship in Hennig's sense, by closer common ancestry, is evinced only by shared derived characters (synapomorphies) inherited from that ancestry. Shared primitive characters (symplesiomorphies), inherited from a more remote ancestry, are irrelevant or misleading in the search for relationship. For example, the teeth and long bony tail of ARCHAEOPTERYX are irrelevant to its relationship with birds, for lizards, salamanders and fishes also have teeth and long bony tails. Feathers and a furcula, however, are synapomorphies unique to *Archaeopteryx* and birds. The third type of character, those unique to any one species or group, Hennig named autapomorphies. The three terms autapomorphy, synapomorphy and symplesiomorphy describe the distribution of characters relative to a particular problem: feathers are an autapomorphy when one is interested in what (featherless) group is most closely related to birds, a synapomorphy when one is interested in the relationships of *Archaeopteryx*, and a symplesiomorphy if the problem is one of relationships within birds.

From these ideas, Hennig derived definitions of three types of group. Monophyletic groups contain all and only the descendants of a common ancestor (ABCD, BCD or CD in Fig. 1), and are characterized by synapomorphies or evolutionary novelties. A paraphyletic group is created when one or more parts of a monophyletic group are removed because of autapomorphies (e.g. Reptilia—those amniotes remaining when birds and mammals are removed; Invertebrata—metazoans lacking vertebrate characters). All 'ancestral groups' are paraphyletic. Polyphyletic groups are those whose defining characters are assumed not to have existed in the latest common ancestor of the group: they are characterized by convergence or non-homology (e.g. a group of all winged animals).

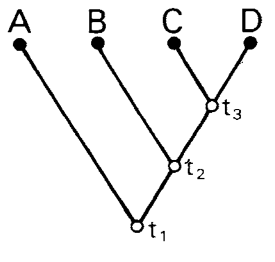


Fig. 1. Hennig's definition of relationship. Two species (e.g. C and D) are more closely related to each other than to a third (A or B) if they share an ancestral species (at t_3) not shared with the third.

Cladists argue that classifications should contain only monophyletic groups. Paraphyletic groups, which are permitted or recommended in evolutionary classifications, should be avoided because they have no historical reality (they cannot become extinct, for example), and no defining characters. Reptiles, for instance, can be defined only by listing characters they lack, such as feathers, hair and homothermy.

Cladistic analysis consists of evaluating the distribution of characters, and ordering homologous characters in 'transformation series' from primitive to derived. Ontogenetic transformation is the only unambiguous method of ordering the polarity of such series, but ancillary methods such as outgroup comparison are available. That cladogram is accepted which is congruent with the distribution of the greatest number of characters rated as synapomorphous. The cladist method is epitomized by 'search for the sister group'—sister groups are species or groups which are each other's closest relatives, such as C and D or B and C + D in Fig. 1.

In forming classifications, cladists recommend that the cladogram be directly translated into the classification; in other words, that sister groups be given equal rank. A cladistic classification of Fig. 1 would be:

- taxon ABCD
  - subtaxon A
  - subtaxon BCD
    - infrataxon B
    - infrataxon CD
      - species C
      - species D

The structure of the cladogram determines the relative rank of the taxa, but not their absolute rank. Hennig proposed ranking by age, for example that groups originating in the late Palaeozoic be ranked as orders, but this practice is not general. Various devices and notations have been proposed to simplify cladistic classifications (Wiley, 1981).

Cladistic analysis is now accepted by many evolutionists as the best approach to systematics. The principal remaining difference between cladists and non-cladists is that the latter wish to retain paraphyletic groups, since they are held to be consonant with evolutionary theory in allowing divergent groups higher rank than their sister groups (e.g. class Aves versus order Crocodilia). Modern developments in cladistics tend to divorce systematics from evolutionary theory, by drawing a distinction between cladograms (summaries of character distribution) and trees (character distribution plus ancestry and descent) (Nelson and Platnick, 1981).

In biogeography, application of cladistics has resulted in the development of vicariance biogeography, in which species cladograms are used to specify the historical interrelationships of geographic areas (Nelson and Platnick, 1981). C.P.

Hennig, W. 1966. Phylogenetic Systematics. (2nd edn. 1979) Urbana.
Nelson, G. & Platnick, N. 1981. Systematics and Biogeography: Cladistics and Vicariance. New York.
Wiley, E.O. 1981. Phylogenetics. New York.

CLADOGENESIS: see SPECIATION.

CLADORNITHES: see under PELECANIFORMES.

CLAMATORES: see under PASSERIFORMES.

CLAP-NET: see TRAPPING.

CLASS: a primary taxonomic category; all birds, including those known only from fossils, constitute a single 'class' of animals, the Class Aves (see ANIMAL KINGDOM; AVES; TAXON): even so, birds are reduced to the rank of a subclass of the Class Reptilia by some authors (Wolters 1975–82). A class is divided into 'orders', but these may be grouped in intermediate categories such as subclasses and superorders.

Subclasses. The division of the Class Aves into subclasses has no practical application to the taxonomy of geologically recent birds, all the orders of which fall in the subclass Neornithes; the most ancient of the fossil birds, the Archaeornithiformes of the Jurassic, are placed by Wetmore in his only other subclass, the Archaeornithes. There are, however, other possibilities, particularly adhered to by palaeontologists, e.g. by Brodkorb (1963): Class Aves, Subclass Odontoholcae (with Hesperornithiformes, tooth-billed birds), Subclass Ornithurae (all orders known as Neornithes).

Superorders. Wetmore divides the Neornithes into the superorders Odontognathae, Ichthyornithes, Impennes, and Neognathae. Of these, the first and second include only fossil birds; the third includes only the Sphenisciformes (penguins); and all other recent (and some fossil) birds are assigned to the Neognathae. So far as birds of today are concerned, therefore, use of the superordinal category involves nothing beyond the question whether the penguins differ more fundamentally from all other recent orders than these differ from each other—a point on which many disagree with Wetmore. At present the systematic arrangement of birds is in a state of intensive re-consideration at all levels and with all kinds of experimental, biochemical methods and cladistic re-interpretations, the end of which is not yet in sight.

Brodkorb, P. 1963. Catalogue of fossil birds. Bull. Florida State Mus. Biol. Sci. 7: 179–293.
Wetmore, A. 1960. A classification for the birds of the world. Smithsonian Misc. Coll. 139 (11): 1–37.
Wolters, H.E. 1975–82. Die Vogelarten der Erde. Hamburg.

CLASSIFICATION: the grouping of organisms into categories or taxa and the subsequent grouping of these into a system, usually hierarchical; also the finished product of the grouping. The work of classification is known as taxonomy or systematics. Both names at present are usually considered synonymous and in common usage are often interchangeable. In fact, since A.P. de Candolle (1813), the term taxonomy has been formerly more regularly applied to the classification of plants, whereas the term systematics has remained more directly based on the title of Linnaeus' *Systema Naturae* (1735 and subsequent issues) and has been for a long time the exclusive term in zoology. In modern literature taxonomy more often refers to the analytical, systematics to the more synthetic part of the work of classification. Nomenclature, the naming of categories, is a practical, not an essential part of classification (see SYSTEMATICS; TAXON; TAXONOMY; NOMENCLATURE).

Theories of classification. The primary goal of classification is to see order or rather reveal basic systems, if present, in the multitude of forms of life that occur and have occurred on earth. It does not aim merely to provide a general reference system for universal scientific use; instead it is an expression of basic biological theories. For it has not always been self-evident that the diversity in nature can be theoretically classified and there are still various philosophical approaches to classification known as essentialism, empiricism, nominalism, and evolutionism. All classifications start with noting differences, hence with discriminating between groups. At first, these groups were based on easily observable differences in outward appearance, which in birds mean particularly bill and feet, leading to groups such as 'birds with curved beaks', order XIV of Linnaeus, including Hoopoe *Upupa*, Treecreeper *Certhia*, Hummingbird *Trochilus*. This was followed by more biological classifications such as that by Carl Illiger (1811) who arranged birds into: *Scansores, Ambulatores, Raptatores, Cursores, Grallatores, Natatores.* With acceptance of the existence of organic evolution, the notion of relationship as the basic principle in classification has replaced that of appearance or structure and through this arose the difference between the *artificial* (based on similarities) and *natural* (based on relationships) classification systems. At present nearly all classifications of birds are intended to be natural and attempt to reflect the evolutionary history of birds.

Methods of classification. For a long time linear sequences of hierarchically arranged categories could meet the needs of classificatory work. Linnaeus recognized 6 taxonomic categories in which to arrange the organic and inorganic world in his *Systema Naturae* (1735): *regnum, classis, ordo, genus, species, varietas.* The now generally used category 'family' was introduced in ornithology by F.M. Daudin not before 1800. It should be stressed that these categories are not natural categories; according to most present-day authors the only 'natural' entities in nature are individuals and (at their best) species. Therefore the number of categories recognized is theoretically unlimited and this is acceptable as long as the principle of hierarchy is adhered to. The following taxonomic categories, arranged according to hierarchy, are at present in wide use: *regnum* (Animals), *phylum, subphylum, superclass, class* (Birds), *subclass, cohort, superorder, order, suborder, superfamily, family, subfamily, tribe, genus, subgenus, superspecies, species, subspecies.*

Usage of categories and recognition of characters on which distinctions are based are subject to the personal judgement of the taxonomist. There are no special specific, generic, familial etc. characters; all those in use are a matter of comparison and tradition. In the better known animal groups, such as birds, most recent authors tend to incorporate any distinctive character in the complex of data used to discriminate between taxonomic categories, irrespective of whether these characters are of a morphological, structural, genetic, biochemical, physiological, ethological or ecological nature. In this way classification has become a matter of the study of the living bird rather than exclusively that of the cabinet specimen. The need to do this was fully explained in *The New Systematics* (1940, editor Julian S. Huxley), which heralded the revival of systematics as a biological science. The different methods of classification used today and described below reflect basic differences in classification theory.

Evolutionary systematics. Several attempts have been made to reduce the traditionally subjective aspects of classificatory work. One of these is the mainly neo-Darwinian evolutionary systematics which judges on 'weighted phenetic similarities' in the context of evolutionary relationship. This method was followed by nearly all bird taxonomists during the first half of this century and by a majority for many years after the publication of Mayr's *Systematics and the Origin of Species* (1942).

Phylogenetic systematics. More recently the so-called phylogenetic systematics has given a strong impetus to classificatory work and achieved notable results. This kind of approach is based on the theory of CLADISTICS (the description of the course of evolution through clades, which are delimitable monophyletic units) developed by the entomologist Hennig (1950, English translation 1966). Basic to this theory is the search for those points in evolution where clades start to diverge, a method which is only possible by rigid distinction between primitive or original similarities (symplesiomorphies) versus progressive or derived similarities (synapomorphies). All forms sharing a certain derived character must have branched off together, i.e. in the same clade, from other related forms which have kept the same character in an original, relatively primitive state. Basically this is the same reasoning as that of the classical comparative anatomists of the decades around the turn of the century. The strict application of the method means that all groups sharing a derived character must be placed in a taxonomic category of the same hierarchical value as the 'sister group' of related forms which retains the character in its primitive state—a procedure that sometimes produces apparently absurd results. The method has been most efficiently applied in birds by Cracraft relating to cranes and rails (1973) and the ratites (1974), by Feduccia (1977) relating to perching birds, and by Raikow (1978) relating to New World nine-primaried songbirds. The rigid application of the theory of cladistics to classification has been severely criticized by Mayr (1974, reprinted 1976).

The method results in a system of cladistics, named cladograms, with fixed points at the supposed beginnings of divergence between clades, the whole resembling the branches of a tree of descent. The main drawback is that, as in the heyday of comparative anatomy, no one can be sure which characters are analogous (similar structure and function but not same origin) and which are homologous (same origin but not necessarily similar structure and function). Hence the course of evolution remains as difficult to trace as ever, and the reality of the branching points may be illusory. Moreover, a cladistic system may be representative of the possible phylogenetic history of one or more organs or structures rather than of the organisms themselves (birds).

Numerical taxonomy. To avoid a classification based on one or a few characters, the choice of which is subjective, several authors have suggested that as large a number of characters as possible should be taken into consideration and quantified; those organisms scoring the highest number of similarities are likely to be most closely related. In birds this was practised not very successfully for osteological characters by Verheyen (1961), but in general zoology (and bacteriology) it received balanced mathematical (in later years computerized) treatment by Sokal and Sneath (1963), and became known as Numerical Taxonomy. The method, which uses measurable phenetic characters known as Operational Taxonomic Units (OTU's), results in the construction of so-called phenograms. These are static, not evolutionary or phylogenetic, illustrations of observable degrees of similarities and differences. Numerical taxonomy was applied to birds among others in the methodologically most interesting works by Schnell (1970) on gulls and Robins and Schnell (1971) on North American grassland sparrows.

On the whole, numerical taxonomy has not yet provided new insight in avian systematics; probably it will not, as the number of bird species is small and, compared with other animals, the structural resemblances among birds are larger than the differences among them, so that the human brain can still master the details of similarities and distinctions and weigh their importance in phylogenetic history. This also applies to the recognition of characters of great adaptive plasticity, such as bill, feet and wings, which often obscure the results of numerical taxonomy, and to 'the role of adaptive mechanisms in the origin of higher levels of organization', to cite a title by Bock (1965).

To avoid the trap in numerical taxonomy of the subjective choice of taxonomic characters used, and to help combine the advantages of numerical taxonomy and cladistic analysis, a new method has been proposed by Estabrook (1972) and others: the method of *character compatibility*. This method is based on the old concept of the occurrence of character combinations, particularly applied in plant taxonomy, and works with Evolutionary Units (EU's) rather than with species or other taxa. Hence, though theoretically it can fall into the same trap as that of orthodox comparative anatomy, it is less liable in practice to do so. The method is complicated and has been applied to birds, e.g. by Strauch (1978) in a review of the phylogeny of Charadriiformes.

Evaluation of methods. Present classifications of birds at their best are based on mixtures of evolutionary and phylogenetic systematics, the ultimate results of which are neither very satisfactory nor notably unsatisfactory. Avian systematists lack the fossil information available more prolifically for mammals. As a result, knowledge of the relationship of higher systematic groups (categories from families upwards) has proved in particular to be more imperfect than had been realized, so that numerous changes of insight and opinions of basic importance can be envisaged in the near future. This not only refers to details (e.g. suggested close relationship of flamingos (Phoenicopteridae) with stilts and avocets (Recurvirostridae)), but also to methods of theoretical approach, for which see the numerous outstanding papers in recent issues of the journal *Systematic Zoology*. Mention should also be made of the biochemical papers by Sibley and Wilson and their collaborators, dealing with DNA-hybridizations and differences in the rates of change in evolution of proteins and morphological structures, respectively (see references under DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA). All these recent studies mark a renewed interest in macro-classification as applied to the biology of birds.

Current systems in practice. To quote Landsborough Thomson, 'One must not seek to stereotype systematic thought and thus deter progress; but with such diverse views on the part of specialists, it is for most purposes of ornithology desirable to standardize—at least for a time—one particular system.' That followed in the present work down to familial level, and set out at the beginning of the volume, is a combination of the arrangements and linear sequences by Wetmore (1960), Stresemann (1959), Sibley, Ahlquist and collaborators (1970, 1972) and Storer (1971). Quite a number of other lists have been published in recent years. The most elaborate and well-balanced is that by Morony, Bock and Farrand (1975); the most unorthodox and wholly cladistic is that by Wolters (1975–1982). No classification can be final, as our knowledge of the course of evolution cannot be otherwise than imperfect; hence classification and sequences will always be liable to change and will remain in a happy stage of continued progress. K.H.V.

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CLAVICLE: a paired bone ('collar bone') of the pectoral girdle, the two clavicles in birds being fused to form the furcula ('wishbone' or 'merrythought')—see SKELETON, POST-CRANIAL.

CLAW: for those on the toes, see LEG; also MOULT; for those sometimes borne on the manus, see WING.

CLEIDOIC: term descriptive of the totally enclosed condition of eggs of the type produced by birds. Such an egg represents a virtually sealed physiological system (except for some gaseous exchange) during the period of incubation, a condition that makes certain adaptations necessary, e.g. as regards EXCRETION. See DEVELOPMENT, EMBRYONIC; EGG; EXCRETORY SYSTEM; NUTRITION.

CLIMACTERIDAE: a family of the PASSERIFORMES, suborder Oscines; TREECREEPER (2).

CLIMATIC ADAPTATION: an adaptation serving to fit the species for occupation of a particular climatic region, or to optimize on the opportunities and limitations of such. It includes breeding modifications, seasonal movements, etc. (see ADAPTATIONS, ENVIRONMENTAL).

CLIMAX COMMUNITY: a biotic community representing the maximum ecological development possible in the particular environment (compare SERAL COMMUNITY).

CLIMAX VEGETATION: see HABITAT.

CLIMBING: see LOCOMOTION, TERRESTRIAL.

CLIMOGRAPH: an ecological method of combining experimental data and field observations in the form of a contoured diagram expressing the effects of temperature and humidity, acting together, in the range of a species under study (see ECOLOGY).

CLINE: a term introduced by Huxley for a geographical gradient in a phenotypic character within the range of a species, for example the increasing darkness of plumage from east to west found in many European bird species; sometimes, but less satisfactorily, used for the aggregate of populations showing such variation. A cline has itself no status in nomenclature. It may include forms to which subspecific names have been attached, although where the gradation is continuous (as happens in the absence of barriers) the validity of such subspecies becomes questionable (see SUBSPECIES; and DEME). Nevertheless, the forms at the extremities of a cline may show striking differences when directly compared with each other, and this may be true also of intermediate forms taken from points sufficiently far apart in the clinal range; in such cases the use of subspecific names may have a practical convenience in providing taxonomic points of reference. Notations have been suggested for the designation of clines in terms of their geographically extreme forms, but this procedure seems to import a concept too rigid for the reality. The fact is that different characters may show clinal variation independently of each other, and sometimes in different directions, e.g., some from east to west and others from north to south.

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CLIPPING: rendering a captive bird temporarily incapable of flight by cutting the primary feathers of one wing; these feathers are replaced at the next moult (compare PINIONING).

CLOACA: the combined terminal opening of three physiological systems (see ALIMENTARY SYSTEM; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; EXCRETORY SYSTEM). This single opening in birds (and reptiles) contrasts with mammals, wherein the ailmentary system has a separate terminal opening to the exterior.

CLOCK, BIOLOGICAL: see RHYTHMS AND TIME MEASUREMENT.

CLOSE RINGING: see CAGE BIRD; CONSERVATION; MARKING.

CLOSE SEASON: period of protection, covering the breeding season, for birds shot for sport.

CLOUD: see MIGRATION; NAVIGATION; WEATHER AND BIRDS.

CLOUD-SCRAPER: substantive name of some *Cisticola* spp. (see WARBLER (1)).

CLUB: term generally applied to a gathering of non-breeding seabirds on the edge of a breeding colony. Although club sites vary from day to day with, for example, prevailing wind and tidal conditions, they are essentially traditional, offering a sufficient area for congregation, a good vantage point, and ready access and exit. In the great majority of cases, those attending are non-breeders of both sexes, whether immature or adult, also failed breeders. At any colony, the size and composition of the club will vary with the availability of immature birds to join it, depending in turn on factors such as season and the colony's previous breeding success.

Apart from loafing and comfort activities, club members typically perform a wide repertoire of sexual and territorial behaviour, including copulation. The club thus serves as a place where birds may encounter others of comparable age and status, and provides a venue for mate attraction and in some cases at least, preliminary pair formation. Often, as in, for instance, the Gannet *Sula bassana* and Guillemot *Uria aalge*, the males defend temporary sites within the club from which they advertise for females.

CLUMPING: see ROOSTING.

CLUTCH: a set of eggs, i.e. the complete number laid by one female and incubated simultaneously (written c/1, c/2, c/3 etc.) (see CLUTCH-SIZE; EGG; LAYING; also ECOLOGY). For exceptions see BROOD-PARASITISM.

CLUTCH-SIZE: number of eggs laid in a discrete group within a clearly defined, often elaborate NEST. The number of eggs laid varies markedly for a number of reasons.

Natural selection; optimal and most productive clutch-size. It is presumed here that the clutch-size of any species is the product of natural selection, adjusted so as to maximize the parents' contribution to future generations. Three main factors contribute to the clutch-size evolved by any species. Firstly, in species which feed their young, an increase in brood-size means that the parents have to work harder to provide food for them. In practice, however, any increase in feeding rate is not proportional to the increase in brood-size, so that the individual young in large broods receive less than those in small broods. As a result, compared with young in small broods, the young in large broods either fail to fledge or leave the nest lighter in weight and with a lower chance of survival. The outcome is that birds starting off with very large clutches may actually raise fewer young than those with smaller clutches.

Secondly (and this may apply particularly to nidifugous birds such as Anseriformes, Galliformes and most Charadriidae) any increase in clutch-size makes the nest or brood more conspicuous so that losses from predation outweigh the advantages of laying the larger clutch.

The combination of these two factors will dictate the *most productive clutch-size* (that which produces the largest number of surviving young per nest). Nevertheless, a third factor will also influence the clutch-size evolved; this relates to the survival of the parents. Compared with parents of smaller clutches, the parents of the most productive clutches may suffer higher mortality because they have to work harder to feed the larger broods and either put themselves at greater risk from predation or are less able to lay down reserves for moulting and surviving the winter. If this is the case, natural selection will favour an *optimal clutch-size* (that which yields the largest number of surviving young in the parents' life-time); this will be somewhat smaller than the most productive clutch-size.

The number of eggs laid in a clutch varies considerably, both between and often within species. The mechanism by which the number of eggs in a clutch is determined physiologically is not fully known (see LAYING).

Inheritance of clutch-size. All evolutionary arguments have as their basis the assumption that the feature concerned is heritable. Heritability of clutch-size has not been studied widely in birds, but has been shown to exist in the Great Tit *Parus major*. In this species, the female and, by inference, the male both contribute to the clutch-size of the daughter. (Perrins and Jones 1974; van Noordwijk *et al* 1980).

The relationship between food and clutch-size. The production of a clutch of eggs may impose considerable demands on the laying female. In extreme cases such as some of the tits Paridae, some ducks Anatidae, and game-birds Phasianidae, the weight of a complete clutch may exceed the weight of the female herself. The production of such a clutch obviously requires very considerable amounts of extra food, and it seems possible that clutch-size is related to the food supply available to the laying hen. Such a relationship has been demonstrated for 2 migrant species. The Red-billed Quelea *Quelea quelea* migrates short distances between breeding areas. Its body reserves of fat and protein (the latter mainly in the flight muscle) decrease to such a low level during laying that the female's clutch is almost certainly limited by the level of her reserves. The Lesser Snow Goose *Anser caerulescens caerulescens* and other geese which breed in the high Arctic, arrive on the breeding grounds when these are still largely snow-covered. They lay their eggs and sometimes undertake much of the incubation before feeding is possible, relying on the food reserves with which they arrived. In the Lesser Snow Goose these reserves affect the size of the clutch; in the Barnacle Goose *Branta leucopsis* there is evidence that the breeding success is affected by the winter feeding conditions. But in many cases there are good reasons for believing that clutch-size is not controlled by food supply. Firstly, if a bird loses its clutch to a predator during or shortly after laying it, the bird may quickly lay a repeat clutch; the total number of eggs may be considerably in excess of the normal clutch. Secondly, in a few experiments where extra food has been provided early in the breeding season, the laying date, but not the clutch-size, has been altered (see BREEDING SEASON).

Hence it seems likely that the clutch-size of most birds is related to the amount of food the parent birds can collect for their brood, not the amount that is available for the laying hen (but see *Food Supply* below).

Phenotypic variation in clutch-size. Not only are there differences between individuals in the clutch-size laid, but individual birds lay clutches of different size under different circumstances (see ii below). A number of observers have recorded that large clutches may produce more survivors than clutches of average size, an observation which, at first sight, contradicts what has been said above. But evidence suggests that the larger clutches are laid under circumstances when the birds are likely to be able to raise large broods (Perrins and Moss 1974). Two types of circumstance may be involved, though they are not easily separated.

Firstly, clutch-size may vary with the 'quality' of the individual female herself. If more 'able' females (perhaps ones which are better at foraging) lay larger clutches than less 'able' females, large clutches will result in a larger number of surviving offspring than the normal clutches of less able females. The evidence for such an effect comes from experiments in which females who have laid clutches of different sizes are, artificially, given broods of the same size; among these females (who now have broods of the same size) those who laid the largest clutches are most successful at raising young.

Secondly, individual birds may respond adaptively to small changes in the environment; they may lay larger clutches in good habitats (see (vii) below) than in poor ones. There is some recent evidence that birds can respond to the quality of the territory; Magpies *Pica pica* lay larger clutches in territories where breeding success (by other pairs in previous years) has been more successful than they do in territories where breeding success has been lower in earlier years. Such responses will lead to the observation of large clutches yielding higher numbers of surviving young than smaller clutches.

Birds, then, do not simply inherit the ability to lay a clutch of a fixed size; more likely they can be thought of as inheriting the ability to lay a clutch which varies within certain limits and, at the same time, the ability to vary that clutch by 'recognizing', and responding adaptively to, certain environmental features which affect the ease with which the brood can be raised.

Variations in clutch-size. Clutch-size varies both between and within species. Indeed, the same individual bird may lay clutches which differ markedly in size in different years or at different stages of the season. The main features with which variations in clutch-size are associated are listed below:

(i) Taxonomic groupings. Perhaps the most striking variation observed is that between different taxonomic groups (see Lack 1968). While doubtless this can be partly explained by the tendency for birds in each group to be ecologically similar, the differences in clutch-size between different groups are very marked: at the low end are the Procellariiformes in which all species, from the smallest storm petrels (Hydrobatidae) to the largest albatrosses (Diomedeidae) lay only a single egg. At the other extreme are the game-birds, whose precocial or nidifugous young leave the nest soon after hatching and fend for themselves, although they are usually guarded by the hen. Although a few species such as the Argus Pheasant *Argusianus argus* have small clutches (only *c.* 2 eggs), most have much larger clutches. The European Grey Partridge *Perdix perdix*, which in Finland lays clutches of *c.* 19 eggs, has possibly the largest clutch of any nidifugous bird.

Within-species variation in clutch-size can also be correlated with taxonomy, being much larger in some groups than others. Within the Charadriidae, for example, each species has a very constant clutch-size (commonly 4), whereas in other groups such as the owls, the clutch-size of many species varies markedly (see ix below).

(ii) Body-size. Within any given taxonomic group there is a tendency for the smaller species to lay the larger clutches. For example most ducks (Anatinae) lay 7–9 eggs while most geese and swans (Anserinae) lay only 5–6. In some orders, a number of the largest species may lay only a single egg although smaller species have larger clutches (e.g. eagles (Accipitridae); penguins; cranes; auks).

(iii) Egg-size. Egg-size tends to be inversely related to clutch-size, those birds which have large clutches tending to have small eggs and vice-versa. Such a generalization only really holds within taxonomic groups, because different groups have large differences in clutch-size and relative egg-size. A negative correlation between egg-size and clutch-size also holds between individuals of the same species and even between different clutches of the same individual. This has the interesting implication that the bird 'knows' how many eggs will be laid in a given clutch when the first egg is ovulated.

(iv) Nest-type. Many hole-nesting birds lay larger clutches than closely related species which nest in open sites. For example, in the sub-family Anatinae, hole-nesters have an average clutch of 10.4 eggs compared with other species whose average clutch is 5.0. In hole-nesting passerines in Central Europe the average clutch is 6.9 compared with 5.1 for open-nesting species. In general, the hole-nesters also tend to have young that develop more slowly; in the passerines quoted above, hole-nesters fledge at a later age (17.3 days) compared with open-nesters (13.2 days). The difference is believed to be associated with the relative safety of nests in holes. Since nests in such sites are less liable to be found by predators, it has proved advantageous to lay larger clutches and take longer over raising them. In contrast, open-nesting species have smaller clutches with faster development and they tend to have more broods within a season. The hole-nesting Blue Tit *Parus caeruleus* lays a clutch of 11–12 eggs in good habitats in Europe (this is an average figure; individuals may exceptionally lay as many as 18 or 19 eggs); this is the largest clutch laid by any nidicolous species.

(v) Nest-size. Within species, variation in clutch-size has sometimes been related to the size of nest. In a small number of hole-nesting species the female appears to modify the size of her clutch in relation to the size of the hole, laying larger clutches in larger sites; presumably, this is in response to the ability to raise a brood in a certain size of nest. There is some evidence that exceptionally large broods may be stressed, inasmuch as they have difficulty preventing themselves from overheating.

One feature of nest-size which needs explanation relates to the open cup-shaped nest which is so characteristic of many species of passerine. No species seems normally to lay a clutch larger than 6 or 7 eggs in such a nest.

(vi) Latitude. Clutch-size varies markedly with latitude, increasing from the tropics northwards. This holds both when comparing closely related species, and even different populations of the same species, over a wide latitudinal range. Although the variation has been attributed to longer days, enabling birds to find more food in the north, this can at best be only a partial answer. For example, owls have larger clutches in temperate areas than in the tropics, yet most of these birds feed at night and the nights get shorter with increasing latitude. Further, the Snow Bunting *Plectrophenax nivalis* lays increasingly large clutches even beyond the Arctic Circle, although the amount of daylight available to parents for collecting food can hardly differ in such areas in mid-summer.

The most convincing explanation of this phenomenon has been provided by Ashmole (1963) and Ricklefs (1980), that clutch-size is related to the abundance of food per bird. The argument is that in the tropics there is a relatively stable environment, and in the equable non-breeding season, mortality is low. Consequently, populations of all species remain near to the food limit. Furthermore, the spring 'flush' of food is relatively small. As a result of both these factors, parent birds at low latitudes are not able to get large quantities of extra food to raise young, so large clutches are not productive. In contrast, the higher latitudes have a harsher environment outside the breeding season, hence fewer birds in spring and larger spring flushes of food; these factors combined lead to very rich supplies of food per pair and permit the raising of large broods.

(vii) Habitat. Within the tropics, clutches of closely-related species tend to be larger in savanna and grassland habitats than in rain forest. The explanation put forward is the same in principle as that given for latitude, that there is more food available per bird in habitats in which seasonal fluctuations are most marked (Lack 1968). The 'carrying capacity' of savanna outside the breeding season is lower than that of rain-forest, but in the breeding season parents can raise larger broods in savanna because there is more food available per pair.

The above refers to differences in clutch-size between closely related species. In addition, some studies have shown that clutch-size of the same species tends to vary in different habitats. The reasons for this may be related to the density of breeding pairs (see below) or to the quality of the habitat. At least in some areas, pairs breeding in marginal habitats lay smaller clutches, but whether they are poorer quality birds or whether the habitat is a poorer one for raising young is usually not known. Again, the assumption is that natural selection has favoured the laying of smaller clutches in circumstances where it is difficult to raise large broods.

(viii) Density. Clutch-size may vary inversely with breeding density. However, breeding density may affect reproductive output in a number of ways other than by affecting clutch-size. Non-breeding individuals may be more common at high than at low density. This may be either because more birds fail to obtain territories at high densities or, as in the Red Grouse *Lagopus lagopus*, because only the males with the largest territories can obtain a mate.

The reproductive output of the Great Tit is also related to density, but in this case the relationship arises because both clutch-size and the proportion of second broods (see below) decrease as density increases. As a result, there is a strong correlation between reproductive output per pair and breeding density.

The reduction in clutch-size with increasing density tends to be small and is by no means fully compensatory; a doubling of the density does not lead to a halving of the clutch-size. As density increases, the number of eggs per unit area of habitat increases steeply. Hence the most likely explanations for the lowering of clutches at high densities are:

(a) that at high densities the parents find it more difficult to form the eggs, or

(b) that the nests are at greater risk from predation under these circumstances, or

(c) that it is harder to find food for the young at high densities. Natural selection has favoured reducing the clutch under these circumstances since, by so doing, the chances of raising some successful young are increased.

(ix) Age. Clutch-size may vary with the age of the laying hen. The most common situation is perhaps that found in passerines where one-year old, and sometimes 2-year old birds lay smaller clutches than older birds. In some cases there are parallel variations in breeding ability, older birds being more successful than young ones. In multi-brooded species, the annual production of young of the older females may be larger both because they lay more eggs in a clutch and because they make more nesting attempts. For example, in the European Blackbird *Turdus merula*, older females raise on average 6.3 young per season compared with the 3.4 of one-year old birds. The difference arises only partly because of clutch-size (0.4 eggs larger in older birds); the older birds make an average of 3.1 nesting attempts per year compared with the 2.3 of young birds.

Often the male selects the territory and provides food for his mate during laying. It might be expected that older males would be more successful at such activities and that the females would lay larger clutches in response to the increased 'living standards' provided by the older males. Studies in North America on the Common Tern *Sterna hirundo* showed that the female laid a larger clutch if the male brought her an above average quantity of food; it is not known whether the males which brought more food were older than the others.

There are few convincing data demonstrating that when a breeding female becomes 'old' her clutch-size decreases; but this is true for the Hawaiian Goose *Branta sandvicensis*, at least in captivity.

(x) Season. Many birds show no seasonal variation in clutch-size, but among those that do there are perhaps two main trends. In certain species, especially those that are largely single-brooded, clutch-size may decrease as the season proceeds (Fig. 1a). This may be related to either of two factors. There is evidence for some species that the food supply for the young may be less abundant later in the season so that the parents who lay later may find it harder to raise large broods than those that lay earlier. Secondly, and probably inter-related with the first, the birds that breed later may be less efficient, or may be younger birds, and lay smaller clutches accordingly.

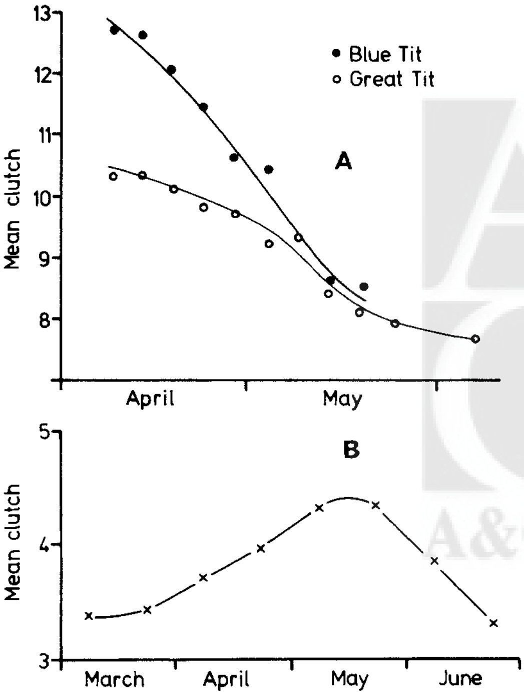

Fig. 1. Seasonal variation in clutch-size. (a) Blue Tit *Parus caeruleus* and Great Tit *P. major*. (b) Blackbird *Turdus merula*. Note the much longer laying season in the Blackbird. (From Lack 1966, Snow 1958).

In other species, such as the European Blackbird, the clutch-size increases during the early part of the season and then declines (Fig. 1b). This trend seems to be related to the food supply, the high clutches in mid-season coinciding with the maximum abundance of woodland caterpillars. Species which lay more eggs in the middle of the season than at either end tend to be multi-brooded.

(xi) Food supply. There is little evidence for most birds that food supply influences clutch-size. However, in certain game-birds it has been suggested that food supply affects not only clutch-size, but also egg quality (and through this, hatching success and subsequent survival). Certain owls, in particular the Tawny Owl *Strix aluco*, Short-eared Owl *Asio flammeus*, and Snowy Owl *Nyctea scandiaca*, lay larger clutches when their small mammal prey are more abundant than when prey are scarce. It is not known whether the female owls lay more eggs because they themselves can obtain more food or because the increased clutch is an adaptive response to the fact that larger numbers of young can be raised on the plentiful supply of food.

(xii) Islands. In a few cases, there is evidence that clutch-size of an island form is lower than on the adjacent mainland. For example, the Coal Tits *Parus ater* on the island of Corsica lay clutches which are about 2–5 eggs smaller than those on the adjacent mainland of France. A number of species breeding in the British Isles have slightly smaller clutches than their European counterparts. Little Owls *Athene noctua*, which were introduced to Britain from Europe in the late 19th century, apparently now lay a smaller clutch than those in nearby Europe, although it seems the reduction in clutch took a few years to occur.

The reason for such differences is not known. However, in some cases islands have a smaller range of species than adjacent mainland areas, but (and perhaps because of this) higher densities of the species which are present. Hence possibly, this situation is a special case of a density effect on clutch-size (see viii above).

(xiii) Non-breeding. One possible clutch-size is zero! For obvious reasons it is difficult to assess the frequency of non-breeding birds. However, in some of the owls and other birds-of-prey, many or even most pairs may fail to breed in years of unusually low prey populations.

In certain other species, such as some of the flamingos, whole populations may not attempt to breed in some years. The reasons for such failures may be related to food supply, though the details are not known.

(xiv) Type of young. The type of development of the young might be expected to affect clutch-size and yet does not appear to do so in most species. Newly hatched young birds fall roughly into two types; those which hatch well-feathered and able to leave the nest and those which are quite incapable of such activity (see YOUNG BIRD). The former (nidifugous or precocial) young hatch with well-developed legs and brains and with their eyes open. In the case of the waders (Charadriidae) the young, and hence the eggs, are relatively large. Presumably, because of the problems associated with incubating such large eggs, the clutch is small, only 2–4. It might therefore be thought that nidifugous young would be associated with large eggs and small clutches. However, clutch-size is quite large and egg size relatively small in some other groups with nidifugous young, e.g. rails, game-birds, ducks, so that there is no correlation between the state of development of the young at hatching and clutch-size.

Reproductive rates and other reproductive tactics. A very large number of species lay a single clutch each year and raise a single brood, but there are a number of ways in which the reproductive rate of birds may be increased.

(i) Multiple broods. A larger number of birds, especially passerines, have more than one brood in a year (see BREEDING SEASON).

(ii) Hatching synchrony. In many birds, incubation does not start until about the time the clutch is completed. As a result all the young hatch at about the same time (synchronously). If food is scarce, all the young will be equally deprived and, if conditions are very bad, they all become weakened and perish. In other species, the female may start to incubate before the clutch is complete and the young will hatch asynchronously over a period of days. Because the young are very different in age and hence in size, the smallest young cannot compete for food on equal terms with its larger siblings. If the food supply is insufficient for the whole brood, the youngest die without depriving their larger brood-mates of food. Hence even when food is scarce, one or two young may be successfully raised. In species which exhibit asynchronous hatching, clutch-size may not vary greatly with conditions, but the brood size is adjusted to match the available food supply. Asynchronous hatching occurs mainly amongst nidicolous birds which catch animal prey; perhaps in these species it is difficult at the time of laying for the female to 'predict' what the level of food supply will be when the young hatch. The main groups which exhibit marked asynchrony in hatching are the cormorants, herons, birds-of-prey, owls and swifts. Other species, such as the House Sparrow *Passer domesticus*, hatch some young together but the last one or two hatch a little later. In the Great Tit early broods tend to hatch synchronously and later ones asynchronously. Such a pattern appears to match the caterpillar food supply which seems to be more predictable early in the season than it is later on (see also GROWTH).

(iii) Polygamy. In a number of species one sex may take two or more partners of the opposite sex; this may be done either sequentially or concurrently (see MATING SYSTEM). Usually it is the male which takes two or several females; less commonly the female may have more than one mate.

In many cases, the advantage to the sex which has several mates is obvious in that more young can be raised per year. The advantage, if any, to the sex which has to share a mate is less obvious since raising young on its own may result in fewer young being raised than when assisted by a mate. Usually, such mating systems involve species with an unbalanced sex ratio, hence possibly the choice for the more common sex may be to accept a polygamous situation or run a high risk of not finding a mate at all.

(iv) Double nesting. In a few species the pair is apparently monogamous but the female may lay two clutches, one of which is incubated by the male while the female herself incubates the other. Species for which this habit are known include the Mountain Plover *Charadrius montanus*, the Spotted Sandpiper *Actitis macularia* and the Red-legged Partridge *Alectoris rufa*; all nidifugous.

(v) Multiple nestings. The nesting pattern is even more complicated in a number of tinamous, the Ostrich *Struthio camelus* and possibly the Rhea *Rhea americana*. In the Ostrich and the tinamou *Crypturellus variegatus* the female lays eggs for a succession of different males, leaving the male to incubate (though in the case of the Ostrich, each nest has a dominant female which shares the incubation). In the tinamous *Crypturellus boucardi* and *Nothoprocta cinerascens* the females go around in small groups laying a 'clutch' jointly before moving on to another male. Such pattern shortens the length of the laying period and hence the risk from predation. The details of these nesting patterns are very poorly known.

(vi) 'Insurance' eggs. In a number of species which raise only a single chick, 2 eggs are laid. For example in the Brown Booby *Sula leucogaster* on Ascension Island, the White Pelican *Pelecanus onocrotalus* and the Lesser Spotted Eagle *Aquila pomarina* 2 young are almost never raised.

The most likely explanation for such apparently wasteful behaviour is that a proportion of all eggs fail to hatch for one reason or another, and if the energy requirements for manufacturing a second egg are not great, the parents can increase their chances of raising a chick by laying a second egg. It does not matter which egg hatches.

In some of the penguins the eggs within a clutch (usually 2) may be of quite different sizes; normally only one of the young survives. Such a strategy may combine the advantages of asynchronous hatching and having insurance eggs (see PENGUIN *Eudyptes*).

(vii) Parasitic birds. Although this subject is covered elsewhere (see BROOD-PARASITISM) it is mentioned here in relation to reproductive output. Since eggs are usually laid at the rate of only one or two per nest, the term clutch-size is not strictly appropriate. The number of eggs laid per season by parasitic birds is not well known. Individual Cuckoos *Cuculus canorus* may lay up to 25 eggs per season (though this was under unusual circumstances where nests of the host were made freely available to the Cuckoo), while the Cowbird *Molothrus ater* may lay 30 or more, possibly in runs of 5 or 6, followed by a gap of a few days; presumably this reflects the ancestral situation when the clutches were laid and incubated by the birds themselves. These numbers of eggs are far higher than the numbers laid by most species and perhaps serve to emphasize the influence of parental care.

(viii) Mound-builders. One group of birds, the megapodes or mound-builders, incubates its eggs by laying them in sand warmed by one means or another (see MEGAPODE). The number of eggs laid by a female is not known for most species, but in the Mallee Fowl *Leipoa ocellata* 72 recorded 'clutches' varied between 5 and 33 with a mean of 18.6.

Rates of evolution. Some of the ways in which birds maximize their reproductive output have evolved over long periods of time, while others may be quite recent. For example, 5,000 years ago few North Temperate birds were breeding where they are today. Hence local differences in clutch-size must have evolved since that time.

Indeed, selective pressures can lead to changes on a much shorter time scale than this. It has been shown for the Great Tit that observed selective advantages could lead to changes of 1.5 eggs per clutch in as little as 10 years (van Noordwijk *et al* 1980). Although some larger species which lay a small clutch do not seem able to alter its size rapidly, this is not likely to hold true for smaller species with larger clutches. Clutch-size should be considered as a dynamic feature, capable of rapid changes if environmental conditions alter. C.M.P.

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CNEMOPHILINAE: see BIRD-OF-PARADISE.

COB: special term for a male SWAN.

COCHLEA: part of the ear (see HEARING AND BALANCE).

COCHLEARIIDAE: a monotypic family of the CICONIIFORMES (suborder Ardeae) recognized by some authors (e.g. Wetmore, Peters) for the Boat-billed Heron *Cochlearius cochlearius*, which in this work (following Mayr, Amadon and Bock) is treated as a member of the Ardeidae (see HERON).

COCHOA: substantive name generally used for the 3 species of *Cochoa* of south east Asia, a distinctive genus within the Turdidae (see THRUSH).

COCK: a male bird; applied without qualification to the male of the domestic fowl—compare HEN. Special terms apply to the males of some species, e.g. DRAKE, GANDER, COB, TIERCEL, BLACKCOCK. The names of certain species have also a special use as terms for the male, e.g. RUFF, and formerly MALLARD.

COCKATIEL: the Australian Parrot *Nymphicus hollandicus* (Cacatuinae) (see PARROT).

COCKATOO: substantive name of the species of the Cacatuinae; in the plural, general term for the subfamily (see PARROT).

COCK-FIGHTING: also called 'cocking', the sport of pitting male domestic fowls against each other in combat; the 'game-cocks' used are specially bred and trained for the purpose (see DOMESTICATION). Betting on the results is a major element. The word 'cockpit' originally signified an enclosure where the 'mains' were held. The sport originated in ancient times in Asia, where the natural spurs on the tarsi were often made more deadly by fitting them with iron spikes. It spread to Greece in classical times, later to Rome, and thence to other parts of Europe, and eventually to the New World. It has been prohibited by law in Great Britain since 1849, and it is now generally banned in many countries, including Canada and the United States. In eastern Asia, female Barred Bustard-quail *Turnix suscitator* are caught and kept for fighting, as also are male Quail *Coturnix coturnix*; and the Russians have a fighting breed of domestic goose.

COCK-OF-THE-ROCK: substantive name of *Rupicola* spp. (see under COTINGA).

COCK'S NEST: see NEST, COCK.

COEREBIDAE: a family of PASSERIFORMES, suborder Oscines; see HONEYCREEPER, also BANANAQUIT; CONEBILL.

COEVOLUTION: reciprocal evolutionary change in 2 (or more) interacting species, whereby each becomes adapted to the interaction. Coevolution may involve an animal and a plant (e.g. a hummingbird (Trochilidae) and a plant which it pollinates) or 2 animals (e.g. a predator and its prey). The interaction may be immediately beneficial to both parties, as in the first of these examples, or immediately beneficial to only one of them, as in the second; both qualify as examples of coevolution, but in practice the term is most often used for interactions that are mutually beneficial. Mutualism is sometimes used as a general term for this kind of interaction. In birds, such interactions mainly involve nectar-eaters (see POLLINATORS) and fruit-eaters (see SEED DISPERSAL). A very different and complex case involves colonially nesting oropendolas and caciques (Icteridae), the nest-parasitic Giant Cowbird *Scaphidura oryzivora*, and several kinds of insects (see BROOD-PARASITISM), and there may be other complex interactions of this kind so far undiscovered.

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COHORT (1): a taxonomic category sometimes interpolated between subclass and superorder (see CLASSIFICATION).

COHORT (2): in population studies, a term used for a group of individuals of similar age within a population, especially a year-class.

COITION: see COPULATION.

COLD: see ADAPTATIONS, ENVIRONMENTAL; WEATHER AND BIRDS.

COLD SEARCHING: see HOT SEARCHING.

COLETO: name, in the Philippine Islands, for *Sarcops calvus* (see STARLING).

COLIIDAE: see below.

COLIIFORMES: an order comprising only the Coliidae (see MOUSEBIRD).

COLLAR: a band or patch of distinctive colour, in some plumage patterns, at least partly encircling the neck (see TOPOGRAPHY).

COLLECTING: see CONSERVATION; MUSEUM.

COLONIALITY: spatio-temporal clumping of nests. At present, there are no objective (nor even widely accepted) criteria as to how clumped nests must be to constitute a true colony, but most are beyond question. The term 'loose colony' is sometimes used for rather more dispersed nests that are still judged to be in a clump relative to the density of nests in the general vicinity (Lack 1968). In other colonies, by contrast, the spacing can be extremely close—often the area that a parent can defend without physically leaving its nest.

Coloniality has evolved independently many times in the Class Aves. Currently, about one-eighth of all avian taxa nest in colonies and there is no major taxonomic restriction to the practice.

Species categorized as 'colonial' often exhibit solitary nesting also, sometimes near major colonies. The reasons for this variability are not known, but it offers a convenient point of research leverage via intraspecific comparisons. Various suggested advantages of coloniality may be tested by studying colonial versus solitary pairs of the same species under the same ecological pressures.

Mixed-species (or 'heterospecific') colonies, though very common, have been little studied. The vague proposition that such colonies are best viewed as 'super-organisms' suffers both from a lack of evidence and from theoretical flaws (specifically, an apparent misunderstanding of natural selection). At present, it seems most reasonable to assume that individuals join colonies to promote their own selfish interests and not on behalf of some higher-level 'systems' function. This does not preclude the likelihood that there may be certain advantages in having a variety of neighbouring species (e.g. nesting near a pugnaciously defensive species), while other advantages (e.g. the selfish herd effect) may be independent of the neighbour's taxonomic identity.

Though many studies address the subject of colony substructure, no general principles have emerged. In a few species, it has been shown that older, experienced breeders occupy the central (safer) territories, giving an age-related 'organization' to the colony. Many more studies have shown merely that the placement of nests (within and between species) is non-random. Perhaps this is due to competition for sites.

The ecological features and life-history of species may show the reasons for clump-nesting. Lack pointed out that most colonial bird species are nidicolous and that most forage in flocks. Darling (1938) noted that there is often high within-colony synchrony of nesting activity, which can make both direct and indirect contributions to individual breeding success. The inter-relation of three characteristics, synchrony, offspring vulnerability during an extended nestling period, and social foraging, is a main topic in the literature of bird coloniality.

The evolutionary question of why clumped nesting arose is a subset of the larger problem of animal group-living in general, with the important difference that bird nests are sedentary. Thus a colony can be regarded as a 'flock' of individuals that must leave a sizeable component of their inclusive fitness in one place throughout the nesting period (see FITNESS). This stationary component (eggs and young) constrains the behavioural options of the parents.

There are several automatic disadvantages associated with any form of group membership (Alexander 1974): (1) increased competition for mates, (2) increased competition for food and space, (3) increased

King Penguins *Aptenodytes patagonicus*. The nests are spread just out of reach of each other. The eggs are incubated on their feet. (*Photo: N. Rankin*).

Quelea *Quelea* nests in Uganda. (*Photo: F. Pölking*).

conspicuousness to predators, and (4) increased risk of disease and ectoparasite transmission. For colonial birds, Hoogland and Sherman (1976) added (5) increased risk of misdirected parental care (resulting from cuckoldry, brood mixing, and possible brood-parasitism). In the many species where colonial nesting has evolved, there must have been one or more benefits of sufficient magnitude to override these disadvantages. There are many proposed benefits for coloniality: here, 7 of the most important are summarized.

Limited nest sites. One simple reason for nest clumping can be that a discontinuous habitat gives the birds no alternative to crowding together. Although simple in principle, this factor probably applies mainly to seabirds nesting on oceanic islands (e.g. albatrosses Diomedeidae). This factor is seldom separable from others (e.g. nesting on remote islands discourages land predators). In non-marine habitats there may be difficulties in judging whether 'suitable' nest sites are discontinuous or not.

Predator detection. An individual's survival chances can be enhanced when there are more eyes watching for danger. This does not necessarily imply any degree of true cooperation: in maintaining vigilance to protect self and offspring each bird inadvertently protects its neighbours by providing useful information. Such information may be communicated via specialized warning signals or automatically by escape behaviour. In foraging flocks of various species, it has been shown that group members generally learn of approaching predators more quickly, more reliably, and at a lower expenditure of watchfulness than solitary birds. Animals in colonies apparently enjoy similar benefits (Hoogland and Sherman 1976); they can use the information for trying to repel the predator, for giving mobile young time to hide or flee, and/or for saving themselves.

Group resistance. Many colonial birds perform collective defensive behaviour to repel intruders and predators. Presumably, the effectiveness of such mobbing attacks is increased by the additional birds in a colony (Kruuk 1964, Hoogland and Sherman 1976). Even if the predator is not driven away outright, it may be distracted enough to reduce its hunting efficiency, thus allowing other lines of defence (e.g. egg crypsis) to work (Tinbergen *et al* 1963).

Numerical swamping. Perhaps the most universal antipredator benefit of colonial nesting is from the reduced risk to each bird's eggs and young, as there are alternative targets for predators: the colony functions as a 'selfish herd' (Hamilton 1971). The fact that predation is often heaviest at colony edges may explain why many colonies are densely packed. (Kruuk 1964, Patterson 1965). On the other hand, colonies are far more conspicuous than a concealed nest (Horn 1968).

Most of the mathematical advantage from this sort of 'hiding behind conspecifics' is gained by the first few dozen pairs (depending on the number and type of major predators). But that advantage continues to be available to the later-joining pairs and the colony may continue to grow for this reason alone. Also, the critical group-size for numerical swamping may be higher for bird colonies than for fully mobile mammal groups because of the extended period of vulnerability to predators.

Cooperative foraging. If individuals feed more efficiently as members of a flock, colonial nesting may be advantageous in helping birds form flocks more easily. There are various ways in which flock-membership can improve individual foraging success (see FLOCKING), including most of the general group-living anti-predator advantages mentioned above (e.g. early detection). In addition, some birds hunt cooperatively. Thus cormorants and pelicans drive schools of fish into shallow water where they are concentrated and more easily captured (Bartholomew 1942).

Various kinds of information about food types, locations, and abundances may also be shared among the members of a feeding flock (see Information Centre Hypothesis, below). Murton (1971) showed that subordinate Woodpigeons *Columba palumbus* watch dominant flock-mates closely and switch food preferences when the dominants do, apparently benefitting from the older birds' experience. In flock-feeding experiments with Great Tits *Parus major*, it has been shown that flock-mates move nearer to a successful individual and search that area for small hidden food concentrations. This type of interaction, known as SOCIAL FACILITATION or local enhancement, is probably very common among flock-feeding birds and may promote coloniality indirectly, via recruitment.

Travel minimization. If the food supply exists in unpredictable but relatively rich patches, exclusive defence of small individual territories may not be profitable. Horn (1968) showed that clumping of nests in the geometric centre of such a zone of patches minimizes the travel/search distance for each bird. Because the patches contain more food than an individual can use anyway, tolerating colony-mates at the food supply incurs no significant cost.

Information centres. In addition to the simple geometric advantage just described, colonial birds may be in a position to monitor the hunting success of neighbours and then follow them to favourable foraging sites. Ward and Zahavi (1973) called such assemblages 'information centres' and proposed that this function was the primary factor promoting the origin and evolutionary maintenance of most bird colonies and roosts. Direct evidence, however, supporting the hypothesis—much less this contention—is in very short supply. Horn actually observed 3 cases of such a system in Brewer's Blackbirds *Euphagus cyanocephalus*: adults that had been feeding on low-yield upland prey followed neighbours who had brought larger aquatic prey to their nestlings.

Several of the same ecological factors are required for this model as for cooperative foraging. Food must be clumped, unpredictable, and locally abundant. In addition, the birds must tolerate close-feeding neighbours: if feeding territories are defended effectively, it is hard to see what advantage is gained by following.

Finally, the adaptive significance of laying synchrony within bird colonies presumably varies from case to case. If predation pressure be significant, it seems likely that pairs breeding in synchrony with their neighbours will obtain more group anti-predator benefits (via detecting, mobbing, and/or swamping) than pairs breeding out of synchrony. Similarly, the group benefits associated with foraging can be more available to birds whose neighbours face similar food demands simultaneously. Mere demonstration of higher reproductive success as a function of synchrony is not, by itself, sufficient for assigning adaptive significance to any of these potentially contributing factors.

The proximate cause of nesting synchrony in colonies is not clearly understood. Although mutual reproductive stimulation by breeding neighbours (the so-called 'Fraser Darling Effect') has been demonstrated in the laboratory (Lott *et al* 1967), its importance to wild populations remains equivocal. D.W.M.

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COLONIZATION: see RANGE CHANGES.

COLONY: a number of birds breeding gregariously, the term vaguely including the location and the nests. For special terms see ASSEMBLY, NOUN OF.

COLORATION, ADAPTIVE: embraces those visual phenomena that subserve survival or reproductive functions in the various relationships between predators and prey, between members of the same or the opposite sex or of a social group, or between parent and offspring. The term may thus be used to include not only modifications of colour, but all aspects of form, adornment, pattern, posture, activity, and background that together determine an animal's appearance in nature and are of value in the struggle for existence. Animal coloration must always be considered in relation to the behaviour associated with it, and to the effect of this upon a potential observer. (For the physical basis of coloration see COLOUR.)

Coloration characteristics fall broadly into two groups; those promoting concealment (cryptic) and those enhancing conspicuousness (phaneric). The former, making for effacement, hinder detection; the latter, acting as advertisements, facilitate identification. The optical-psychological principles upon which recognition of a bird (or of any other solid object) depends include: differences of hue and tone between object and background; differential effects of light and shade, or of relief, that convey the appearance of solidity; shape, or surface-continuity framed by a characteristic contour; cast shadow; and movement. The effectiveness of cryptic and phaneric coloration is due to the suppression or exaggeration, respectively, of these visual characters.

Cryptic coloration. The biological role of cryptic coloration is limited to predator-prey relationships, either affording protection against enemies (procryptic) or facilitating capture of food (anticryptic). Among birds procryptic coloration is common, and anticryptic rare. Again, cryptic coloration may afford either general concealment or special disguise; instances of the latter are rare in birds. The two categories intergrade in a type of coloration known as 'background picturing'.

General resemblance. Every major habitat provides examples of birds that wear cryptic plumage—white in snowlands, e.g. Snowy Owl *Nyctea scandiaca*, Ptarmigan *Lagopus mutus* in winter dress; ochre, buff, or sandy-grey in deserts, e.g. sandgrouse, thickknees, wheatears *Oenanthe* spp., larks; green in the rain-forest canopy or dense foliage, e.g. toucanets (Ramphastidae), some parakeets and conures (Psittacidae), fruit pigeons (Treroninae); variegated browns among grass and reeds, e.g. many waders (Charadrii), crakes (Rallidae), bitterns (Botaurinae), buntings (Emberizidae), grass warblers *Cisticola* spp. (Sylviinae). Of special interest in this connection are species and races of desert larks (*Ammomanes, Mirafra, Spizocorys*) with plumage closely matching the particular ground on which they occur—whether black lava, red or brown earth, or white sand. Such birds have clearly defined habitat preferences, and are reluctant to leave their own terrain for adjoining ground of a different hue (see LARK).

Obliterative shading. Graded coloration, ranging from darkest on the back to lightest on the under parts, neutralizes relief and thus renders the solid body as an apparently flat surface. Obliterative shading forms a basis for the coloration of nearly all cryptic birds, whether or not they carry a superimposed pattern; it reaches its highest perfection in various terrestrial birds of open country, such as bustards, thickknees, buttonquails, francolins *Francolinus* spp., and sandgrouse.

Disruption. In its concealing role, pattern prevents or delays recognition by attracting an observer's attention to itself and away from the form that bears it. Such a distractive effect depends upon the colours being characteristic also of the background (Woodcock *Scolopax rusticola*, Grey Partridge *Perdix perdix*) and embodying strongly contrasted tonal elements that transgress anatomical form and contour and so visually break up surface continuity (Turnstone *Arenaria interpres*, Killdeer *Charadrius vociferus*, Cream-coloured Courser *Cursorius cursor*). Many birds carry dark head-markings so disposed as to coincide with and include the otherwise conspicuous eye. Such coincident elements may take the form of horizontal stripes, e.g. Bobwhite *Colinus virginianus*, Quail *Coturnix*

Willow Grouse *Lagopus lagopus* male in winter plumage. (*Photo*: *E.J. Hosking*).

Lava Gull *Larus fuliginosus* blending with background in Galapagos. (*Photo: E.J. Hosking*).

Grey-breasted Seedsnipe *Thinocorus orbignyianus* incubating. (*Photo: G.L. Maclean*).

Ringed Plover *Charadrius hiaticula* chick showing protective colouring. (*Photo: R.J. Chandler*).

coturnix, Snipe *Gallinago gallinago*, Whimbrel *Numenius phaeopus*, Dotterel *Eudromias morinellus*; or of vertical bars, e.g. Woodcock; or of a combination of both, e.g. Ringed Plover *Charadrius hiaticula*.

Immobility, and shadow concealment. Effective concealment is possible only when it is accompanied by cryptic quiescence. Immobility and the squatting posture, as a reaction to danger, are most highly developed in various cryptic ground-nesting birds of several groups—some female ducks and game-birds, snipe, woodcock, plovers (Charadriidae), coursers *Cursorius* spp., bustards, nightjars, larks; also in highly cryptic nidifugous young, such as Ruffed Grouse *Bonasa umbellus*, Stone-curlew *Burhinus oedicnemus*, Lapwing *Vanellus vanellus*, Ringed Plover, Oystercatcher *Haematopus ostralegus*, and Little Tern *Sterna albifrons*. The crouching posture also serves to obscure or reduce the tell-tale shadow cast by the body.

Background picturing. Disruptive patterns afford concealment in relation to a generalized background. The coloration of species that rest or nest in a specialized habitat may be correlated more closely with the environment; in such species the disruptive design is scenic, and tends to reproduce the background configuration against which it is likely to be displayed—whether of heath, grass, or reed. Such colour schemes are always rendered more effective by appropriate cryptic postures, for example, prone in Owl Parrot *Strigops habroptilus*, Ptarmigan, and Golden Plover *Pluvialis apricarius*, vertical and frontal in Bittern *Botaurus stellaris* and Little Bittern *Ixobrychus minutus*.

Special resemblance. In a few highly specialized cases, cryptic coloration exerts its effect by disguise rather than concealment—colouring, form, and posture combining to produce a more or less exact resemblance to some familiar object of the habitat. Various nightjars afford the best examples among birds. In their usual prone position on the ground, many species resemble fallen bits of wood; frogmouths (Podargidae), which nest on a horizontal tree-fork, adopt an oblique posture and so simulate a broken branch; while the Grey Potoo *Nyctibius griseus*, which lays its single egg on top of a broken tree-stump, incubates in a stiffly erect posture. All these birds close the eyes when in the presence of an intruder, and remain motionless. Nestlings of the Bar-winged Flycatcher-shrike *Hemipus picatus* face one another with their bills pointing upwards and nearly meeting, their coloration and attitude causing the lichen-garnished nest with its contents to resemble a snag on the branch.

Phaneric coloration. Conspicuousness, the basis of all phaneric characters, depends upon the exaggeration of those visual attributes—colour, relief, form, and movement—that tend to be suppressed in cryptic species. Brilliant hues and textures alien to the environment are widely developed, notable examples being seen among gallinules *Porphyrio* spp., macaws (Psittacidae), turacos, toucans, kingfishers, woodhoopoes, glossy starlings *Lamprotornis* spp., tanagers (Thraupinae), and the males of many ducks and game-birds. Countershading is replaced by self-coloration, which reaches the height of conspicuousness in uniformly white or black birds, e.g. swans *Cygnus* spp., pelicans, egrets *Egretta* spp., spoonbills (Plataleinae), cockatoos (Cacatoeinae), and crows *Corvus* spp. Colours and patterns are generally displayed constructively (crest, breast, ruff, tail, and so on); and the contour is often conspicuously framed with a marginal pattern (tail of Ruffed Grouse, throat of King Bird-of-paradise *Cicinnurus regius*). Frequently, the eye is made prominent in its setting of feathers, e.g. owls, white-eyes *Zosterops* spp., or ornamental skin, e.g. many vultures (Aegypiinae), storks, cranes, game-birds, hornbills, and toucans. Eye-spots are displayed (Argus Pheasant *Argusianus argus* and peacock pheasants *Polyplectron* spp.) and reach their most extravagant appearance in the huge paired ocelli, each formed by a purple-red gular sac framed in a broad circle of white feathers, in the Blue Grouse *Dendragapus obscurus*. Adornments (plumes, fans, ruffs, wattles, inflatable air-sacs, and the like), and above all specialized activity (including orientated postures, antics, dances, and utterance of sounds both vocal and instrumental) contribute further to the impact made upon the observer.

Phaneric (unlike cryptic) coloration subserves a wide range of biological functions, both interspecific and intraspecific—in relations between enemies and prey (warning, adventitious warning, bluff, BATESIAN MIMICRY, and deflection); between rival males (threat and distance recognition); between opposite sexes (sex recognition and epigamic display); between members of the same or different species (social, and specifically distinct signals); and between parent and offspring (feeding releasers and indicators).

Warning coloration and adventitious warning. Warning characters (proaposematic) are associated with deterrent or noxious attributes that render a species relatively unacceptable to predators (see PALATABILITY OF BIRDS AND EGGS). In another category (allosematic) are certain relatively defenceless birds that habitually nest close in association with aggressive aposematic aculeate hymenoptera such as *Polybia*, *Polistes*, *Apis*, *Azteca*, *Oecophylla*. The insects tolerate the presence of the birds (which build pensile or covered nests) but not other intruders; thus the birds secure themselves from attack by most enemies. Such nesting associations are known among tropical birds of widely different groups—caciques (*Cacicus*) in South America; mannikins (*Lonchura*), estrildid or weaver-finches (*Uraeginthus*), and striped swallows (*Hirundo*) in Africa; bayas (*Ploceus*) in Malaya; and bush-warblers (*Gerygone*) in Australia (see also NESTING ASSOCIATION).

False warning coloration. Bluffing characters (pseudaposematic) include so-called 'terrifying actions'—fluffing of feathers, spreading wings, demonstrating with claws or bill—as in the intimidating displays of young owls and hawks, and Batesian mimicry. Instances of the latter are rare among birds e.g. *Oriolus* ('*Mimeta*') and *Philemon* in Indonesia (see MIMICRY). In an aggressive (pseudepisematic) rather than a protective role are the wonderfully detailed mimetic resemblances that the eggs of various cuckoos bear to those of the foster-parents (see BROOD-PARASITISM).

Deflection displays. These serve to deflect the attention of enemies away from the more to the less biologically valuable or vulnerable members (incubating parent, or nestlings) of a social group. Inter-individual deflection (parasematic) operates both in the relations between the sexes and in those between parents and offspring. In the former category is the conspicuous appearance of various male ducks and pheasants, and the delayed moult of certain male ptarmigan *Lagopus* spp., which diverts attention from the incubating female; in the latter, the so-called 'injury-feigning' behaviour of the brooding parent, whose movements and posturing (falling, lying on one side, leg-trailing, wing-dragging, wing-flapping, or quivering) advertise its whereabouts at a distance from the nest. Such displays are known to occur in many avian orders—Gaviiformes, Anseriformes, Galliformes, Gruiformes, Charadriiformes, Columbiformes, Strigiformes, Caprimulgiformes, Passeriformes; they do not appear to have been recorded in any other class of animal (see DISTRACTION BEHAVIOUR).

Social signalling characters. Social recognition, or guide-marks (proepisematic), such as those displayed in flight on the wings, tail, and rump of many waders (Charadrii), serve to ensure contact between members of a flock, or to release and direct following behaviour. The patterns have few components and are striking and distinctive. In cryptic nidifugous young (Lapwing, Ringed Plover, Egyptian Plover *Pluvianus aegyptius*) a white nuchal band, when displayed, assists the parent to locate and reassemble the brood. The predominantly white plumage of many sea birds—gannets, albatrosses (Diomedeidae), gulls, and some terns—is socially advantageous as a signal of the whereabouts of a locally and sporadically plentiful food-supply (fish shoals, etc.). In a different category are the specifically distinctive characters that serve to prevent confusion with members of closely related species. Notable examples are the almost heraldic colour-schemes of toucans, the speculum in ducks, and the head and neck characters of penguins and auks.

Threat and distance recognition. Threat characters are directed against rivals, usually of the same sex (antepisematic), and associated with combat, actual or potential. Under this head are included close-range aggressive threat, in which the characters displayed indicate a readiness to fight (Blackcock *Tetrao tetrix*, Junglefowl *Gallus gallus*, and Ruff *Philomachus pugnax*); and recognitional threat, which advertises the presence of a potential competitor at a distance. Characters (both visual and auditory) used in the latter context are generally significant in relation to territorial defence (monogamous, and some polygamous, territorial species); by deterring a rival from intrusion, they obviate the need for combat.

Courtship and display. Characters that promote the meeting and mating of the sexes and subsequent phases of the reproductive cycle (epigamic) are discussed elsewhere (see DISPLAY).

Feeding indicators and releasers. Adornments with a releasing and directing function connected with the feeding of nidicolous young are found in several orders. Nestlings that are directly fed by parent or fosterer (e.g. Passeriformes, Cuculidae) commonly have the gaping display enhanced by wide bill flanges and a brilliant mouth-lining (see TONGUE). Red, orange, and yellow (the colours displayed by ornithophilous flowers) are frequent in these quasifloral displays, which may, as in the Bearded Tit *Panurus biarmicus* (white projections set on a background of red and black and surrounded by the yellow gape), be detailed and elaborate. The mouths of various nestlings reared in dimly lit surrounding are bordered with white (Jackdaw *Corvus monedula*, glossy starlings *Lamprotornis* spp.). In some species of which the young are nidifugous, or thrust their heads into the parent's mouth to obtain food, the parent carries the relevant ornaments. Thus the red spot on the gonys of the adult Herring Gull *Larus argentatus* releases and directs the pecking response; while in the Gannet *Sula bassana* and Cormorant *Phalacrocorax carbo* the mouth-lining of the adult displays conspicuous colour—black in the former, yellow in the latter (see RELEASER). H.B.C.

Armstrong, E.A. 1947. Bird Display and Behaviour. (2nd edn.). London.
Cott, H.B. 1957. Adaptive Coloration in Animals. (2nd edn.). London.

COLOUR: in birds especially that of the feathers (see FEATHER; PLUMAGE). The colours are due to the reflection of some but not all the components of the incident white light. When all the components of white light are reflected the bird will appear white. Colours can be removed from incident white light—(a) by the physical nature of the reflecting surface, giving structural colours, and (b) by certain chemical attributes, giving pigmentary colours. Some colours are due to a combination of these two methods. The removal of some parts of the spectrum by these methods results in the reflection of the remaining parts.

Structural colours. Those of birds are due either to interference, giving iridescent colours that change with the viewing angle, or to the scattering of light, giving non-iridescent structural colours. The structure responsible for iridescence is present in barbules that are flattened for part of their length and twisted so that one of the flat sides comes to face the observer. Barbule torsion is accompanied by loss of the hooklets and flanges; this reduces the mechanical strength of the vane, and so fully iridescent colours are not found in flight feathers. It was formerly thought that all iridescent colours were due to interference in the thin outer layer of the barbule keratin. It has now been found that in some feathers, including those of hummingbirds, highly refractive melanin granules beneath the barbule surface are responsible for the interference.

Non-iridescent structural colours, produced by the scattering of the shorter waves in white light by very small particles (Tyndall scattering), do not alter with the angle of vision. If the diameter of the particles is less than the wavelength of red light, more of the short-wave components of white light will be reflected and the structure will appear blue. In non-iridescent blue feathers the scattering particles are actually minute air-filled cavities within the barb keratin. Such feathers appear blue in reflected light, but dull brown in transmitted white light owing to the background of melanin.

Pigmentary colours. These are widespread in the bill, 'soft parts' and feathers of birds. The commonest pigment of birds is melanin which usually occurs as granules, is insoluble in most solvents (but can be dissolved in alkalis), and has no characteristic absorption bands. Melanin is not always black (eumelanin), but may be brown, red-brown, or even yellow (phaeomelanin). Eumelanin occurs in crows, the Blackbird *Turdus merula*, some gallinaceous birds, and many others; brown or red-brown phaeomelanin gives the dull colours of many birds showing protective coloration, and yellow phaeomelanin, the yellow colour of the down in domestic chicks. Melanin formation in birds may be influenced by sex, age, and season (see PLUMAGE, ABNORMAL).

Carotenoids are organic compounds consisting of carbon and hydrogen (carotenes) or carbon, hydrogen and oxygen (xanthophylls). They are soluble in organic solvents, are characterized by their behaviour on a chromatographic column, and by their absorption spectra. They are responsible for the colour of many red and orange feathers. Egg yolk has two carotenoids, lutein and zeaxanthin, and the red wattles of the Pheasant *Phasianus colchicus* contain astaxanthin. Growing feathers of Canaries *Serinus canaria* can be made red by feeding with paprika, which contains capsanthin.

Like other animals, birds are unable to synthesize carotenoids, and they obtain them directly or indirectly from plants. The bright red yolk of the Gentoo Penguin *Pygoscelis papua* is due to astaxanthin in the crustacean diet, and the pink of flamingos to a similar pigment derived from blue-green algae and aquatic invertebrates. Carotenoid deposition is often selective; thus feathers have only xanthophylls, whereas bill and skin may have both carotenes and xanthophylls.

Haemoglobin, the red tetrapyrrole respiratory pigment of vertebrates and some invertebrates, is not normally seen as an external colour in birds. It does, however, colour the wattles of the Turkey *Meleagris gallopavo* and the bare head and neck of some vultures (Aegypiinae). There are also other tetrapyrrole pigments, e.g. the protoporphyrin of most egg-shells (Kennedy and Vevers 1976); a fragment of domestic hen eggshell shows absorption bands when seen in transmitted light, and also the typical red fluorescence of porphyrin in ultraviolet light. Porphyrin also occurs in the feathers of owls and bustards and in the pink down of some birds.

The bright red wing-feathers of turacos are coloured by turacin, a copper porphyrin, which is extracted by dilute ammonia to give a purple-red solution. The green feathers of some turacos contain turacoverdin, the relationship of which to turacin is not completely understood. See also TURACO.

Two types of pigment, of unknown composition, occur in certain parrots. In one type the pigment is pale yellow in visible light and fluorescent yellow-gold, sulphur-yellow, or green in ultraviolet light. The fluorescence disappears in alkali, but is not affected by acid. The crest of some cockatoos *Cacatua* spp. is coloured by one of these pigments.

The second type consists of non-fluorescent red or yellow pigments, chemically quite distinct from carotenoids, found in the Budgerigar *Melopsittacus undulatus* and some other parrots.

Combined effects. Some colours are due to the combined action of two or more pigments, or of pigment and structure. Thus in many green feathers the outer layers of the barbs contain yellow pigment that filters some of the short-wave rays out of the incident white light. Below this filter, box cells containing minute air spaces scatter the remaining short waves; as a result, the feather appears green. If the filter pigment is dissolved out the feather becomes blue, as in ordinary Tyndall scattering. When the filter is carotenoid it can probably be bleached out under natural conditions, e.g. in the tropical magpie *Cissa*, which is green in subdued forest light, but blue when living in open sunny country.

Olive-green is caused by the juxtaposition of tiny black and yellow pigment spots. Thus in the Greenfinch *Carduelis chloris* and in some tits there is melanin in the barbule tips and yellow carotenoid in the barbs and barbule bases.

Purple occurs as a mixture of Tyndall scattering and red pigment, e.g. in the Blossom-headed Parakeet *Psittacula cyanocephala*, in which the barbs have a structure producing scattered blue, and the barbules contain red pigment.

Colours may be modified by a structural attribute which alters the surface texture. Short feathers growing out perpendicularly from the body produce the appearance of velvet, e.g. the nape feathers of Teal *Anas crecca*. Twisting of the barbs to expose their flat shiny surfaces gives an effect of lacquer, e.g. in some *Pitta* spp. Powder particles on the feather surface reflect light at numerous surfaces, giving the dull, greyish colours of some pigeons and cranes.

Cosmetic coloration. Some birds adorn their plumage with coloured secretion from the preen gland (see OIL GLAND). The Great Indian Hornbill *Buceros bicornis* rubs its bill on the outlet of this gland and transfers the yellow secretion to some of the white wing feathers. The pigment (a carotenoid) bleaches in air and light, and is frequently renewed. Such cosmetic coloration may also account for the pink suffusions seen on the breast of the Black-headed Gull *Larus ridibundus* and the White (or Rosy) Pelican *Pelecanus onocrotalus* during spring (Stegmann 1956). These colours are known to disappear quickly in most museum skins. G.V.

Fox H.M. & Vevers, G. 1960. The Nature of Animal Colours. London.

Kennedy, G.Y. & Vevers, H.G. 1976. A survey of avian eggshell pigments. Comp. Biochem. Physiol. 55B: 117–123.

Stegmann, B. 1956. Ueber die Herkunft des flüchtigen rosenroten Federpigments. J. Orn. 97: 204–205.

COLOUR DYING: see MARKING.

COLOUR PHASE: see PLUMAGE.

COLOUR RINGING: see MARKING.

COLOUR STANDARDIZATION: involves the integration of (1) language or symbols, (2) either colours of which the names are widely understood or else colour samples in an atlas or chart, and (3) the variables in biological materials being described. The result should be comprehensible to persons other than the describer. Standardization can be done at different levels. One is by use of generally understood colour terms, in combination with modifiers as needed, as is done in most non-technical works on ornithology. Another consists in comparing biological materials with colour samples on a chart or in an atlas, these being designated by words or symbols. The latter can be more precise, but the reader of descriptions prepared in this manner must have access to an equivalent copy of the chart or atlas in order fully to comprehend the descriptions.

In practice in taxonomy, and in view of the range of variation in most biological materials, one compares specimens or series of them—not colour descriptions of each; describing is an aftermath of comparing. The specimens then become the points of reference, not named colours in an atlas (although the describing may be in terms from an atlas—see TYPE SPECIMEN). To utilize the results of such comparisons to the full one must again refer to the same or equivalent specimens.

In written descriptions that are intended to be meaningful to the majority of readers, it is desirable to use as few colour terms as possible. For most persons, such a list probably does not exceed 50 terms. An analysis of all terms used in all descriptions in several standard works reveals that a larger list is unnecessary.

The following includes the *colours* that are in widespread accepted use, the *names* being those in general use except that certain 'pure' or 'spectral' colours are more accurately designated; after a 'spectral' colour is listed, any of its 'impure' derivatives that are included here follow in parentheses: ruby (rose, dusky brown, pink), scarlet (blackish brown), scarlet-orange (chestnut, brownish red, fuscous, rufous, flesh, sepia, tawny, cinnamon), orange (brownish olive, buffish brown, smoke-grey), orange-yellow (olive, buffish yellow, cream, straw-yellow), yellow, yellow-lime, lime, lime-green, green, emerald, turquoise-cobalt, cobalt (pearl-grey), cobalt-ultramarine, ultramarine, ultramarine-violet, violet (sooty black), violet-magenta, magenta.

Such colour terms can be modified, as required and where logical, by terms of 'lightness'—pale, light, medium, dark, deep. Or they can be modified by combination with neutrals; pale greyish, light greyish, etc. Note that *black* and *white* are absolutes; attempts to modify them, such as 'greyish white' or 'brownish black' are incorrect. Metallic colour names widely used in ornithology are: bronzy, coppery, golden, leaden, silvery. They combine colour and texture. The following terms or phrases, which refer to texture alone or are used in combination with colours, are also widely used in ornithology: burnished, dull, glossy, hoary (or frosted), iridescent, having a sheen, silky, velvety, waxy.

If one departs from generally understood terms and uses a chart or atlas, the standard used should always be clearly indicated. Many coloured descriptions have been based on Ridgway's *Color Standards and Color Nomenclature* (Washington, D.C. 1912), now a rare book. A more workable standard, but using symbols instead of words, is the Villalobos-Dominguez and Villalobos *Atlas de los Colores* (Buenos Aires. 1947); it includes a concordance of symbols and Ridgway names. R.S.P.

Palmer, R.S. 1962. Handbook of North American Birds, vol. 1. New Haven, Conn., and London. (See Introduction, at pp. 4 and 8, with colour chart.)

COLOUR VISION: see VISION.

COLUMBIDAE: see below.

COLUMBIFORMES: an order, alternatively 'Columbae', comprising 3 families: Columbidae (PIGEON), Raphidae (DODO, extinct), Pezophapidae (Solitaire, extinct, see under DODO).

COLUMELLA AURIS: the ear ossicle, alternatively 'stapes' (see HEARING AND BALANCE; SKULL).

COLY: alternative name for MOUSEBIRD.

COLYMBIDAE: together with 'Colymbiformes' (alternatively 'Colymbi'), discarded familial and ordinal names formed from the generic name *Colymbus* Linnaeus 1758, applied to the Gaviidae (see DIVER).

COMB: see INTEGUMENTARY STRUCTURES.

COMBASSOU: substantive name, alternatively 'indigo-bird' or 'indigo-finch', of *Hypochera* spp. (see WHYDAH (1)).

COMET: substantive name of *Polyonymus caroli* and *Sappho sparganura* (see HUMMINGBIRD).

COMFORT BEHAVIOUR: general term for a complex of basic, highly stereotyped maintenance activities concerned with the care of the plumage and covering associated behaviour (see also ROOSTING). Such phenomena are broadly similar throughout the whole class Aves, the main differences, especially between aquatic, terrestrial and arboreal birds, being related to structure and habits. In original or ritualized form they often occur as pre-flight or other displays, and are also a source of so-called 'DISPLACEMENT ACTIVITIES'.

Feather maintenance. It is essential that the plumage, especially the wings, be kept in sound order, both for the primary purposes of insulation and flight and for use in e.g. display and camouflage. This is achieved by routine maintenance, including repair of the feather structure, dressing with preen-oil and other organic liquids, and the removal of unhygienic or damaging substances, both those originating from the bird itself (e.g. excess or stale preen-oil, other lipids, carbonic and other exudates shed via the skin and feathers) and from the external environment (e.g. dirt, ectoparasites). In several cases, special movements are used to care for the more inaccessible parts, especially the head and undersurface of the primaries. The main patterns of feather care in the majority of birds include bathing, drying, oiling, preening and plumage-scratching. These appear to form a homogeneous functional group to which the activities of DUSTING, ANTING, SUNNING or even SMOKE-BATHING could be subsidiary.

Bathing. It seems best to restrict this term to cases of true bathing in water involving special movements used deliberately to wet the plumage, either 'spontaneously' in routine feather care sessions or in direct response to the soiling of the plumage; in non-passerines particularly, these bathing movements may be accompanied by 'washing' actions—the rolling of the head over flanks and back, plumage-scratching, and vigorous preening (see below). Most species bathe but a few groups that dust themselves do not (see DUSTING).

There are 7 methods of bathing shown by passerines and other land-birds: (1) stand-out bathing (so-called 'splash-bathing') while settled on land at the edge of the water; (2) stand-in bathing while standing or crouching in the water itself (practised by most taxa); (3) in-out bathing while jumping repeatedly into the water and out again (babblers); (4) flight-bathing on the wing by a series of dips and rises (swifts and swallows); (5) plunge-bathing by diving from a perch onto the surface of the water, sometimes repeatedly (kingfishers and tyrant flycatchers); (6) rain-bathing by deliberate exposure to precipitation (parrots, woodpeckers and larks); and (7) foliage- and dew-bathing against wet vegetation (hornbills).

In typical stand-in bathing, the bird e.g. a Robin *Erithacus rubecula* ruffles its feathers and wets the plumage by repeatedly dipping head and breast into the water while shaking the body from side to side and flicking both wings rapidly up and forward, this being the limit of the movements performed by the stand-out bather. It next wallows with head raised and rear-end submerged, tail fanned, while flipping water across its back with one wing at a time. Feather ruffling and the shaking of head, wings and body also occur in the other bathing methods, but the details are hard to follow. Specialist rain-bathers have characteristic postures with feathers ruffled, wings fully extended horizontally, and tail spread. Most families or subfamilies use one of these methods exclusively, but some two or even more. For example: as well as stand-in bathing, pigeons will rain-bathe, adopting a posture similar to that used in SUNNING; vireos will stand-in bathe briefly at times during spells of plunge-bathing into shallow water; wrens will in-out bathe at times instead of or before their more usual stand-in bathing, apparently when cautious or testing the depth of the water; and babblers will foliage-bathe as well as in-out bathe. True rain- and especially foliage-bathing seem to be employed by many taxa as an alternative, if subsidiary, bathing method to their main one. However, rain-bathing is often confused with a bird's attempt to dry itself when caught in the rain (see below)—though a special RAIN-POSTURE may be adopted. Some species that normally stand-in bathe will sometimes make incomplete, often clumsy, attempts to bathe in the rain or in wet vegetation.

Blackbird *Turdus merula* juvenile bathing. (*Photo: E.J. Hosking*)

Many seabirds and waterbirds, e.g. penguins, divers, grebes, gannets and boobies and most other pelecaniform birds, and waterfowl, swim-bathe while floating in deep water. Some, e.g. gulls and certain rails, also stand-in bathe in shallow water. Highly aerial seabirds, such as frigatebirds and certain terns, are solely flight-bathers. The swim-bathing of grebes, typified by the Great Crested Grebe *Podiceps cristatus*, is of two main types. When surface-bathing, the bird performs a series of ducking-and-rubbing actions, dipping head, neck, and forebody under water and rubbing the head against the flanks, and also a series of wing-thrashing actions, beating the partly open wings against the water; it may also shuffle the folded wings in the water, and 'barge-swim' with rear-end submerged and wings extended below the surface. When dive-bathing, the grebe makes a series of kick-dives to submerge entirely with feathers ruffled and wings loosely open; between dives, it floats immobile, low in the water, wallowing or soaking. The surface-bathing of the Anatidae (swans, geese, and ducks) is basically similar to that of grebes, with head-ducking and wing-thrashing sequences; there is no barge-swimming, but waterfowl often somersault. Dive-bathing in the Anatidae, however, takes the form mainly of sudden total submergences with the wings open; especially when a number of birds take part, it is interspersed by flapping over the surface and by short flights—as if the birds are fleeing from a predator ('dashing-and-diving'). The surface-bathing of gulls too is basically similar, that of penguins apparently rather less so, but no dive-bathing has been described for either group. Gulls have a sideways rolling action (so-called 'plunging') and penguins a special 'body-thrashing'. The Brown Booby *Sula leucogaster*, like most other sulids, often starts a bathing session with a series of shallow flight-plunges; when surface-bathing, it interrupts the usual activities of head-dipping, wing-shuffling, etc. by banging the carpal joints of the wings against the water and also by rolling laterally with wings fully extended onto its side or back. It may roll from side to side or at times turn a complete somersault.

In many cases, a bird bathes just to dampen its plumage evenly as much as possible without actually soaking it. The main aim then would seem to be to facilitate the oiling and preening which typically follow. At times too, a bird will bathe in order to cool itself. A distinction needs to be made between ordinary routine or standard bathing, performed fairly frequently (in grebes, several times a day) and a thorough bathe, performed less often (in grebes, perhaps just once a day). The thorough bathe of a grebe consists of prolonged, intense surface-bathing and dive-bathing; it is followed by a session of long and thorough feather care, special attention being given to the wings. Even so, such a bathe must fall short of a real drenching which would destroy the waterproofing and buoyancy of the plumage. In landbirds however, a thorough bathe can involve a really good soaking—providing that the feathers are not damaged or flying efficiency totally impaired. A passerine indulging in such a bathe will on occasion turn itself into a mass of dishevelled, watersoaked feathers, repeatedly exposing and closing its feather tracts, forcing water into the apteria and squeezing it through the tracts, thus rinsing the skin and feather bases most efficiently. In all cases of such bathing, the bird needs the opportunity and sufficient time afterwards to groom itself thoroughly in safety, so the frequency and timing of such sequences has to be strictly controlled.

Pied Shag *Phalacrocorax* ('Hypoleucos') *varius* wing-drying posture. (*Photo: G. Moon*).

Drying. All birds make deliberate movements to remove surplus water from the plumage quickly, both during and after bathing, accidental wetting from precipitation, etc.; these drying movements may continue intermittently during the oiling and preening session that typically follows. In grebes, waterfowl, and many other non-passerines, the drying actions after bathing are basically the appropriate comfort-movements (e.g. body-shaking, wing-flapping) performed more frequently or more intensely than usual and often interspersed by head-rolling and rapid preening (so-called 'wiping') and by other feather care actions—see below. Some birds (e.g. ducks, gulls) shake themselves in flight, and, especially in those species that leave the bathing area to oil and preen, normal flight also facilitates drying. Diving birds when feeding perform drying movements from time to time during pauses and lulls on the surface and at the end of the diving session. Cormorants and darters adopt a characteristic spread-wing posture after diving for food or bathing, perching thus often for long periods; similar attitudes being found also in a number of other large birds when wet; however, such behaviour may well have other functions besides drying, including thermoregulation (see HEAT REGULATION; SUNNING). Passerines do not wing-flap but, in addition to wing-oiling type and other preening actions (see below), perform various shaking movements to dry themselves; of these last, the most distinctive is 'whirring', a rapid vibration of the tail and wing tips simultaneously, together with a general ruffling of the plumage. The passive use of air currents and the heat of the sun at times is probably widespread in birds as auxiliary means of drying.

Oiling. In species with a functional OIL GLAND, the plumage is typically anointed with the fatty secretion (preen-oil) of that gland immediately following bathing and initial drying. The oil is obtained, a few or several times, during the first minutes of the oiling and preening bout: the bird reaches back and squeezes the nipple of the gland between the mandibles; it may also push the bill and chin across the gland or its associated tuft of feathers or down, and in the case of species with long necks (e.g. grebes), rub or roll the head on it. Oil is then distributed over the plumage mainly by rubbing and preening with the bill and by rubbing and rolling with the head (so-called 'oil-preening'); also by scratching with the foot. In most taxa, the head is oiled indirectly by contact with other parts of the plumage, including the wings. In passerines the bird also gets oil on the bill directly, then transfers the oil to one foot by scratching the bill and finally to the head feathers by scratching all over the head rapidly, moving the head under the foot while so doing. The undersurface of the primaries also presents problems of access for efficient oiling and preening. Many non-passerines oil this area by lowering the carpus, raising the wing-tip, and turning the head round to it over the back for treatment with the bill as in normal preening. Grebes rub the primary tips alternately on the oil gland direct by persistent wing-twitching after a thorough bathe. Passerines oil the under surface of the wings with the bill or with the bill and head together, extending one wing at a time sideways and forwards, carpus uppermost, and often alternating from wing to wing rapidly. Wing-oiling type movements also help to dry the wings (see above). Typically, oiling follows on directly from bathing and drying; in some taxa however (e.g. boobies) there may be a further oiling and preening session long after the initial bathing-drying-oiling-preening sequence, perhaps stimulated by secretion of fluid from the nasal-glands.

Powdering. In those taxa with powder-down patches and tracts (see PLUMAGE), the material produced permeates the plumage, aided by preening, and appears to supplement preen-oil or, in those birds lacking a functional oil gland (e.g. many pigeons), to replace it. After fouling the feathers of head and neck with slime from their fish prey (eels, etc.), bitterns and herons rub the affected parts on the powder-down patches, then scratch off the slime and powder using the pectinated claw, apply preen-oil, and finally preen thoroughly.

Preening. True preening (so-called 'nibble-preening'), the arrangement, cleaning, and general maintenance of the plumage using the bill, is the basic and most important activity of feather care. It occurs frequently, in short or more prolonged bouts, throughout the day especially during loafing, either as the climax of the bathe-dry-oil-preen sequence or independently. In the latter case, it may be done as routine or in response to the soiling or disarrangement of the feathers or because of irritation. When preening without prior bathing, some birds e.g. grebes, wildfowl, and waders (Charadrii) will deliberately wet the bill by dipping it in the water periodically during the bout. Longer preening sessions in particular tend to be structured, certain areas of the plumage being treated in fixed sequence.

Two main sets of bill actions are used in preening: (1) with the mandibles opening and closing, the cutting edges operating against each other (nibbling); (2) with the mandibles closed or passively open, and operating as a single unit (stroking). The first set is especially important for working in preen-oil, re-arranging the plumage, repairing split webbing, and removing waste matter. Nibbling (mandibulating) is the most thorough and accurate preening method: an individual feather or small group of contour feathers is seized in the mandibles and passed between them, working from base to tip; or attention is concentrated at or near the calamus of the feather and on the adjacent area of skin. In birds with fine or small bills, especially passerines, nibbling often consists of repeated tiny peckings with the tips of the mandibles, but birds with large or broad bills have less precise and delicate movements. Waterbirds may perform particularly vigorous nibbling actions during bathing (so-called 'washing' in Anatidae) or during oiling and the initial phase of the subsequent preening ('snapping' and 'biting' in gulls). Drawing or 'feather-stripping' is related to nibbling, and often alternates with it, single feathers or groups being pulled through the bill in one movement. The stroking actions are less skilful than the others, which they supplement, and are used to dry the feathers, smooth them down, and apply preen-oil. When stroking, the bird moves the closed bill rapidly down the feathers, usually in the direction of the alignment of the plumage. A more vigorous treatment of whole areas, with closed or partly

Bar-tailed Godwit *Limosa lapponica* preening. (*Photo: J.B. & S. Bottomley*)

Robin *Erithacus rubecula* preening. (*Photo: J.B. & S. Bottomley*)

open bill, is termed 'stropping' in grebes; similar movements occur in gulls and penguins, while the 'wiping' of penguins involves the head also and is associated particularly with drying. Quivering is a trembling action of the closed bill down the feather; this and stroking are used to preen the primaries, particularly in passerines.

As well as the bill, the head and foot are employed subsidiarily in preening, especially for drying and oiling. The head itself is preened by scratching (see below) and by being rubbed against other parts of the plumage. In some taxa, one individual may preen another (see ALLOPREENING); though this is often thought to be primarily of social significance, it must also function in feather care at times—especially if reciprocated and confined to the head and other areas inaccessible to the bird's own bill. Parents may preen their helpless young.

Red-footed Falcon *Falco vespertinus* scratching. (*Photo: P. Munsterman*).

Plumage-scratching. This is effected by one foot at a time, usually while the bird supports itself on the other though some species will scratch in flight, and is of two types: (1) simple head-scratching, so-called 'basic scratching' or 'scratching reflex', an immediate response to sudden irritation on the head-parts; and (2) scratch-preening, so-called 'extended scratching', a supplementary form of preening, usually of the head-parts, but in some cases also of other areas. The first type may occur at any time, and is by far the more common, the second mainly during bouts of feather care. The head-oiling of most passerines provides a good example of scratch-preening; in those taxa with a pectinated claw, this preening comb is used for prolonged scratch-preening (true combing). Hummingbirds with particularly long bills will scratch-preen the dorsal plumage, wing, and vent, while others confine their attention to head, bill, hindneck, chin, and upper throat; in all cases, the scratch-preening movements tend to be slower and more deliberate than those of simple head-scratching. Some parrots use similar movements for scratch-preening the face, employing the toes like fingers, or rub the face against the clenched toes. The Budgerigar *Melopsittacus undulatus* scratch-preens its vent area using the upper part of the toes, the joint between them, and the tarsus.

There are two methods of scratching the head: direct or 'underwing' scratching, with the foot brought straight up to the head without involving the wing; and indirect or 'overwing' scratching with the foot brought up above the humerus after the wing has been lowered. In simple head-scratching, each species typically uses one method only, and that is usually characteristic of related species up to the family or subfamily level; in only a few groups, e.g. the American wood-warblers (Parulidae), differences exist at the genus level. No direct-scratching species, however, has ever been seen to use the indirect method for either simple head-scratching or scratch-preening. Indirect-scratching species may use the direct method but mainly during ontogeny or in flight. Other variation in scratching method may be related to the type of plumage-scratching involved, the indirect method being used for simple head-scratching and the direct at times for scratch-preening—especially of areas other than the head, as in hummingbirds. Avocets and stilts scratch the head indirectly but the bill directly.

Care of skin and bare parts. The skin and feet are attended to by use of the bill mainly during routine feather maintenance, particularly bouts of true preening. Many birds will examine the feet and pick off dirt at other times too. Waders deliberately clean the feet in water before going to the nest. The eyes are cleaned and also protected during feather care sessions by use of the nictitating membrane (see VISION). Dirt or other sources of irritation in the eye itself or on the surrounding area elicit an immediate shoulder-rubbing response; this should not be confused with rather similar movements used by grebes and waterfowl during bathing and oiling and by penguins for drying after bathing. Grebes and other water birds will clean the bill by dipping it in the water; ducks and other waterfowl also submerge the bill and blow air through the nostrils, probably both to clear the nasal passages of mucus and to get rid of dirt. Similar 'sneezing' behaviour has been recorded in penguins. Such activities are often supplemented by head-shaking (see below) as is the special throat-touching movement of the grebes whereby water is drained from the bill after diving. The bill is also cleaned by scratching with one foot, by seizing or pecking hard objects, or (in gulls) by being plunged into the ground. After bathing and at other times, many landbirds wipe the bill and gape-flanges on a perch or other firm surface in a species-characteristic way, either by stropping it from side to side with a sharpening-like action or by rubbing one side several times and then the other. Many taxa lubricate the bill with preen-oil, more or less incidentally during oiling spells; passerines (at least) also anoint the feet similarly and will deliberately treat the tarsi with bill-quivering movements.

Comfort movements. Term now sometimes used to cover the whole field of what is here called 'comfort behaviour' but best restricted mainly

Dunlin *Calidris alpina* wing-stretching. (*Photo: M. Holliday*).

to various shaking and stretching actions. Others, relating to the bare parts, are mentioned in the section above. All are often associated with feather-maintenance activities, occurring during loafing breaks, but often occur quite independently. As well as putting the feathers in order and stretching muscles, the main comfort movements may well prepare the muscular and circulatory systems for activity.

Shaking. The head-shake, usually a brief mainly lateral movement, seems common to all birds. Wildfowl also have a distinctive head-flick in which there is a rotary component of head and neck with the bill rising vertically; in most other groups, this action seems incorporated into high-intensity head-shaking—as with the head-fling of grebes. The body-shake is more complex, involving the rapid ruffling up and lowering of the contour feathers often with rotation of trunk, neck, and head to a greater or lesser extent. In grebes, body-shakes occur on the water only, as the bird lifts itself by paddling with the feet (rise-and-shake); wildfowl have similar swimming-shakes but also perform standing-shakes in shallow water or on land. Some birds e.g. falcons and gulls, will body-shake on the wing (flying-shake or so-called 'aerial rousing'). When wing-flapping, the bird beats the wings deliberately a number of times. The wing-flap is most characteristic of non-passerines such as grebes (the rise-and-flap) and wildfowl (swimming-flap, standing-flap); in some, e.g. gulls and waders, it may be prolonged and vigorous, the bird even rising from the ground meanwhile. The closed wings may also be vibrated in a wing-shake, and many groups have a lateral tail-wag. Wildfowl also incorporate tail-wagging and wing-shaking into the body-shake, and tail-wagging into the wing-flap. Body-shaking, tail-wagging, and wing-flapping especially act as feather-settling movements; they are also drying ones (see above).

Stretching. The one-wing stretch seems common to all birds, the wing being extended sideways and downwards or backwards until it is nearly or fully open, held still briefly, then folded away again. In many species, there is also a co-ordinated stretching of the corresponding leg (wing-leg stretch)—but both can occur independently. Passerines and near-passerines especially accompany these movements with a sideways fanning of the tail. In the both-wings stretch, the wings are lifted together above the back—typically while still remaining flexed or only partly open at the carpal joints. Passerines often follow this with the two-leg stretch as they straighten the tarsal joints and lift the body. Wildfowl lack this movement but combine the both-wings stretch with a forward extension of the neck, etc, and grebes with a neck-stretch, head-rotating, and a head-stretch (chin-brace); in penguins, the sequence of activities is even more complex. The term 'full-stretch' seems therefore better suited for such co-ordinations. In addition to the two standard wing-stretches, plovers and many other waders have a vertical wing-raising posture in which the fully extended wings almost touch; at times this appears to be a comfort movement but it serves as a social signal as well, especially before and immediately after flight. Finally, many birds have a movement in which the mandibles are deliberately opened then closed. It is still argued whether this represents a jaw-stretch or a true yawn (see YAWNING). In wildfowl it appears to be a jaw-stretch, in the Ostrich *Struthio* and in penguins a yawn, while in grebes and at least some pelecaniform birds there is both a jaw-stretch and a distinctive yawn.

Snipe *Gallinago gallinago* loafing. (*Photo: F. Pölking*).

New Zealand Kingfisher *Halcyon sancta* juvenile wing-stretching. (*Photo: G. Moon*).

Resting postures. Adult birds usually rest and sleep while standing on one or both legs; some cursorial and wading birds, including plovers and storks, will also at times squat half-down, taking their weight on the tibio-tarsal joints. Aquatic birds, such as divers and grebes, normally loaf only while floating on the water, except when incubating; a few highly aerial species, such as terns and swifts, will rest on the wing even through the night. Young birds often rest by squatting right down on the belly, as do adults of certain groups such as gamebirds (Galliformes), gulls, pigeons, and babblers, when feeling safe from danger, or when ill. In the most typical of the full resting postures, the bird relaxes, ruffles its contour feathers, fluffing them over the folded wings, and turns the head round and inserts the bill 'behind the wing'; one leg may be drawn up into the plumage. A minority of groups merely draw the head in close to the body in a hunched attitude (e.g. pigeons), rest the bill on the foreneck (e.g. storks), or insert it into the side of the neck (e.g. herons, grebes—the latter in the well-known 'pork-pie' posture with the opposite foot stowed away up in the flank 'pocket' under the wing). See also ROOSTING.

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COMMENSALISM: the rare situation where species A benefits from the presence of species B, but where B is indifferent to the presence of A, neither gaining nor losing from the association, e.g. sparrows *Passer* spp. nesting in the bases of nests of larger species. Commensalism differs from Symbiosis or Mutualism, in which both species benefit from the association.

COMMISSURE: the line of apposition of the closed mandibles, as viewed laterally (see BILL).

COMMON BIRDS CENSUS: see CENSUS.

COMMUNITY: a natural assemblage of species, the term being usually restricted to assemblages occurring in defined habitat types; frequently further restricted to assemblages of related species, e.g. the bird community of oak woodland. Community ecology is concerned with the patterns that characterize such assemblages and with the interactions, especially competitive, between the species. There has been a rather general consensus among ecologists that interspecific competition is fundamental for the interpretation of community patterns (e.g. MacArthur 1972, Cody 1974; and see COMPETITION); but for a critical re-assessment of the role of competition, and of the probable importance of chance factors in determining community structure (and indeed of the reality of any such 'structure'), see Connors and Simberloff (1979) and Wiens (1983).

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COMPETITION: the interaction which occurs when two or more individuals, of the same or different species, use a resource (food or nest sites, for example) in short supply.

Competition may either be by 'exploitation'—as the limiting resource is simply used up; or by 'interference'—behavioural interactions in which individuals or species pre-empt valuable resources for their exclusive use, by direct aggression or display.

The interactions are intra-specific when individuals of a single species are involved, or inter-specific when two or more species utilize the same limiting resource. Inter-specific competition cannot occur without intra-specific competition.

The abundance of a species in a habitat may be markedly reduced by inter-specific competition, and in the extreme, it may be excluded altogether by a superior competitor or competitors. The combined competitive effects of several species on another species are sometimes referred to as diffuse competition.

COMPETITIVE EXCLUSION: the exclusion (usually from a particular habitat) of one species by another, competitively superior species, in cases where each is exploiting the same environmental resource(s). Ecologically less similar species may still compete, without one excluding the other. The precise conditions determining competitive exclusion or competitive coexistence can be stated mathematically. They depend not only upon how similar the species are in their ecologies, but also on their abundances in the absence of competition. See also ECOLOGY.

COMPLEX: in taxonomy, a neutral term used when the precise status and interrelationships of a group of forms is in doubt.

COMPROMISE BEHAVIOUR: see AMBIVALENCE.

CONCHA: part of the ear (see HEARING AND BALANCE; OWL).

CONDITIONING: see LEARNING.

CONDOR: substantive name of the 2 species of Cathartidae that are placed in *Vultur* and *Gymnogyps* respectively (see VULTURE (2)). See photo FLIGHT.

CONDYLE: an articulating process on a bone (see SKELETON, POST-CRANIAL).

CONEBILL: substantive name of the 10 species of *Conirostrum* and of *Oreomanes fraseri* (Giant Conebill) (Passeriformes, suborder Oscines). The systematic position of this small group of Neotropical birds is problematical; they are here placed together with *Coereba* in a family Coerebidae (see HONEYCREEPER, BANANAQUIT), but future research may well lead to a different arrangement. The typical conebills are small (10–14 cm) warbler-like birds with short, pointed bills. Their plumage is not brilliant, mostly grey or bluish above and paler, with chestnut brown and buff tints, below, and black or white head markings in some species. They fall into two groups ecologically, one group inhabiting swampy tropical forest, including mangroves, and the other group subtropical to temperate woodlands in the Andes. They are not well known ecologically, but are evidently mainly gleaners of insects from arboreal vegetation, some species at least being also partly frugivorous. Unlike the Bananaquit, those species whose nests are known build deep open cup nests. The Giant Conebill, a considerably larger bird (length *c.* 18 cm), is found in very high-altitude *Polylepis* woodland in the Andes, where it forages by searching the tree trunks for insects concealed beneath the bark.

D.W.S. (1)

CONFIDENCE LIMITS: see BIOSTATISTICS.

CONGENERIC: of two or more species, meaning that they are, or should be, placed in the same GENUS.

CONGRESSES, INTERNATIONAL: gatherings for scientific discussion and for establishing personal contacts and, on occasion, for reaching agreement on courses of action. International Ornithological Congresses are now held at intervals of 4 years. Continuity is provided by an International Ornithological Committee of 100 members, meeting during the course of each Congress; this body fills vacancies in its own number, decides general questions concerning the regulation of Congresses, chooses the country in which the next is to be held and elects a President for the succeeding Congress. A small Permanent Executive Committee makes recommendations to the International Ornithological Committee and deals with matters arising in the interval between Congresses; the constitution of this body is governed by the rule adopted in 1954—Acta XI Congressus Internationalis Ornithologici: 42, Decision 3 (pub. Basel, 1955).

The following International Ornithological Congresses have been held, under the Presidents named.

I 1884 Vienna: Dr Gustav Radde (Austria)
II 1891 Budapest: Prof. V. Fatio (Switzerland)
III 1900 Paris: Dr Emile Oustalet (France)
IV 1905 London: Dr R. Bowdler Sharp (Great Britain)
V 1910 Berlin: Prof. Anton Reichenow (Germany)
VI 1926 Copenhagen: Dr Ernst Hartert (Germany and Great Britain)
VII 1930 Amsterdam: Prof. Einar Lönnberg (Sweden)
VIII 1934 Oxford: Prof. Erwin Stresemann (Germany)
IX 1938 Rouen: Prof. Alessandro Ghighi (Italy)
X 1950 Uppsala: Dr Alexander Wetmore (USA)
XI 1954 Basel: Sir A. Landsborough Thomson (Great Britain)
XII 1958 Helsinki: Prof. Jacques Berlioz (France)
XIII 1962 Ithaca, N.Y.: Dr Ernst Mayr (USA)
XIV 1966 Oxford: Dr David Lack (Great Britain)
XV 1970 The Hague: Prof. N. Tinbergen (Great Britain), Dr Finn Salomonsen (Denmark)
XVI 1974 Canberra: Prof. Jean Dorst (France)
XVII 1978 Berlin: Prof. D.S. Farner (USA)
XVIII 1982 Moscow: Prof. L. von Haartman (Finland)

The 19th Congress is due to be held in Ottawa in 1986 under the presidency of Prof. Klaus Immelmann (West Germany).

Each Congress is followed by the publication of a special volume of *Verhandlungen, Proceedings, Comptes Rendues* or *Acta*, edited by its General Secretary. The proceedings of the 3rd and 4th Congresses constituted volumes of the former international journal *Ornis*. The Presidential Address at the 8th Congress gave the history of the earlier meetings.

The International Congresses of Zoology, held at intervals of 5 years, are also of interest to ornithologists in a more general way. They are important in that they constitute the final authority on questions of zoological NOMENCLATURE and appoint the standing International Commission on that subject. (A.L.T.) B.C.

CONNECTIVE TISSUE: a general term for a variety of fibrous and other tissues of the body, including ligaments and tendons (see also under MUSCULATURE).

CONSERVATION: measures, including legislation, preservation and management of habitat, control of environmental pollution, education and research, to promote the wellbeing and survival of wild birds. Their purpose is to achieve as wide a variety of species, and the greatest number of each, compatible with and appropriate to the ecological conditions existing in an area, and to guard against the extinction of species or races. During the second half of this century they have replaced an earlier approach which relied on legal protection for individual species or groups of species.

This protectionist approach was based on the assumption that birds could co-exist with Man, provided they were safeguarded against excessive persecution and exploitation. Since then land pressures have enormously increased. Initially, expanding towns, motorways and airports were responsible, but recent intensification and mechanization of agriculture and forestry have made extensive areas of remaining countryside inhospitable to wildlife. A more flexible approach is needed and one which, since all change cannot and indeed should not be stopped, allows for the integration of wildlife. Because of the mobility of birds (see MIGRATION), and world trade in birds (alive and dead), plumage and their eggs (see UTILIZATION BY MAN), international aspects also apply.

Legislation. Different approaches have been adopted but all emanate from one of two fundamentally different attitudes. Either birds are considered as something to be hunted as quarry, which is the possession and right of the owner or occupier of the land, or as being within the public domain, regardless of the ownership of the land on which they may be found.

British legislation. This evolved from the former approach. Thus in the Middle Ages birds such as the Grey Heron *Ardea cinerea* were protected as quarry for falconry, a royal sport (see FALCONRY). Continuing interest in hunting led to the concept of a special group of huntable species referred to as GAME-BIRDS. The development of game preservation and the need for further protection of owners' rights was reflected in the Game (Scotland) Act 1772 and the Night Poaching Act 1828. A series of Acts then followed, which were still principally aimed at upholding the rights of owners and occupiers, and only indirectly benefiting birds. This narrow British definition of game is not easily understood in other countries, where all birds shot for food are regarded as game and covered by legislation.

The second half of the 19th century saw a change in attitude and increasing public concern towards wild birds in general. A number of Acts extended protection to a wider variety of species. The privilege of owners and occupiers of land was retained by local exemptions, and it was not until the mid-20th century that a really effective and comprehensive Act was achieved. The Wild Birds Protection Act 1954 started with the concept that all wild birds and their eggs should be protected. There were exceptions for hunting and in the interests of agriculture, science and education. This enlightened and straightforward approach, already adopted in 1914 in the Netherlands and 1929 in Prussia, not only facilitated enforcement, but represented an important educational advance with acknowledgement by Government that wild animals represented a common heritage. The 1954 Act continues to this day to underlie protection for wild birds in Britain. Modified in 1967, in 1981 it was incorporated, with further changes to bring it into line with the European Community Directive (see below), into the Wildlife and Countryside Act.

Legislation outside Britain. By contrast this was based on the alternative approach to birds which, with other wild animals, are part of the public domain. In the USA protection of birds is divided between federal (national) government and state governments. Federal government legislates when the matter is deemed by Congress to be of interstate, national or international concern.

This system includes provision for hunting certain species for sport, but not commercially. Migratory birds that are considered to be game—most ducks (Anatidae), some rails (Rallidae), and a few waders (Charadrii) and doves (Columbidae)—are subject to licence and annual regulations by the Federal Fish and Wildlife Service. Non-migrating game, such as the Turkey *Meleagris gallopavo*, grouse (Tetraonidae) and quail (Odontophorinae) are covered by state regulations.

To achieve its purpose legislation must be effectively enforced. Understandably wildlife laws come low down the priority list of overworked police forces, who find it difficult to act without specialist knowledge of wild birds and their eggs. In the United States, Canada, Australia, New Zealand and certain other countries, the task of investigation and enforcement is largely undertaken by federal and state wildlife enforcement agencies, whose officers have special responsibilities and training in wildlife legislation, conservation work and species identification. Most European countries lack these specialist services and as in Britain, rely on voluntary bodies, such as the Royal Society for the Protection of Birds and the Royal Society for the Prevention of Cruelty to Animals, who either undertake prosecutions themselves, or co-operate with police by carrying out much of the preliminary investigation work and providing the expertise.

International action. An increase in knowledge of migratory movements led to the realization that birds could not be regarded as the property of one country alone. The first international convention between two countries was the Migratory Bird Treaty of 1916, which provided reciprocal legislation for the protection of migratory birds between the United States and Canada; this was extended in 1937 to include Mexico.

In Europe the international aspect of bird protection was first raised at Vienna in 1868, when a meeting of German agriculturists and foresters resolved to procure international agreements for the protection of birds and other animals useful to agriculture and forestry. Although efforts were made to bring the proposal into effect, it was not until 1902 that an International Convention for the Protection of Birds useful to Agriculture was signed in Paris. This accorded protection to birds enumerated as useful and to their nests, eggs and young, while other species were pronounced harmful and exempted from protection. Various methods of taking and killing birds were prohibited, and also the sale of protected birds during the close season.

During the first two decades of the 20th century, an increase in field observations, and experience of the dire results of commercial exploitation of certain species, led in 1922 to the founding by Dr T. Gilbert Pearson of the United States of the International Council (then Committee) for Bird Preservation (ICBP)—the first international organization concerned with the preservation of wildlife.

In 1925, Professor Einar Lönnberg of Sweden drew attention to the urgent need for international co-operation for the protection of the Anatidae, pointing out that Scandinavian countries bred the birds and countries further south shot them. His efforts led to active co-operation between European countries and to the passing of the Wild Birds (Ducks and Geese) Protection Act 1939 in the United Kingdom, and similar protective measures in other European countries, and eventually to the establishment of the International Wildfowl (now Waterfowl) Research Bureau (IWRB).

In addition to these exclusively bird-orientated organizations, international conservation was strengthened by the formation in 1948 of the International Union for the Conservation of Nature and Natural Resources (IUCN), the World Wildlife Fund (WWF) in 1961 and the United Nations Environment Programme (UNEP) in 1972. The IUCN represents government and non-government organizations and an important part of its output has been the Red Data Books listing rare species (see ENDANGERED BIRDS). The ICBP and IWRB act as specialist advisory bodies to IUCN. WWF is primarily a fund-raising body giving major financial support to IUCN and ICBP. The UNEP, which relates to the total environment, also gives funds for conservation work. In 1980, IUCN, WWF and UNEP jointly published a World Conservation Strategy.

In 1935, at a meeting of ICBP in Brussels, representatives of the Finnish, Swedish and Norwegian Governments produced a draft convention for the international protection of birds. It was eventually agreed that an entirely new convention was not practicable, and proposals should be incorporated in the revision of the Paris Convention of 1902. Although now restricted to Europe, it took 12 years before the requisite number of countries ratified in 1963. More recently there was renewed impetus for international co-operation, and in 1979 three international instruments were agreed: the European Communities Directive on the Conservation of Wild Birds; the Council of Europe Convention on the Conservation of European Wildlife and Natural Habitats (the Berne Convention); and the Convention on the Conservation of Migratory Species of Wild Animals (the Bonn Convention). Of other conventions perhaps the most important was the Convention on the Conservation of Nature and Natural Resources in Africa.

Protection of habitats. As the human population of the world continues to grow, the necessity to preserve habitats for wild birds becomes increasingly urgent. It is now known that most species of birds will flourish if an adequate ecological base, including cover, food, water and the necessary conditions to satisfy behavioural needs is provided for them, with freedom from disturbance. In many countries a start has been made with the establishment, both by governments and voluntary bodies, of national parks, nature reserves, refuges and sanctuaries. Internationally the first major action directed specifically to safeguarding habitats for birds was the Convention on Wetlands of International Importance signed in Ramsar, Iran, in 1971. Since then both the European Community Bird Directive and Berne Convention have provided for habitat protection, particularly of those more sensitive to outside influences and of importance to migratory species as staging, wintering or breeding sites.

It is now realized that the protection of sites is not sufficient by itself and that without management many will deteriorate. To guard against unwanted changes, most reserves are now subjected to a management plan which lays down objectives and a programme of research and estate work. With increasing experience gained from site work and the accumulation of ecological information, management work is now highly successful, and there are numerous examples of sites which have had their scientific value considerably increased. For example, when the Minsmere Reserve on the east coast of England was acquired by the Royal Society for the Protection of Birds, it was not rated as of outstanding importance since much of the area had been transformed into agricultural land. An intensive management programme has won it national status and inclusion as one of the British internationally important wetland sites under the Ramsar Convention. This enrichment of habitat and re-creation of lost sites is one of the most exciting and important recent achievements of Conservation.

In addition to major site management, considerable efforts have been made to produce diversification within the main habitats. These include the best siting and density of nestboxes; the artificial provision of food in frosty weather or where the natural food is polluted; and different treatments of woodland clearings and fringes. In Scandinavia, substantial increases of breeding range of the Goldeneye *Bucephala clangula* have been achieved by provision of suitably designed nestboxes, and in America Wood Duck *Aix sponsa* have been locally much increased by provision of raccoon-proof nestboxes. The attraction of ducks to artificial decoy ponds has a long history in Europe (see DECOY), and recently pools to encourage wildfowl have been constructed in large numbers in North America with some incorporating artificial islets giving cover for nesting wildfowl. Floating rafts have also been used to extend the breeding area of the commercially exploited guano cormorants on islands off Peru (see GUANO).

Research. A considerable body of empirical knowledge now exists on management techniques. This has not yet been assessed or related scientifically to fundamental studies in ethology, ecology and population dynamics. Studies with this object in view are now in progress in several countries.

Conservation will also benefit from a wide range of applied and fundamental research. Certain projects are more immediately valuable and offer practical solutions to urgent problems. An autecological study of a diminishing species may reveal the cause of the decline and enable action to reverse it. Thus in the United States it has been shown that the survival of the rare Kirtland's Warbler *Dendroica kirtlandii* depends on burnt areas to stimulate regeneration of pines, on which the species is largely dependent.

General studies of broad geographical distributions with population estimates, such as numerous recent national bird atlas projects (see ATLAS), provide basic material on which national conservation programmes are based, and long term surveillance studies give early warning of unsuspected problems. In Britain these take many forms e.g. the Common Birds Census, run by the British Trust for Ornithology, which calculates an annual index of abundance for widely distributed farmland and woodland plots; the Beached Bird Survey of the Royal Society for the Protection of Birds which records the number of dead birds and the proportion oiled that wash ashore over measured stretches of coast; the annual census of heronries started in 1928. North America conducts annual surveys of waterfowl to allow calculation of permitted hunting levels for the forthcoming season. Research will also establish whether claims of damage by birds are valid.

Black-headed Gulls *Larus ridibundus* and Common Terns *Sterna hirundo* nesting on artificial island. (*Photo: E.J. Hosking*).

Difficult and controversial issues arise in connection with proposals for introduction not only of exotic species, but of species perhaps native to similar habitats not far away, and even in some cases formerly indigenous at the place in question (see NATURALIZED BIRDS). So much harm has been done by thoughtless introductions, and the indirect consequences of such interference are so unpredictable, that most authorities at present take an ultra-cautious attitude towards any such projects. In principle there may be no logical objection to introductions in a world where so much other human interference is unavoidable, but its practice in the present state of ignorance about possible repercussions can rarely be justified. Artificial attraction of birds and artificial increase of their numbers may also have dangers, but these tend to be more easily controlled if need arises. Recently there has been a growing interest in research into captive breeding and reintroduction of species in an attempt to re-populate areas. In Britain the Wildfowl Trust has successfully bred the Hawaiian Goose *Branta sandvicensis* in captivity, and reintroduction to the wild is underway. In the United States, Canada and other countries a massive captive breeding programme involving the Peregrine *Falco peregrinus* is in progress and the first successful breeding of pairs reintroduced into the wild was recorded in 1980. In contrast, in certain instances e.g. where large gulls compete for nesting sites with terns, the gulls' numbers may have to be reduced.

Environmental pollution. A country possessing excellent, well enforced bird legislation and large numbers of nature reserves may still find itself faced with a conservation disaster caused by a widely dispersed man-made environmental pollutant. The most recent alarming example was the serious widespread effect, particularly on birds of prey and fish-feeding birds, of persistent organochlorine pesticides such as DDT and dieldrin (see TOXIC CHEMICALS). In some instances pollution may have its origin outside the immediate control of the country affected. Pollution of the seas by oil from shipping operations and disasters and mining operations (see OIL POLLUTION) is an example. In such circumstances conservationists have to press for international action through agencies such as the United Nations and the Organization for Economic Co-operation and Development.

Education. Effective conservation of wildlife in the modern world requires considerable finance and deployment of resources. Governments and peoples will not support this expenditure unless they understand the necessity for it and believe it to be worthwhile. Educational activities aimed at both adults and children are now promoted in many countries. These include television and radio programmes, work in schools involving field courses and the publication of books and magazines. Nature trails and public viewing 'hides' or 'blinds' on reserves enable large numbers of people to observe and study at close range rare and shy birds without disturbing them or affecting the scientific interest of the site.

Voluntary bodies have played an outstanding role in this work. In North America the National Audubon Society and many affiliated state and local Audubon societies continue to be extremely active in promoting public awareness and participation. In Britain the development of public interest is clearly reflected in the growth of the Royal Society for the Protection of Birds, whose adult membership has increased from 5,000 in 1940 to 375,000 in 1984. Its Young Ornithologists' Club is also expanding with a membership now standing at over 80,000.

Elsewhere in many countries of the world, new voluntary societies are being formed and established ones are gaining in strength. To encourage such growth in Europe, a Working Group of European Bird Protection Societies (WEBS) was formed in 1976 to exchange experience and ideas. I.P.

CONSPECIFIC: of two or more subspecies or other forms, meaning that they belong to the same species (or should be so regarded, although considered by others to be specifically distinct)—see SPECIES.

CONSUMMATORY ACT: 'an act which constitutes the termination of a given instinctive behaviour pattern or sequence' (Thorpe 1951), bringing about a sudden drop in motivation—compare APPETITIVE BEHAVIOUR; BEHAVIOUR, HISTORY OF; SPECIFIC ACTION POTENTIAL.

CONTACT CALL: a noise made by a bird as a means of keeping in touch with others of its species (see FLOCKING).

CONTINGENCY TABLE: see BIOSTATISTICS.

CONTOUR FEATHER: the predominant feather type, characterized by the presence of vanes, which, at least in their distal parts, are firm and flat. Includes remiges and rectrices. Sometimes highly modified (see FEATHER; PLUMAGE).

CONTROL (1): deliberate action by man to limit or reduce the numbers of a wild species, where potential increase or existing abundance is thought to be detrimental to human interests; a negative aspect, so to speak, of CONSERVATION. See EMU WAR; QUELEA CONTROL.

CONTROL (2): recovery and release of a bird already marked (see MARKING).

CONTROL (3): standard of comparison for checking inferences deduced from experiment (Concise Oxford Dictionary). A classic ornithological example is the experiment by Keeton (1971) to test whether magnets mounted on pigeons *Columba livia* could affect their homing behaviour. Individual birds were released alternately from 2 treatment groups, chosen randomly from a flock housed in a single pen. Birds in the 'experimental' group wore a magnetic bar glued, just before release, to the back at the base of the neck. The 'control' group wore a brass bar of identical size, weight and placement, the important 'control' factor being that brass has no magnetic properties. The birds were liberated at various sites and their orientation to home observed. Under overcast conditions the magnet-bearing birds were significantly more disorientated than the brass-bearing birds, indicating that the magnets were a confusing factor. One possible interpretation of the results, therefore, was that, under certain conditions, pigeons can use magnetic cues in homing (see also NAVIGATION). E.K.D.

Keeton, W. 1971. Magnets interfere with pigeon homing. Proc. Nat. Acad. Sci. 68: 102–106.

CONURE: substantive name of the species of several Neotropical parrot genera, e.g. *Aratinga* (Psittacinae, Arini) (see PARROT).

CONVERGENCE: evolution on lines tending to produce similarity between unrelated or only distantly related forms as a result of adaptation to a like mode of life—the antithesis of radiation in its evolutionary sense (see ADAPTATIONS, ENVIRONMENTAL; EVOLUTION; RADIATION (1)). Examples of modes of life leading to convergent adaptations are running (in place of flight), aquatic habitat, aerial pursuit of insect prey, and raptorial feeding habits; but there are many others.

Convergence is all the more important as a phenomenon of avian evolution because it is superimposed on a high degree of uniformity in basic structure within the class. For that reason it is confusing to taxonomists, who have difficulty in distinguishing between characters that are primary, and therefore of phylogenetic significance, and characters that are secondary in that they are the result of special adaptations (as contrasted with the general adaptations common to all birds).

Convergence can be extremely subtle in its manifestations, producing similarity not merely in a few characters but in a whole series of characters, even of minute detail, that are advantageous for the particular mode of life. The resemblance may indeed have so many facets as to arouse scepticism concerning the absence of a close relationship. This is a frame of mind induced by the misleading process of enumerating points of similarity as if they were quite independent instead of being items in a 'constellation of characters' contributing to a single adaptation.

At the same time it has to be realized that phylogenetic relationship and convergent adaptation need not be mutually exclusive. Convergence may occur between forms that had diverged not very far back in the evolutionary process.

CONVERSION TABLES: for factors for converting between the British and the metric systems see Tables at the end of the volume.

CO-OPERATIVE BREEDING: the phenomenon of non-breeding birds attending the nests of breeding members of their species and carrying out some or all of the behaviour patterns associated with nesting, including nest-building, incubation, and feeding of the nestlings. The presence of non-breeders at the nests of many species of Central American birds was pointed out by Skutch (1961), who coined the term 'helpers at the nest' to describe the supernumeraries. Subsequently this behaviour has been found to be widespread among birds, particularly those of terrestrial ecosystems at tropical and sub-tropical latitudes.

Occurrence. Co-operative breeding is most frequent among passerines, where it has been recorded, at least casually, for 32 families and sub-families, but it also occurs in groups as diverse as rails, kingfishers and bee-eaters, swifts and woodpeckers, suggesting that the behaviour has evolved independently on many occasions (Brown 1978). It occurs almost invariably in species where groups of more than two birds defend common territories throughout the year and in such cases it is normal for non-breeding members of the group to participate in feeding the nestlings and, less frequently, in incubation.

Co-operative breeding is also found among many colonial birds, particularly those nesting in holes (e.g. bee-eaters, kingfishers) where the non-breeders may participate in breeding activities at several different nests during the same season. The same applies in the case of territorial groups where more than one pair breeds. In some species where groups hold territories outside the breeding season but individuals pair to breed, failed breeders may become helpers at adjacent nests.

The extent of co-operative breeding varies widely in different species, from those in which only a small proportion of nests are attended by non-breeders, with usually no more than one at each (e.g. todies *Todus* spp. and long-tailed tits *Aegithalos* spp.), to species in which several non-breeders are nearly always present at each nest, (e.g. the babblers *Turdoides* spp., Whitewinged Chough *Corcorax melanorhamphus* and Mexican Jay *Aphelocoma ultramarina*). In the former case the non-breeders are generally males and this sex also predominates where larger groups occur. This bias apparently results from the earlier dispersal of females from their natal group, with a consequently higher mortality.

Among species in which stable, territorial groups persist over several years, co-operative breeding forms one of a number of behaviour patterns typical of prolonged adaptation to a group-territorial existence. These include allopreening, roosting clumped together, giving communal vocalizations, and maintaining sentinels while feeding. Species which have reached this stage generally exhibit little or no sexual dimorphism, produce no distinctive song and frequently appear to suppress any signs of courtship behaviour, courtship displays and mating being carried out infrequently and well away from other group members.

Evolution. Among group-territorial species, groups frequently arise through the deferred dispersal of young reared within the territory, so that breeders and non-breeders are closely related. This observation has led to speculation that KIN SELECTION may have played an important role in the evolution of co-operative breeding. Among colonial species which exhibit co-operative breeding, however, breeders and helpers are not necessarily closely related and a satisfactory evolutionary explanation for this type of co-operative breeding is not yet forthcoming. For the group-territorial Florida Scrub Jay *Aphelocoma coerulescens* Woolfenden and Fitzpatrick (1978) have pointed out that by helping to increase the number of young reared within the territory, non-breeding males increase their own chances of 'budding-off' a new territory to become breeders themselves. With such a strong selection pressure operating on the individual it appears that kin-selection may be unimportant. Where territorial boundaries are relatively inflexible, moreover, non-breeders may compete with one another for the privilege of eventually breeding in the parental territory, creating a selection pressure against the rearing of further young within the territory. This may account for the fact that in some species where co-operative breeding is normal the actual production of fledglings per pair is no higher than for similar species where helpers are not found (Gaston 1978).

Environmental correlates of co-operative breeding are difficult to define. Virtually all co-operative breeders are sedentary, however, and those in which co-operative breeding is obligatory, with several helpers at each nest, are often medium-sized passerines feeding by searching on the ground. They are found particularly in savanna and seasonal rainfall areas of the tropics. In a few genera co-operative breeding occurs among island populations, but not among continental species (e.g. mockingbirds *Mimus*, Seychelles Brush Warbler *Bebrornis sechellensis*). Demographic factors are probably responsible for the origin and maintenance of group territories and hence co-operative breeding, being the result of high population densities existing close to the carrying capacity of the habitat. If the dispersion of food supplies in space and time favours the defence of year-round territories, then where adult survival is high there is little scope for young birds to establish new territories. Under these conditions the best option for young birds is apparently to remain in the parental territory to await the best moment to establish a new territory or take over a vacant one, while perhaps contributing at the same time to their own inclusive FITNESS by assisting their parents in rearing further offspring.

The relative dearth of co-operative breeding species in cool temperate climates is apparently related to the high proportion of migrants and the unpredictable winter mortality of residents, making the deferment of breeding a chancy business. In Britain the only species known to exhibit co-operative breeding regularly, the Long-tailed Tit *Aegithalos caudatus* and the Dunnock *Prunella modularis*, both belong to genera particularly associated with high altitudes in the Himalayas, an area with a high concentration of co-operatively breeding species. In both cases the occurrence of co-operative breeding in the temperate Palearctic may result from pre-existing behavioural adaptations common to all members of the genus. A.J.G.

Brown, J.L. 1978. Avian communal breeding systems. Ann. Rev. Ecol. Syst. 9: 123–156.

Gaston, A.J. 1978. The evolution of group territorial behavior and co-operative breeding. Am. Nat. 112: 1091–1100.

Skutch, A.F. 1961. Helpers among birds. Condor 63: 198–226.

Woolfenden, G.E. & Fitzpatrick, J.W. 1978. The inheritance of territory in group breeding birds. Bioscience 28: 104–108.

CO-ORDINATE: term used in taxonomy to mean 'of equal nomenclatural status' (see GROUP (1); NOMENCLATURE).

COOT: substantive name of *Fulica* spp.; used without qualification in Britain for *F. atra*; has also been misapplied to gallinules *Porphyrio* spp. (see RAIL).

COPPERSMITH: *Megalaima haemacephala* (see BARBET).

COPPERTAIL: substantive name of some *Metallura* spp. (for family see HUMMINGBIRD).

COPRODAEUM: name sometimes applied to the part of the cloaca into which the rectum opens (see ALIMENTARY SYSTEM).

COPULATION: the sexual act, leading to fertilization of the ova of the female by spermatozoa from the male (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM); also termed 'coition'. This usually occurs with maximum frequency a day or two before the first egg is laid, although the precise interval varies with species, clutch-size, and other factors.

Although the Anatidae have penes, the males of most species of birds have no specialized intromittent organs. Furthermore, copulation involves bodily contact with another individual, which is avoided at other times. For these reasons many, and perhaps most, copulation attempts are unsuccessful, the principal cause of failure being a sudden changeover to aggressive or fleeing behaviour in one of the partners (see PAIR FORMATION; DISPLAY).

Redshanks *Tringa totanus* about to mate. (*Photo: P. Munsterman*).

Normally, of course, the male mounts the female, but reversed mounting occurs as a usual sequel to copulation in many species. Homosexual mounting has been observed in a number of cases. Such phenomena are, as might be expected, more frequent in species in which the sexes are alike in colour; but it is probable that in most species each sex can show the sexual behaviour characteristic of the other if appropriate conditions arise.

Red-necked Phalaropes *Phalaropus lobatus* mating. (*Photo: H. Schouten*).

In a successful copulation the tail of each bird is displaced laterally, and the feathers round the cloacae are turned back so that the engorged lips of the two cloacae can come into juxtaposition. Copulation usually occurs on the ground or on a perch, but some species may copulate on the water (e.g. Anatidae) and a few even on the wing (Apodidae). R.A.H.

COQUETTE: substantive name of *Lophornis* spp. (see HUMMINGBIRD).

CORACII; CORACIIDAE: see below, and ROLLER.

CORACIIFORMES: an order comprising 4 suborders, Alcedines, Meropes, Coracii, Bucerotes; 10 families: Alcedinidae (KINGFISHER), Momotidae (MOTMOT), Todidae (TODY), Meropidae (BEE-EATER), Coraciidae (ROLLER), Brachypteraciidae (GROUND-ROLLER), Leptosomatidae (CUCKOO-ROLLER), Phoeniculidae (WOOD-HOOPOE), Upupidae (HOOPOE), Bucerotidae (HORNBILL). The classification adopted here differs in minor detail only from that used by Wetmore and Peters. Among structural points, there is a tendency for the 3 forward toes to be connected together; syndactyly is most marked in the Alcedinidae and Meropidae.

Very many members of the order are birds of brilliant plumage. Other striking features often present include long tails, crests, and large bills. Most of the species are partly arboreal, but many find their food (largely animal) on the ground—some in the air (bee-eaters) or in the water (some kingfishers). They usually nest in holes, some excavating burrows for themselves (KINGFISHERS, TODIES, MOTMOTS, BEE-EATERS); the nesting habits of the HORNBILLS are especially remarkable. The eggs are white or slightly tinted. The young at hatching are blind, helpless, and (except in hoopoes) naked.

The order as a whole is cosmpolitan, but of the families this is true only in respect of the Alcedinidae; of the rest, 2 families are Neotropical and the others confined to the Old World. In some cases the distribution is very restricted, e.g. to the West Indies (Todidae) or to Madagascar and the Comoros (Leptosomatidae).

CORACOID: a paired bone (not present in mammals) of the pectoral girdle (see SKELETON, POST-CRANIAL).

CORCORACIDAE: a family of the PASSERIFORMES, suborder Oscines; MAGPIE-LARK.

CORDON-BLEU: substantive name of some waxbills *Estrilda* spp. (see ESTRILDID FINCH).

CORELLA: substantive name for the 2 Australian smaller white cockatoo species, *Cacatua sanguinea* (Little Corella) and *C. tenuirostris* (Long-billed Corella) (see PARROT).

CORMORANT: substantive name of some species of Phalacrocoracidae (Pelecaniformes, suborder Pelecani); used without qualification in the British Isles for one of the species found there, *Phalacrocorax carbo*; in the plural, general term for the family. The substantive name for other species of Phalacrocoracidae is 'shag'; used without qualification in the British Isles for the other species found there *P. (Stictocarbo) aristotelis*; in the plural, alternative general term for the family, which includes *c.* 34 species in 5 genera or sub-genera, although some authors have recognized only 1–3 genera. Several groups of allopatric forms are treated either as species or as superspecies. Some authors prefer to place the darters as a subfamily Anhinginae in the Phalacrocoracidae (see DARTER).

Characteristics. Cormorants are medium to large in size (0.5–1.0 m long), found on both salt and fresh water. The bill is of moderate length, cylindrical and hooked. The neck is long and S-shaped. The short legs are set far back and the large feet are totipalmate. The wings, relatively short, are strong and the tail very stiff. The plumage is predominantly dark, and in fresh adult plumage has a bronze, greenish or bluish sheen. Many species have white throats, forenecks, breasts and abdomens, and may have individually variable amounts of white in patches and bars above and below the wings and on the back. Some have black or white crests, and have white nuptial plumes irregularly distributed with concentrations on the head, neck, rump and thighs. A few species have large pale grey areas, and one a brown head and upper neck. In most species the wing coverts are grey with a black margin. A few also have a black terminal spot on the wing coverts. Immatures may be brown where the adults are black, white or grey. The plumage of juveniles is dark, silky, and adult-like. In all ages the dark plumage may fade to sandy brown.

Facial colours, including the bill, the mouth lining, and the naked parts of the throat, may be bright yellow, orange, red, purple, violet, blue, green and/or black. The iris may change from brown in juveniles to green or blue within a year, but in some species it remains brown. The tarsi of cormorants are less scutellated than those of shags. All cormorants and some shags have black feet, while other shags have pink, red or yellow feet. Most species of shag have seasonally a shaggy tuft of black feathers as a crest on the forehead. Modified barbs on the contour feathers allow air to escape and water to penetrate the body plumage, thus reducing buoyancy (see SWIMMING AND DIVING). Ingested pebbles also reduce buoyancy, and may serve to adjust the centre of gravity. Cormorants swim low in the water. Ashore the water is shaken and aired out of the plumage. Secretions from the OIL GLAND help the plumage shed rain and spray. Most species spread their wings to dry, but not sub-antarctic forms of *Leucocarbo*. In addition to drying, the spreading of wings may have several other functions, including thermoregulation and grooming.

Sustained flight consists of steady wing-beats and an occasional glide. During an onshore wind cormorants may even soar. Flocks may form V's and lines flying low over the water, occasionally rising as if trying to look for prey or get their bearings. Cormorants fly with their heads held high and shags with their heads held low.

Distribution. The cormorants may be divided into 3 genera or subgenera, *Phalacrocorax*, *Hypoleucos*, and *Microcarbo* (= *Halietor*). *Phalacrocorax* includes *carbo*, *lucidus* and *capillatus*. *P. carbo* is the most

Shag *Phalacrocorax aristotelis*. (*J.B.*).

widespread in the family and occurs from the North American and Arctic shores of the North Atlantic across North Africa and Eurasia to Australasia and its sub-antarctic islands. *P. lucidus*, which occurs in Africa south of the Sahara, has been treated either as a species or as a sub-species of *P. carbo*. *P. capillatus* is restricted to some of the Asian shores of the North Pacific. The 3 forms are very similar in plumage and bare part colours. As adults they have a median erectile crest on the nape and upper hind neck.

Hypoleucos includes 2 large species, *auritus* in North America and *varius* in Australia and New Zealand; and 3 small species that form a superspecies with *auritus*; *olivaceus* in South and Middle America, *fuscicollis* in southern Asia, and *sulcirostris* in Indonesia and Australasia. They are relatively slender and have long bills, bodies, tarsi and tails.

Microcarbo consists of 6 small species or subspecies that occur in an arc around the Indian Ocean. *Microcarbo* is characterized by a short stubby bill, a broad body, short tarsi, and a long tail.

The shags may be divided into 2 genera or sub-genera, *Leucocarbo* and *Stictocarbo*. *Leucocarbo* includes 14 species, mainly around the southern oceans, and the flightless *L. harrisi* of the Galapagos, frequently considered to be in a separate monotypic genus, *Nannopterum*. *Leucocarbo* is robust with sturdy short broad wings. *L. bougainvillei* and *L. capensis* are the main producers of GUANO.

Stictocarbo includes 8 species of world-wide distribution. It is slender with long wings and short tail. The bill is long and thin with a small hook. It nests on small ledges and in alcoves of steep coastal cliffs.

Movement. Movement is mainly in response to weather-induced shortages of food. Inland populations move to avoid frost and drought. Coastal populations disperse following failures of cold, nutrient-rich, oceanic currents, and insular populations are mainly sedentary.

Food. Cormorants and shags feed on a wide variety of fish, crustaceans and cephalopods. They dive from the surface, often taking a forward leap; underwater they use their feet for propulsion and their wings and tail for balance. The catch is commonly brought to the surface before being swallowed. Large flocks (up to 2,000 individual *Phalacrocorax auritus*), moving line abreast, may co-operate in driving shoals.

Voice. Usually cormorants and shags are silent, but when breeding there are individual, sexual, age and species differences in their calls. The Bank Cormorant *Phalacrocorax neglectus* of South Africa has a loud, melancholy cry when disturbed. Visual signals are complex with marked differences between genera and species.

Breeding. Cormorants nest in colonies, sometimes densely packed, on rocky islets, cliffs and in trees, often with other kinds of waterbirds. They are at least seasonally monogamous, though some species breed more than once each year. The male selects the nest site, and the female builds the nest with material gathered by the male. The pair take turns guarding the nest and its contents; in some species, the female forages during the morning and the male during the afternoon. The modal clutch size is 3 or 4. The pale blue or green, usually unmarked eggs are incubated on the feet. The chicks are naked when hatched after about 4 weeks incubation. After a week they are covered in black, grey and/or white down. They squeal for food with a closed bill and beg silently for water with an open bill. Very small chicks take fluid from their parents' lower bill; when larger they take solid bits of regurgitated food from their parents' throats. They leave the nest after about 4 weeks and fledge when about 7 weeks old, but are fed sometimes for several months afterwards. First breeding is generally deferred until about 2–3 years old.

Fishing with cormorants is an ancient kind of aquatic 'falconry', formerly pursued in many parts of the world. Its origins are in Asia where it is still practised, with its highest development in Japan (see DOMESTICATION). See photos COMFORT BEHAVIOUR; FLIGHTLESSNESS; SWIMMING AND DIVING. (A.L.T.) G.F. VAN T.

Bartholomew, G.A. Jr. 1942. The fishing activities of Double-crested Cormorants on San Francisco Bay. Condor 44: 13–21.

Berry, H.H. 1976. Physiological and behavioural ecology of the Cape Cormorant *Phalacrocorax capensis*. Madoqua 9: 5–55.

Coulson, J.C. & Brazendale, M.G. 1968. Movements of Cormorants ringed in the British Isles and evidence of colony-specific dispersal. Br. Birds 61: 1–21.

Devillers, P. & Terschuren, J.A. 1978. Relationships between the blue-eyed shags of South America. Gerfaut 68: 53–86.

Harris, M.P. 1979. Population dynamics of the Flightless Cormorant *Nannopterum harrisi*. Ibis 121: 135–146.

Potts, G.R. 1969. The influence of eruptive movements, age, population size, and other factors on the survival of the Shag (*Phalacrocorax aristotelis* (L.)). J. Anim. Ecol. 38: 53–102.

van Tets, G.F. 1965. A comparative study of some social communication patterns in the Pelecaniformes. Orn. Monogr. 2.

CORNCRAKE: *Crex crex*, sometimes called 'Landrail' (see RAIL).

CORNEA: part of the eye (see VISION).

CORNEOUS: horny.

CORONARY VESSELS: see HEART.

CORONET: substantive name of *Boissonneaua* spp. (for family see HUMMINGBIRD).

CORPUSCLE, RED: see BLOOD.

CORPUS LUTEUM: (plural 'corpora lutea')—see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

CORPUS STRIATUM: part of the forebrain (see NERVOUS SYSTEM).

CORRELATION: statistical (not necessarily causal) association between two (or more) phenomena, one tending to vary directly or inversely as does the other. The degree of correlation may be expressed as a coefficient of which the values range from +1 (complete direct association) to −1 (complete inverse association), lower values than unity representing weaker associations and zero representing none at all. See further under BIOSTATISTICS; STATISTICAL SIGNIFICANCE.

CORRIDOR: term used for MIGRATION on a narrow front.

CORTEX: for that of the cerebral hemispheres (part of the forebrain) see NERVOUS SYSTEM; for that of the adrenal gland see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

CORVIDAE: a family of the PASSERIFORMES, suborder Oscines; CROW (1).

COSMETIC COLORATION: see COLOUR.

COSMOPOLITAN: distributional term applied to species or higher taxa found in all the main zoogeographical regions—or at least in most of them, and certainly in both Old and New Worlds and in both Northern and Southern Hemispheres (see DISTRIBUTION, GEOGRAPHICAL).

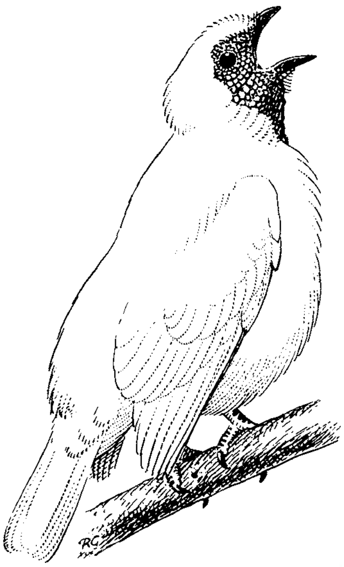
COSTAL: pertaining to the ribs (see SKELETON, POST-CRANIAL).

COT; COTE: a shelter for domesticated birds (or other animals), especially doves, i.e. 'dovecots'.

Hornell, J. 1947. Egyptian and medieval pigeon houses. Antiquity 21: 182–185.

COTINGA: substantive name of some species of Cotingidae (Passeriformes, infraorder Tyranni); in the plural, general term for the family. This Neotropical group contains about 65 species and is allied to the manakins (Pipridae) and tyrant-flycatchers (Tyrannidae). Several genera which were formerly included in the Cotingidae, especially *Tityra*, *Pachyramphus* (becards), *Rhytipterna* and *Laniocera* (mourners), are now placed in the Tyrannidae. It is by no means certain that the family Cotingidae, as currently recognized, is monophyletic; it is extremely diverse, and may consist of several lineages that were independently derived from an ancestral 'tyranniform' stock during the long period of isolation of South America from the rest of the world (see NEOTROPICAL REGION). The cock-of-the-rock *Rupicola* is sometimes placed in a separate family Rupicolidae on the basis of the major artery of the thigh (sciatic in *Rupicola*, femoral in the other cotingas examined).

Characteristics. Cotingas range from 9–45 cm in length, and are very varied in external appearance, although typical cotingas are alike in possessing rather broad bills somewhat hooked at the tip, rounded wings, and short legs. A few depart radically from this general form, notably the purpletufts *Iodopleura*, which have relatively long, pointed wings and resemble small swallows, and the Swallow-tailed Cotinga *Phibalura flavirostris*, which has pointed wings and a long forked tail and, like the purpletufts, feeds in part by aerial hawking for insects. Some species are



Bare-throated Bellbird *Procnias nudicollis* male. (*R.G.*)

of undistinguished appearance, with little difference between the sexes; in others the males have plumage of brilliant or unusual colours (e.g. very deep reds and purples), curiously modified feathers on the wing and the head region, peculiar fleshy wattles, or patches of brightly coloured naked skin; in most of these species the females are inconspicuously coloured.

Outstanding among the cotingas are the 2 species of cock-of-the-rock *Rupicola*, in which the male is brilliant orange or red with a helmet-like crest concealing the bill; the 3 species of umbrella-bird *Cephalopterus*, with black umbrella-like crests and long pendent wattles (feathered in 2 species, nearly bare in the third) hanging from the upper breast; the 4 bellbirds *Procnias*, the males of which have extensible wattles springing from the base of the bill (*P. alba*, *P. tricarunculata*), a 'beard' of fleshy black wattles on the throat (*P. averano*), or a bare green throat (*P. nudicollis*); and the 7 species of *Cotinga*, in which the males are mainly of various shades of brilliant blue. Crimson or plum-coloured throats are a feature of several genera that in other respects are quite dissimilar. In several species one or more of the outer primaries are peculiarly modified, being notched, attenuated or twisted.

Distribution. The family is nearly confined to the tropics; the northern limit is in southern Mexico, well within the tropics, but in the extreme south a few species reach latitudes of 28–31° S in south-eastern Brazil.

Habitat. Many species inhabit lowland primary forest; others occur in montane forest, and a few Andean species live at temperate levels at the upper edge of forest or even higher, in the zone of bushes and stunted woodland. The larger forest-inhabiting species are especially vulnerable to destruction and degradation of primary forest; at least 2 species in eastern Brazil (*Xipholena atropurpurea* and *Cotinga maculata*) have suffered severely from destruction of the coastal forests and are considered endangered.

Movements. Most species are sedentary but several undertake well-marked altitudinal migrations, breeding in montane forest and moving down to the lowlands in the off-season, and in the extreme south 2 species are known only as breeding migrants (*Phibalura flavirostris* and *Procnias nudicollis*) and so presumably move north, to a warmer climate, in the non-breeding season. Some lowland forest species undertake movements which may to some extent be regularly seasonal, probably in response to the changing availability of the fruits on which they depend.

Food. Most cotingas are frugivorous, and some, e.g. the bellbirds, are extreme fruit specialists, feeding not only themselves but their young wholly or predominantly on fruits. The greater part of the diet of the large cotingas of tropical forest is provided by a limited number of plant families (especially the laurels Lauraceae, incense family Burseraceae, and palms Palmae). Probably there has been a long period of coevolution between the cotingas and trees of these and some other families. The largest cotingas, generally known as fruit-crows, have a mixed diet of fruits and large insects. Most cotingas typically pluck fruits on the wing, in short sallies from a perch, and insects are usually seized from the leaves and branches in a similar way. The short-winged, heavy-bodied fruit-eaters of the Andes (*Pipreola* spp.) take fruit from a perch, and all species will do so on occasion when suitable perches are available. As already mentioned, the purpletufts and Swallow-tailed Cotinga make aerial sallies after flying insects.

Behaviour and voice. Some cotingas, in which sexual dimorphism is not very marked, live in pairs (e.g. *Carpornis* and *Pipreola* spp.), but many species, and probably all the larger ones, are polygynous. In these species lasting pairs are not formed, the sexes associate briefly for mating, and the females carry out all nesting duties single-handed. In the males of such species display behaviour, and the ornamentation associated with it, reaches extremes of elaboration. In the Guianan Cock-of-the-rock *R. rupicola* the males gather to display at traditional LEKS. Each male clears a court on the forest floor, and during the breeding season the greater part of the day is spent at or near the court. Screaming Pihas *Lipaugus vociferans* also display in leks; the males (dull-coloured like the females) are much more widely spaced than the cock-of-the-rock and advertise themselves by very loud ringing calls from perches in the middle strata of the forest. Male bellbirds utter extremely loud, metallic calls from special display perches, either in the tree-tops (for long-range advertisement) or low down in the forest under-storey (for the later stages of courtship). Individual males are widely spaced, but form discrete groups ('dispersed leks'). In the Calfbird *Perissocephalus tricolor*, one of the large fruit-crows, the males display communally in small leks on branches below the forest canopy, advertising themselves by loud mooing calls associated with extravagant postures. Analogous displays occur in the Red-ruffed Fruit-crow *Pyroderus scutatus* and umbrella-birds. In 2 genera in which the males have white wings (*Xipholena*, *Carpodectes*), males make conspicuous display flights above the forest canopy, when their wings are visible at a great distance. The displays of some of the little known species, e.g. the Crimson Fruit-crow *Haematoderus militaris*, are unknown.

Breeding. The breeding of many of the cotingas is unknown. Some of the Andean species build substantial cup nests, which they place in trees or bushes, but most species whose nests are known build very specialized and peculiar nests, which seem to be adapted primarily to escape predation by their inconspicuousness or inaccessibility. Thus the large fruit-crows, bellbirds, pihas, and Pompadour Cotinga *Xipholena punicea* build relatively tiny platforms or saucer-shaped nests of interlocking twigs or coiled tendrils. All of these, so far as known, have single-egg clutches, probably because such nests cannot safely accommodate more than one egg or well-grown young. The cock-of-the-rock attaches a more substantial nest of mud and plant fibres, cemented together with saliva, to vertical rock faces in caves or over streams; its clutch is of 2 eggs. The nest of the White-browed Purpletuft *Iodopleura isabellae* is a tiny cup attached with cobweb to a slender horizontal twig high in a tree, reminiscent of a hummingbird's nest. Cotinga eggs are typically olive or pale brown in ground colour, irregularly spotted and blotched with darker browns and ashy colours. Incubation periods are long (27–28 days in the Guianan Cock-of-the-rock, 26 days in the Calfbird, 25 days in the Purple-throated Fruit-crow *Querula purpurata*, 23 days in the Bearded Bellbird *Procnias averano*), and fledging periods long but very incompletely known (42–44 days in the Andean Cock-of-the-rock *R. peruviana*, 33 days in the Bearded Bellbird, 32–33 days in the Purple-throated Fruit-crow). There is no information on the number of nesting attempts that a female may make per year, but it is probable that the reproductive rate of all the larger cotingas is generally low. Moult seasons follow a well-marked annual pattern in most species, and it is a general rule that in those species in which the female alone attends the nest the males begin their annual moult well in advance of the females. D.W.S. (1)

Gilliard, E.T. 1962. On the breeding behavior of the Cock-of-the-rock (Aves, *Rupicola rupicola*). Bull. Am. Mus. Nat. Hist. 124: 31–68.

Sick, H. 1954. Zur Biologie des amazonischen Schirmvogels, *Cephalopterus ornatus*. J. Orn. 95: 233–244.

Skutch, A.F. 1969. Life histories of Central American birds, III. Pacific Coast Avifauna no. 35 (Cooper Ornithological Society).

Snow, D.W. 1982. The Cotingas. London.

COTINGIDAE: see under PASSERIFORMES; suborder Deutero-Oscines; infraorder Tyranni; COTINGA.

COTYPE: see TYPE SPECIMEN.

COUA: substantive name of *Coua* spp.; in the plural, general term for the subfamily Couainae (see CUCKOO).

COUAINAE: see CUCKOO.

COUCAL: substantive name of *Centropus* spp.; in the plural, general term for the subfamily Centropodinae (see CUCKOO).

COUNT: a method of studying the distribution and the trends in population of a species by making synchronized counts on a widespread sample of sites of the numbers of individuals present in successive years. For the most part the term is used in respect of studies undertaken outside the breeding season, the commonest subjects being the wintering flocks of gregarious species. Studies of breeding populations are usually referred to as 'censuses', but the distinction between the two terms is ill-defined (see CENSUS). The word 'census' is also used to describe an autumn or winter count in which the sample of sites is more comprehensive than usual.

The counting technique has been applied to several groups of birds, including game-birds (Galliformes), waders and gulls (Charadriiformes). It has also been used intensively over many years in the study of wildfowl (Anatidae), a field in which many of the developments and refinements have been pioneered. The current investigation, whereby the European populations of migratory ducks, geese and swans are kept under annual review, is certainly the most ambitious and sustained of the projects attempted hitherto; the remainder of this article is therefore devoted to this one study.

Organized counts of wildfowl were first made in Britain in the late 1930s, mainly around London. These lapsed in 1939, but were restarted in 1948 on a much wider scale. By the mid-1950s some 500 sites throughout the Kingdom were being covered regularly on a set date each month between September and March, and this still continues. Occasional counts have also been made in many other less important areas, bringing the total number of British sites for which data are now available to about 3,000.

Several other European countries began making similar counts of wildfowl during the 1950s, and in 1967 these national investigations were incorporated in a common programme under the aegis of the International Waterfowl Research Bureau. The countries already making the monthly counts were encouraged to continue, using the same prearranged dates throughout, whilst those not yet involved were invited, as a first step, to participate in a single mid-January 'census'. By the 1980s some 6–7,000 sites were being covered annually, and over the years records have been amassed from more than 14,000 different places in Europe, northern and central Africa and south-west Asia. A total of 57 countries have contributed. Counts on a rather smaller scale have also been made in November of the years 1969–1973, and more recently in March.

The great majority of the records have come from northern and central Europe, where virtually all the more important resorts have been covered in at least some of the years since 1967. In these northern districts the populations of most species are dispersed in relatively small flocks over a large number and variety of wetland habitats; counts are therefore required from a correspondingly large sample of sites. These have been undertaken to a very great extent by volunteer observers, working in their spare time and at their own expense. In southern Europe, Africa and Asia the wetlands are scattered more sparsely, but are often much larger in extent; the wintering wildfowl tend, therefore, to concentrate in certain well-defined areas. In the absence of local observers, these major centres have been covered by mobile teams of visiting ornithologists; aerial surveys of some of the more inaccessible wetlands have also been made, both in northern Europe and the regions further south.

Both the national and international wildfowl counts are directed primarily towards the common Palearctic species, with special emphasis on the dabbling and diving ducks (*Anas* and *Aythya* spp.). These are the easiest to count effectively, because by day they congregate to roost or feed on the larger and more open sheets of water. In Britain and north-west Europe the counts are believed to include a substantial proportion of their total populations, perhaps as much as 75% in some species. The sea-ducks (*Clangula, Melanitta* and *Somateria* spp.) are much more difficult, and effective methods of counting their populations are still being sought. Counts from the shore in Morocco and Portugal, and aerial surveys along the coasts of France, Scotland, the Netherlands, Denmark and Sweden have produced local winter totals, and counts of moulting Eiders *Somateria mollissima* have helped to substantiate the size of the Baltic and White Sea populations; radar has also been used to assess the numbers of Long-tailed Ducks *Clangula hyemalis* and scoters *Melanitta* passing on migration through the Gulf of Finland. Nevertheless the information on all these species is far from complete. The geese also require special treatment, in their case a separate effort is made to count the entire north-west European population of each species on at least one occasion each winter. The timing and tactics of these 'censuses' varies from species to species, depending on their daily habits and their distribution at various stages of the winter.

International counts of waders were started as a parallel study in 1966, and have developed along similar lines. The most intensive counts so far have been made around the coasts of northern and western Europe, but surveys have also been conducted in several important areas of western and southern Africa, and in parts of south-west Asia. In Britain, the period of greatest activity was between 1969 and 1975, when the British Trust for Ornithology organized a series of monthly counts throughout the year on all major estuaries. Although directed primarily at the waders, the 'Birds of Estuaries Enquiry' of the BTO and the Royal Society for the Protection of Birds encompassed all species of water birds, including many which had not been counted before. Since 1975 the work has continued on a reduced scale.

The prime purpose of the counts is to provide a scientific basis for the long term conservation of both wetlands and waterfowl. The projects in which the data are currently being used are:

1. to identify the areas of habitat which are of special importance to the various species;
2. to estimate the total numbers of each species in each of the main wintering areas;
3. to formulate the criteria by which habitat importance can be judged, at both national and international level;
4. to compile maps showing the numerical distribution of the species during January, and other months for which data become available;
5. to monitor trends in the north-west European populations of selected species, especially those subjected to heavy hunting pressure.

These studies have already produced a wealth of information; in particular they have shown that the numbers and distribution of the species are subject to constant change. The monitoring of these changes, and the availability of up-to-date information on the local, national and continental situation continues to be a major conservation requirement.

G.L.A.-W.

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Atkinson-Willes, G.L. 1978. The numbers and distribution of sea ducks in northwest Europe, January 1967–1973. Proc. Symposium on sea ducks, 1975: 28–67. Stockholm.
Prater, A.J. 1976. The distribution of coastal waders in Europe and North Africa. Proc. Int. Conf. on the conservation of wetlands and waterfowl, Heiligenhafen, 1974: 255–271. Slimbridge.
Prater, A.J. 1981. Estuary Birds of Britain and Ireland. Calton.

COUNTERSHADING: or OBLITERATIVE SHADING: contrast between dark-plumaged upperparts and light underparts which reduces the effect of shadow cast by the bird, so that it does not stand out from its background.

Allen, G.M. 1925. Birds and their Attributes. Francestown, USA.

COUNTERSINGING: singing in rivalry with another male within hearing; or 'duetting' between male and female of a pair (see VOCALIZATION).

COUNTING: term loosely applied to manifestations of a number sense. Experiments on this number sense or 'counting' ability of birds and other animals have been carried out for over 50 years, but it was not until comparatively recently that the difficulties of the task came to be fully realized. The fact that a bird discontinues ovulation and commences incubation when a certain number of eggs are in the nest (not when a certain number of eggs have been laid) is certainly not evidence for counting ability: the bird may merely be reacting to certain visually observed proportions of egg to nest, or it might be responding to the growing amount of stimulation received through the brood patches.

During the course of some of the early work on counting by mammals, results were obtained that suggested not merely counting, but mathematical ability of a high order. It was eventually shown, however, that the animals could give these results only when they could see the trainer and when the trainer himself knew the answer. In some cases there seems to be no doubt that the trainers actually believed that their pets were displaying intelligence of the highest order. Yet in the end it became abundantly clear that when the horse or the dog was giving its answer, by stopping its stamping or barking when the correct number had been reached, it was not giving evidence of a counting ability at all but had merely been extremely sensitive to minute, probably involuntary, signs and signals which the owner made. These 'clever' animals could never actually solve any problems by themselves; they merely obeyed their master's signs, which—given at the proper moment—stopped the stamping or barking by which they were spelling out their answers. The classic example of this was the horse 'Clever Hans'; and, ever since, mistakes of this kind in animal psychology have been called 'Clever Hans errors'. Precautions at least as rigid, to exclude such errors, are required when dealing with birds.

The study of the counting abilities of birds was explored by the elaborate experiments of Köhler and his school, in which extraordinary precautions were taken to avoid errors of the 'Clever Hans' type. In these experiments, and during training for them, the observer and the animals were always separated by a partition so that the experimenter was never seen by the bird although, while at work, he was able to watch it through the view-finder of a cine-camera fitted into the wall. When a deterrent was required in conditioning there was only one degree of punishment and this was always the same—namely a light touch on the back by means of a mechanically operated stick—so that it was impossible for the experimenter inadvertently to give signs by means of the punishing apparatus. In many of the experiments the bird was left entirely to itself and the result recorded automatically by a cine-camera, so that all possibility of an investigator inadvertently giving cues was ruled out. By such methods Köhler and his associates demonstrated that birds have what he calls an 'unnamed number' concept. The experiments were of two main types, simultaneous presentation and successive presentation. The first problem was presented to birds in a number of different ways, starting with only two groups of edible units (e.g. grains of corn, fruit, pieces of biscuit), the two groups differing by one unit only. In this way a Raven *Corvus corax* and a Grey Parrot *Psittacus erithacus* were taught to open that box which had the same number of spots on the lid as there were on the key card presented to them. These birds thus eventually learned to distinguish between five groups indicated by 2, 3, 4, 5, and 6 black spots on the lids of small boxes, the key being one of these numbers (i.e. a group of one of these numbers of objects) lying on the ground in front of the boxes. As a control, every other factor was changed in a random manner from experiment to experiment.

In presenting the numbers successively many different methods were employed. At first birds were trained to eat only 'x' grains out of many offered in a heap in circumstances such that the configuration of the heap gave no cue. Another task was to take only 'x' number of peas which were discharged from a chute into a cup one after another at randomly varied intervals ranging from 1 to 60 seconds. In this experiment the pigeon never sees more than one pea in the cup. It always has the same view and there is no visible cue for distinguishing the last 'allowed' pea from the first 'forbidden' one.

Another experiment involved opening the lids of boxes standing in a long row until 'x' baits had been secured. Since the baits were arranged in the boxes in 20 or more different distributions from one experiment to the next, the number of lids actually to be opened in order to get the required number was constantly changing. For instance, if the bird is to be trained to take 5 baits it may have to open any number of boxes between 1 and 7. The bird thus learns to open lids for up to 'x' baits, so that the number of lids it has to open to get 5 (when 'x' = 5) changes with each experiment. One Jackdaw *Corvus monedula* could learn 4 problems of this kind at the same time. It learned to open black lids until it had secured 2 baits and green lids until it had secured 3, red lids up to 4, and white lids up to 5. Similar results were obtained from Budgerigars *Melopsittacus undulatus* with a bell indicating 2 and a buzzer indicating 3. In these experiments—since, as far as can be seen, all external cues were successfully excluded—we can assume that only an inner token can be responsible for a bird ceasing action when the required number was reached. It is as if the bird is doing some inward marking of the units it is acting upon. This supposition is strengthened by the fact that sometimes these supposed inward markings show themselves in external behaviour in the form of intention movements. Thus a Jackdaw, given the task of raising lids until it had secured 5 baits, which in this case were distributed in the first five boxes in the order 1, 2, 1, 0, 1, went home to its cage after having opened 3 lids only and consequently having 4 baits. The experimenter was in the act of recording 'One too few. Incorrect solution', when the Jackdaw returned. It then went through a remarkable performance: it bowed its head once before the first box it had emptied, made 2 bows before the second box, 1 before the third. It then went farther along the line, removed the fourth lid (the box with no bait) and then the fifth and took out of this the last, fifth, bait. Having done this it left the rest of the line of boxes untouched and went back to its cage as if regarding the experiment as over. It appears from this 'intention' bowing, repeated the same number of times before each opened box as on the first occasion when it found the baits in them, that the bird remembered its previous actions. It seems as if it became aware that the task was unfinished and so returned and commenced again 'picking up' in vacuo, with intention movements, baits that previously it had actually picked up. When, however, it came to the last 2 boxes, which by mistake it had omitted to open on its first trip, it performed the full movements and thus completed the task.

The simplest explanation Köhler has to offer for this intention marking is that it may consist in equal marks—as if we were to think of or give 1 nod of the head for 1, 2 for 2, and so on. This is called thinking unnamed numbers, and for the great majority of experimental results at present available it is not necessary to suppose that the bird does the marking by unequal or qualitatively different marks in a fixed order, as we do when we think of the words for 1, 2, 3, 4, 5, or, alternatively, a phrase of 5 different syllables. Lögler (1959) has shown that a bird trained to open a box with, say, 3 spots on a lid as a result of seeing 3 flashes of light, will then go, without further learning, to the same box when it hears 3 sounds of varying pitch or 3 random alternations of sound and light. There is good evidence for the ability of birds to transfer the idea of number from one quality to another and also to combine successive and simultaneous recognition of number. This is a big advance on anything previously established, but it still remains a special solution only, i.e. the bird having been trained, say, to open box No. 3 when it sees 3 spots, box No. 4 when it sees 4 spots, and box No. 6 when it sees 6 spots, will not necessarily go and open box No. 5 when it hears 5 blasts of a whistle—provided, of course, that it has not been taught the number 5 before. In other words, there is as yet no evidence that animals have a power of expanding their general concept of number to other numbers of a series, i.e. that they can do arithmetic and have the general power of abstract dealing in numbers.

A possible example of counting by birds is described by Egremont and Rothschild (1979). Chinese fishermen on the Li-Kiang river use Cormorants *Phalacrocorax carbo* to catch fish, the traditional procedure being to prevent the Cormorant from swallowing fish by means of a neck ring. After a bird has brought 7 fish to its master, the neck ring is loosened so that the bird can eat the eighth fish it catches itself. Apparently the birds refuse to move after the seventh fish unless the neck ring is loosened, suggesting that perhaps they can tally up to 7 counts, independent of the time between them. W.H.T. and J.R.K.

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Köhler, O. 1956. Thinking without words. Proc. XIV Int. Congr. Zool., Copenhagen 1953: 75–88.

Lögler, P. 1959. Versuche zur Frage des 'Zahl'-Vermägens an einem Graupapagei und Vergleichsversuche an Menschen. Z. Tierpsychol. 16: 179–217. (English Summary).

Thorpe, W.H. 1963. Learning and Instinct in Animals (2nd edn.). London.

COUROL: alternative name for *Leptosomus discolor* (see CUCKOO-ROLLER).

COURSER: substantive name of all but one species of the subfamily Cursoriinae (Charadriiformes, suborder Charadrii, family Glareolidae); in the plural, general term for the subfamily. For the other subfamily, the Glareolinae, see PRATINCOLE. The coursers consist of 9 species in 3 genera. The largest genus, *Cursorius*, has 2 species in India and 3 in Africa. The genus *Rhinoptilus* has one Indian species (Jerdon's Courser *R. bitorquatus*, now almost certainly extinct) and 3 African species. The aberrant Egyptian Plover *Pluvianus aegyptius* belongs to a monotypic genus and is confined to the larger rivers of tropical Africa.

Characteristics. Coursers are plover-like in size and shape, but are rather longer-legged and have a strongly curved culmen. They are between 20 and 30 cm long and weigh 75–100 g. The toes are short, the hind toe is absent and the claw of the middle toe is pectinate (except in *Pluvianus*); the legs are whitish in most species, but yellow in the Three-banded Courser *Rhinoptilus cinctus* and reddish in the Bronzewing Courser *R. chalcopterus*. The tail is square. There is no obvious sexual dimorphism in any courser.

The genus *Cursorius* is characterized by a long bill (about half of the length of the head), a plain rufous forecrown, plain brown dorsal plumage, a broad white line behind the eye bordered below by a black line, and a dark brown band or patch across the lower belly (except in the Cream-coloured Courser *C. cursor*). The immature plumage is boldly patterned dorsally. The Cream-coloured Courser and Burchell's Courser *C. rufus* of northern and southern Africa respectively have a blue-grey hindcrown.

The genus *Rhinoptilus* is characterized by a short bill (33% of the length of the head), one or more chest bands in black, brown or rufous, bordering broader areas of rufous, white or greyish-brown, and the crown scalloped or broadly streaked with brown and buff. The Three-banded Courser and the Double-banded Courser *R. africanus* have the dorsal plumage boldly patterned in black, brown and buff.

The Egyptian Plover is atypical of coursers in being grey above and buff below with the crown, the centre of the back, a conspicuous chest band and a line through the eye, black. The eyebrow is pure white and, as in *Cursorius*, reaches to the nape. The bill is about 44% of the length of the head. The Australian Dotterel *Peltohyas australis* is a courser-like plover of the central Australian arid zone, formerly included with the Glareolidae, but now unequivocally shown to be a member of the family Charadriidae.

Relationships within the subfamily Cursoriinae are not easy to work out, but it has been suggested, using feather lice (see ECTOPARASITE) as evidence, that the evolutionary trend has been from *Rhinoptilus* through *Cursorius* to *Pluvianus*. Adult plumage patterns seem to confirm this idea. Chick plumage patterns, usually a good source of systematic information, are too variable among coursers to be of any systematic use. The nearest relative of the coursers is the Australian Pratincole *Stiltia isabella* (see PRATINCOLE) which has features of both coursers and pratincoles.

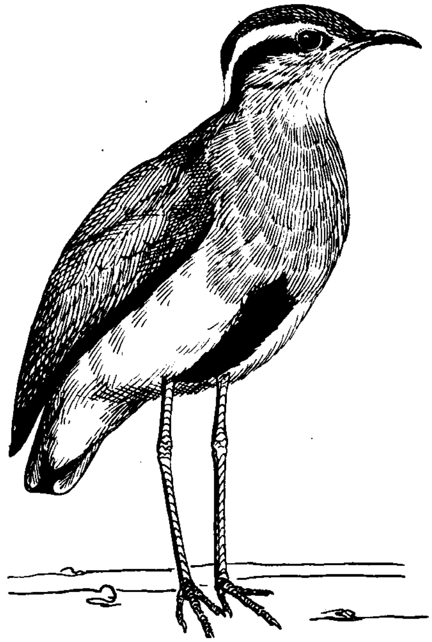
Habitat. Coursers are birds of dry, rather flat savanna, grassland and desert. The Egyptian Plover inhabits sandbars and shores of large rivers.

Distribution. The subfamily Cursoriinae is distributed throughout the non-forested parts of Africa, the Middle East and India.

Movements. The true coursers are mostly nomadic, especially in the more arid areas; those of savannas tend to be more sedentary. No courser appears to be migratory. The Egyptian Plover appears to be more or less sedentary.

Food. Coursers feed largely on insects picked up from the ground, while members of the genus *Cursorius* apparently also eat seeds. The Egyptian Plover feeds on small arthropods found by turning over stones, probing in sand, scratching in damp sand with both feet together; they may be caught in the air by a run, or merely picked from the surface of the sand or a plant. It has also been said to pick food from the mouths of basking crocodiles (see CROCODILE BIRD), but if it ever does so, it has not been seen doing so in recent times.

Behaviour. Coursers of the genus *Cursorius* tend to be gregarious, occurring in small parties of up to about 15 birds. Even during the breeding season, nesting pairs tolerate the close proximity of conspecifics. *Rhinoptilus* coursers are usually found in pairs, or small family parties. *Pluvianus* occurs in pairs when breeding but is said to form small flocks after breeding has ended and the water level in the rivers is high. Most coursers are fairly active at night, but only the Bronzewing Courser is truly nocturnal. When approached in open desert habitat, coursers will run a little way and then stop with neck stretched upright to look at the intruder.



Temminck's Courser *Cursorius temminckii*. (*C.E.T.K.*).

Voice. Coursers have unmusical growling or grunting calls, often uttered on the wing, but some *Rhinoptilus* species have attractive whistled contact and alarm notes that carry a considerable distance.

Breeding. All cursoriines nest on the ground. The true coursers may make a shallow scrape for a nest, or they simply lay the eggs on the bare soil. An exception is the Three-banded Courser which lays its 2 eggs in a fairly deep scrape in loose gravelly soil, partly filling the scrape to bury the eggs until less than half is exposed. The eggs are incubated in this partly buried state. Most coursers lay clutches of 2 eggs, but the Double-banded lays only one egg, and the Bronzewing often lays 3. The Egyptian Plover lays 2 or 3 eggs in a deep scrape on a sandbank; by day the eggs are completely buried under 2–5 mm of sand which is continuously wetted by the parents during the hottest hours of the day (from about 3–4 hours after sunrise to 2–3 hours before sunset) in order to keep the egg temperature from rising too high; water for this purpose is carried in the soaked belly plumage and never by regurgitation as has often been quoted in the past (see BELLY-SOAKING). Small chicks are also buried and wetted in this way.

Cursoriine eggs are cryptically coloured, off-white to yellowish brown in ground colour, finely and densely scrawled or irregularly spotted with dark brown and grey. Burial of eggs by both the Three-banded Courser and the Egyptian Plover is done with the bill and not with the feet as in other waders (Charadrii). Some coursers deliberately lay their eggs among dry antelope droppings for extra camouflage.

Incubation in the Double-banded Courser takes about 26 days (which is average for waders of this size), in the Egyptian Plover about 30 days. It is thought that the latter's long incubation period is facilitated by wetting the sand, which reduces evaporation from the eggs and allows the chicks to develop to a highly precocial condition by the time they hatch. All cursoriines feed their young until they are almost ready to fly, although the young pick up much of their own food after the first few days. The young can fly at 5–6 weeks of age. Coursers with eggs or chicks have no true distraction displays, but the Egyptian Plover has an injury-feigning display in the presence of a human intruder. See photo INCUBATION; PARENTAL CARE. G.L.M.

Howell, T.R. 1979. Breeding biology of the Egyptian Plover, *Pluvianus aegyptius*. Univ. Calif. Publns Zool. 113.

Kemp, A.C. & Maclean, G.L. 1973. Neonatal plumage patterns of Three-banded and Temminck's Coursers and their bearing on courser genera. Ostrich 44: 80–81.

Kemp, A.C. & Maclean, G.L. 1973. Nesting of the Three-banded Courser. Ostrich 44: 82–83.

Maclean, G.L. 1967. The breeding biology and behaviour of the Double-banded Courser *Rhinoptilus africanus* (Temminck). Ibis 109: 556–569.

Timmermann, G. 1955. Die verwandtschaftlichen Beziehungen einiger Watvogelgruppen im Lichte der vergleichenden Parasitologie. Proc XI Int. Orn. Congr.: 356–361.

COURT: alternatively 'arena' (and various special terms)—see LEK.

COURTSHIP: term used, in the study of bird behaviour, to cover a wide range of activities of which the function seems to lie in attracting a mate, maintaining the pair bond, and in facilitating copulation and parental activities (see PAIR FORMATION; also COPULATION; COURTSHIP FEEDING; DISPLAY; LEK; MECHANICAL SOUNDS; TERRITORY; VOCALIZATION). See photo DISPLAY.

Scottish Crossbill *Loxia scotica* male feeding female. (*Photo: E.J. Hosking*).

COURTSHIP FEEDING: the feeding of one member of an adult pair by the other. In sexually dimorphic species it is normally the male that feeds the female, but where the behaviour and plumage of the sexes is similar, the reverse sometimes occurs; further, in species where the female takes the active role in courtship, she may regularly feed the male.

The movements used by each species in courtship feeding are usually closely similar to those of juvenile begging and feeding the young. Thus in cardueline finches the male regurgitates the food, whereas in tits it is passed directly from his bill. Often the posture adopted by the female resembles not only the begging of the young, but also the female copulatory posture and the submissive posture. The movements may, however, become further ritualized, and elaborate ceremonials, such as the fish-flight in terns, may be incorporated (see RITUALIZATION). Billing and scissoring movements may be a further development of courtship feeding, or they may be independently derived from movements used in feeding the young or in aggression.

Courtship feeding is usually most frequent before or during the period of copulation and egg-laying, but often it continues during incubation. During egg-laying and incubation the actual food exchanged may be important as such, but in most species it seems to be primarily of symbolic and stimulatory significance—many cases of a female begging from a male although already carrying food herself have been recorded. Indeed, in many species elaborate ceremonials of billing, scissoring, and the like, in which no food is passed, occur as well as, or instead of, courtship feeding itself.

Courtship feeding does not, in general, occur in birds that do not form pairs. Presumably, where it does not have a nutritive function, it has a survival value relating to the pair bond. Its precise function varies between species. In some it is closely related to copulation, the male feeding the female while copulating, or just before or afterwards. In others it occurs at the same stage in the cycle as copulation, but not in immediate temporal relation with it (see also COPULATION). The food conveyed may be of direct importance to the female, and may also indicate the male's potential as a provider of food for the young. It may also have a function in reducing aggression between the partners, perhaps promoting habituation to the proximity of the mate and thus facilitating sexual and, later, parental behaviour (see PAIR FORMATION); in general it is commoner in sexually monomorphic species (i.e. where both sexes carry the releasers for aggressive behaviour). However, even when the peaks of courtship feeding and copulation occur at the same stage in the reproductive cycle, courtship feeding usually starts well before and lasts after copulation. In other species there seems to be no relation with copulation except that both occur in the breeding season; in such cases little can be said about the functions of courtship feeding except that it presumably plays a general role in promoting and maintaining the pair bond. R.A.H.

Krebs, J.R. 1970. The efficiency of courtship feeding in the Blue Tit *Parus caeruleus*. Ibis 112: 108–110.

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COVERT: also 'tectrix', term for any of the contour feathers that overlie, dorsally or ventrally, the bases of the remiges and rectrices; applied also to the auriculars (ear coverts), concealing the external auditory meatus. There are upper and under tail coverts, and upper and under wing coverts. In the wing, the upper coverts in particular form several distinct rows, designated (from distal to proximal) as primary, greater, median, and lesser coverts (see TOPOGRAPHY; WING).

COVEY: see ASSEMBLY, NOUN OF.

COWBIRD: substantive name of species in several genera (*Molothrus*, etc.) of Icteridae (see ORIOLE (2)).

CRAB-PLOVER: *Dromas ardeola*, sole member of the Dromadidae (Charadriiformes, suborder Charadrii, superfamily Charadrioidea). It is a very distinctive large shorebird, about 40 cm long; the sexes are identical, being white with black mantle and primaries. In immature birds the crown, neck, scapulars and tail are suffused with grey-brown. The large black bill is laterally compressed. The long legs are slaty-blue and the feet are partially webbed. The wings are long and pointed and the tail is short.

Habitat and distribution. The Crab-plover is a coastal bird, breeding in sand dunes and feeding on sandy and muddy beaches, coral reefs and reef flats. As a breeding bird it is endemic to the north-western Indian Ocean, breeding in the Persian Gulf, on southern coasts of the Arabian peninsula, and in Somalia. Out of the breeding season it occurs on most islands of the western Indian Ocean south to Madagascar and on continental Africa south to Natal; in the east it occurs in the Laccadives

Crab-plover *Dromas ardeola*. (*C.E.T.K.*).

and Maldives, Pakistan, peninsular India, Andamans and (rarely) in the Malay Peninsula. On islands of the Malagasy Region non-breeding birds can be found throughout the year.

Foods. Molluscs are eaten, but food consists mainly of crabs taken by both day and night; small crabs are eaten whole but the massive bill is used to break open larger ones.

Behaviour. Crab-plovers are frequently gregarious. In the non-breeding range they occur singly, in small parties and in large flocks, but birds from large roosting flocks generally disperse to feed more or less solitarily on extensive reef flats exposed at low tide. Both near breeding colonies and in the non-breeding range Crab-plovers are usually not very approachable, and when disturbed they are noisy; the call is a low fluty and musical chattering.

Breeding. The birds nest during the northern summer in burrows in colonies, sometimes numbering hundreds of nests, resembling rabbit warrens. Burrows, up to 2 m long, end in an unlined chamber in which is laid a single large white egg (unique in the Charadrii). The downy chick is nidicolous, but older chicks may emerge from their burrows at night. In the Seychelles, Crab-plovers sometimes arrive in autumn in family parties, with juveniles begging and being fed by their parents, suggesting prolonged parental care. (R.M.) C.J.F.

CRACIDAE: one of the families of the GALLIFORMES; comprising the curassows, guans, and chachalacas (see under CURASSOW).

CRACTICIDAE: a family of the Passeriformes, suborder Oscines (see BUTCHER-BIRD (2); CURRAWONG; MAGPIE (2)).

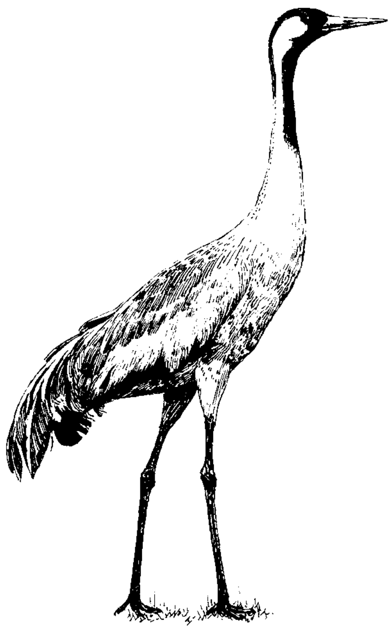
CRAKE: primary or alternative substantive name of many species of Rallidae (see RAIL).

CRANE: substantive name of the species of Gruidae (Gruiformes, suborder Grues); in the plural, general term for the family. Cranes form a homogeneous and phylogenetically very ancient family of large, stately and often very tall (up to 1.5 m) terrestrial and wading birds. There are 14–15 species in 4–5 genera (treated here as 15 in 4): 10 typical cranes *Grus*, Wattled Crane *Bugeranus carunculatus*, Demoiselle Crane *Anthropoides virgo*, Stanley or Blue Crane *A. (Tetrapteryx) paradisea*, Black-necked Crowned Crane *Balearica pavonina* and Grey-necked Crowned Crane *B. regulorum* (these two last, sometimes considered one species, probably represent a distinct subfamily). Recent studies of unison-calls suggest that the Siberian Crane *G. leucogeranus* is closer to *Bugeranus* than *Grus*.

Characteristics. All species are long-legged, long-necked birds with graceful tapering bodies and (except in *Balearica*) ornamental inner secondaries hanging over tail; bills are medium length (short in *Balearica*), straight and sharp. The hallux is raised. Flight is powerful and easy, the wings long and broad, the tail short. *Grus* and *Bugeranus* have bare patches on head and sometimes neck, coloured red, orange or black, the latter with a pair of feathered wattles either side of the chin; *Balearica* has a throat lappet, bare cheeks, bushy crown of bristly feathers and, with *Anthropoides*, elongated breast plumes. *A. virgo* has white post-auricular plumes. Most plumages comprise shades of grey, white, brown, blue and black. The sexes are similar, but males are slightly larger. In *Grus* (except *G. leucogeranus*) the trachea penetrates the sternum with 2 or more loops, assisting volume of calls; it is nearly straight in *Balearica*.

Habitat. Cranes show 3 partially distinct habitat requirements, for nesting, feeding and roosting. Nesting habitats are usually secluded and aquatic, e.g. bogs, marshes, floodplains, wet grasslands and swamps. Feeding habitats (throughout the year) generally extend also to dry uplands, savanna, cultivations and pasture; breeding birds may fly some distance to reach them. Roosting (also flight-feather moulting) sites are usually in remote areas with surface water. *G. leucogeranus* is considered the most aquatic species; the Cuban race of the Sandhill Crane *G. canadensis* is probably the least. The Whooping Crane *G. americana* uses (in winter) the most saline habitats. *Balearica* roosts regularly in trees.

Distribution. The family is represented on all continents except South America and Antarctica. The main area of speciation is central to eastern Asia, which (including north and east Siberia) holds 8 species. Of these the Common Crane *G. grus* breeds from north-east Europe to eastern Siberia, the Black-necked Crane *G. nigricollis* on the Tibetan plateau, the Hooded Crane *G. monacha* in central Siberia between Tomsk and Lake Baikal, the Japanese (or Manchurian) Crane *G. japonensis* in Ussuriland, Manchuria and western Hokkaido (Japan), the White-naped Crane *G. vipio* in Mongolia, Manchuria and the adjacent USSR, *G. leucogeranus* in northern Siberia (north-east Yakutia and the lower reaches of the Ob), *A. virgo* (apart from a tiny number perhaps still breeding in North Africa) from Bessarabia and eastern Turkey across central Asia to Mongolia and adjacent southern Siberia, and *G. canadensis* in north-east Siberia and (patchily) throughout the northern Nearctic, with outpost subspecies in Mississippi, Florida and Cuba. *G. americana* is thus the only purely Nearctic species, breeding in a single area in Canada. The Sarus Crane *G. antigone* occurs from the Indian subcontinent across south-east Asia into northern Australia; its close relative, the Brolga *G. rubicunda*, is confined to parts of Australia and southern New Guinea. In Africa, *A. paradisea* only occurs south of the Tropic of Capricorn, except for an outpost in Namibia; *Bugeranus carunculatus* is thinly distributed south of 5° S and in the Ethiopian highlands; *Balearica pavonina* occurs from West Africa across to Ethiopia; and *Balearica regulorum* replaces it from Uganda to the Cape.



Common Crane *Grus grus*. (*C.J.F.C.*).

Populations. The migratory species tend to occur discretely because birds show a high site-fidelity and philopatry, the young learning the migration routes from their parents; this increases the likelihood of local extinction. Although a few species (notably *G. canadensis* and *G. grus*) retain relatively large populations, probably all have declined considerably and 5–7 are now at risk. *G. monacha* and *G. vipio* each have a few (not more than 3) thousand individuals; *G. japonensis* and *G. leucogeranus* a few hundred; *G. americana* (see also under ENDANGERED BIRDS) less than 100 (more including captive stock). *Bugeranus carunculatus* and *G. nigricollis* have unknown populations, but the former is certainly small and diminishing, the latter possibly so. Two sedentary races of *G. canadensis* (in Mississippi and Cuba) are represented by tiny remnant numbers. The causes of declines are everywhere the same: habitat destruction and disturbance, with some hunting.

Movements. No crane is entirely resident. All Holarctic species are strongly migratory, apart from the Japanese population of *G. japonensis* and the 3 southern races of *G. canadensis*. Birds commonly fly in large V-formations, by day or night, sometimes at enormous heights. Routes are traditional and involve the use of particular staging areas. *G. grus* winters in Iberia, northern Africa, Sudan, and parts of Asia from Turkey across to China. *G. nigricollis* winters in western China; the 'Manchurian' population of *G. japonensis* winters in China, Korea and Japan, *G. monacha* and *G. vipio* in the latter two. The Ob River population of *G. leucogeranus* winters at one site in India but the present wintering grounds of the Yakutia population seem uncertain. The northern races of *G. canadensis* (including the Siberian birds) winter in the southern USA and Mexico; *G. americana* migrates to a small area of coastal Texas. Some *A. virgo* travel further south than any other Holarctic species to winter in north-east and north-central Africa (9–15° N); most, however, visit the

Indian subcontinent and parts of south-east Asia. All the remaining species show at least small local movements.

Food. Cranes are omnivorous, the diet varying with season and local conditions, but preferences for animal or vegetable diet appear also to vary between species (e.g. chiefly animal in *G. americana*, *A. paradisea* and possibly *Balearica*, chiefly vegetable in *G. leucogeranus*, *G. canadensis* and *Bugeranus carunculatus*). All species use the bill to probe and dig for rhizomes, roots and tubers of marsh plants (although *Balearica* also scratch for them with their feet); they also browse, graze and glean for above-ground vegetable matter, especially seed-heads of grasses and sedges, leaves, shoots, buds, fruit (including acorns), etc. Most species also exploit cultivations where possible or at certain seasons; maize is particularly important for *G. canadensis* in both autumn and spring. Animal food is highly varied, but insects (especially Orthoptera and Coleoptera) are always important; also worms, molluscs, crustaceans, crabs, fish (including eels), amphibians, and less commonly small reptiles, birds (eggs and chicks) and small mammals. Only *G. americana* is known consistently to maintain winter feeding territories, probably as a result of its dependence on animal food (blue crabs *Callinectes* and several genera of clam).

Behaviour and voice. Cranes are usually gregarious outside the breeding season, especially when roosting and moulting. All are strictly monogamous, some species evidently pairing for life (but the survivor remates when its partner dies). Pairing appears to occur in flocks of young birds between independence (end of the first year) and maturity (from 3 years onwards). The bond is maintained all year round, most obviously by unison-calling (duetting) and associated displays. The famous and beautiful dancing-displays of cranes (in which birds bow, leap in the air, run wildly and toss vegetation about) may also at times serve this purpose, but they can occur in isolated birds or flocks and seem only to reflect general excitement. Pairs hold large territories, but the traditional and often isolated nature of the nesting site restricts aggression. The rolling, sonorous and often musical calls carry very long distances, perhaps serving both to disperse and to contact pairs; flocks are often extremely noisy. In migratory species, the offspring accompany their parents throughout the winter (when they may still be fed), and are only driven away after arrival back at the breeding grounds the following year.

Breeding is seasonal in the 9 Holarctic species, somewhat more extended in *A. paradisea*, *G. antigone* and *G. rubicunda*, and considerably so in *Bugeranus* and *Balearica*. Nests (often bulky through repeated use, but with little or no material in *Anthropoides*) are always in the open (*Balearica* trample the surrounding area flat, but also sometimes build low in trees) and usually on marshy ground. The eggs are oval or subelliptical, and variable in colour, markings and gloss; usually 2 are laid (but up to 4 in *Balearica*) and one young reared. Incubation is by both birds and typically lasts *c.* 30 days (up to 40 in *Bugeranus*); the young are precocial and nidifugous. Intersibling aggression may lead to the death of the weaker chick, but parents may take charge of one young each, feeding them bill-to-bill. Fledging periods vary, but are shorter in Holarctic species (55 days minimum) and apparently longest in *Bugeranus* (105 days minimum). N.J.C.

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Pomeroy, D.E. 1980. Aspects of the ecology of Crowned Cranes *Balearica regulorum* in Uganda. Scopus 4: 29–35.

Urban, E.K., Fry, C.H. & Keith, S. (eds). (In press). The Birds of Africa, II. London.

Walkinshaw, L. 1973. Cranes of the World. New York.

CRANIAL: pertaining to the skull.

CRÈCHE: an assemblage pooling the still dependent young of several pairs of a species, e.g. Eider *Somateria mollissima*, Emperor Penguin *Aptenodytes forsteri*, Greater Flamingo *Phoenicopterus ruber*. The term seems particularly apt in those cases where only a few adult birds are usually present, although these may not have any special role as guardians. See also PARENTAL CARE.

CREEPER: element in substantive names used (some also as general terms) in several families of Passeriformes; although used alone by American ornithologists for *Certhia*, more often written as part of a compound word—for Certhiidae see TREECREEPER (1); for Climacteridae see TREECREEPER (2); for Rhabdornithidae see CREEPER, PHILIPPINE; for Salpornithidae see CREEPER, SPOTTED; for Tichodromatidae see WALLCREEPER; for Coerebidae see HONEYCREEPER; for Drepanididae see HAWAIIAN HONEYCREEPER; for Timaliinae (bush-creeper) see BABBLER; for Dendrocolaptidae see WOODCREEPER; for Formicariidae (antcreeper) see ANTBIRD; for Furnariidae (earthcreeper, streamcreeper) see OVENBIRD (1). The New Zealand Brown Creeper *Finschia novaezeelandiae* is now placed in the subfamily Mohouinae of the Acanthizidae; see WARBLER, AUSTRALIAN.

CREEPER, PHILIPPINE: in the plural, general term for the members of the endemic Philippine family Rhabdornithidae (Passeriformes, suborder Oscines). The 2 usually recognized species are the Plain-headed Creeper *Rhabdornis inornatus* of Luzon, Mindanao, Samar, Leyte and Negros, and the Stripe-headed Creeper *R. mystacalis* of these islands and Masbate, Panay, Bohol, and Dinagat.

Characteristics. *R. mystacalis* is about 15 cm long, brown above and white below, with a black mask, a white eyebrow, black striping along the sides, and white crown-streaks. Males tend to be greyer above than females (Parkes 1971). *R. inornatus* is larger and duller, with an unmarked crown. Both species have a straight bill, longest in races from the northern Philippines (Rand and Rabor 1960).

Habitat. *Rhabdornis* inhabits rain forest, forest edge and clearings. *R. inornatus*, the less common species, is most often found above 900 m. *R. mystacalis* is common at lower elevations, but may be uncommon to absent at higher elevations on some islands.

Food. Although both species will climb on trunks (duPont and Rabor 1973, M.D. Bruce), they forage primarily in the outer canopy. Here they perch crosswise on branches or walk along them, gleaning insects from leaves and twigs, probing among flowers, and occasionally eating small fruits.

Behaviour and breeding. Little is known of their biology. Both species usually forage either in single-species flocks of under 10 birds or in larger, mixed-species assemblages. Their nests are unknown, although *R. mystacalis* is suspected of nesting in holes in trees or hollow limbs. One call of the Stripe-headed Creeper is a high-pitched, squeaky *tsee-tsee-wit-see*.

Rhabdornis has been allied with *Sitta* (see NUTHATCH), *Certhia* (see TREECREEPER (1)), and *Climacteris* (see TREECREEPER (2)), but its resemblances to these climbing birds are superficial (Mayr 1963). It differs from them in leg musculature, and lacks such climbing adaptations as stiffened rectrices, elongated toes and reduced toe pads (Orenstein 1977). The genus has plumage and anatomical similarities to the babblers *Ptilocichla* and *Kenopia* (see BABBLER), but its true relationships remain uncertain.

As 'Creeper' is a misnomer for these birds, Rabor and Kennedy (MS) suggest that 'Rhabdornis' replace it as the substantive name for the family. R.O. and R.S.K.

duPont, J.E. & Rabor, D.S. 1973. Birds of Dinagat and Siargao, Philippines. An expedition report. Nemouria 10: 1–111.

Orenstein, R.I. 1977. Morphological adaptations for bark-foraging in the Australian Treecreepers (Aves; Climacteridae). Ph.D. thesis, University of Michigan.

Mayr, E. 1963. Comments on the taxonomic position of some Australian genera of songbirds. Emu 63: 1–7.

Parkes, K.C. 1971. Taxonomic and distributional notes on Philippine Birds. Nemouria 4: 1–67.

Rabor, D.S. & Kennedy R.S. MS. A Field Guide to the Birds of the Philippine Islands.

Rand, A.L. & Rabor D.S. 1960. Birds of the Philippine Islands: Siquijor, Mount Malindang, Bohol, and Samar. Fieldiana Zool. 35: 223–441.

CREEPER, SPOTTED: substantive name of *Salpornis spilonota*, sole member of the Salpornithidae (Passeriformes, suborder Oscines). Formerly included in the Certhiidae (see TREECREEPER (1)) or Sittidae (see NUTHATCH), *Salpornis* lacks *Certhia*'s stiffened rectrices, and differs from both families in nest type and details of leg musculature.

Characteristics. The Spotted Creeper is about 13 cm in length, with an elongate, thin, downcurved bill, pointed wings and a nearly square tail with 12 rectrices. It has short legs and long, partly fused toes with strongly curved claws. Adults are blackish-brown, heavily spotted with white above and mottled white, buff and brownish below, with a barred

Emperor Penguin *Aptenodytes forsteri* guarding crèche of young. (*Photo: J. Prévost*).

tail and white eyebrow. Immatures are duller.

Habitat and distribution. Spotted Creepers are locally distributed in the central Indian peninsula, and in Africa south of the Sahara to about 25° S. They are sedentary birds, usually found singly or in pairs in savanna or in semi-open acacia or miombo *Brachystegia* woodland, often in association with mixed foraging parties.

Food. A foraging Spotted Creeper flutters and clambers rapidly from the base of a tree to the upper branches, exploring bark fissures for beetles (e.g. Bostrychidae), ants, spiders and other arthropods. It holds its tail clear of the trunk. Flight between trees is undulating or gliding. The bird lands by 'tumbling' on to a trunk, with open wings.

Voice. Vocalizations include a rapid, shrill whistle *sweepy-swip-swip-swip* . . ., 5 or 6 high-pitched, croaking *kek*'s and a single *tseee*.

Breeding. *Salpornis* nests between August and May, at different times in different areas. The nest is a soft cup of leaf-stalks, bark, lichen and other materials, lined with hair or spider egg-cases and bound together with cobwebs, cocoons and vegetable down. Its walls may be built up during incubation. The nest is usually placed 3 to 13 m up near the fork of a horizontal branch. The 2 or, more usually, 3 eggs (*c.* 18.5 × 3.5 mm) are pale bluish to greenish, with dark markings tending to form a ring around the blunt end. Apparently only the female incubates, fed by the male. Both sexes brood the young. A nest tree may be re-used for several seasons. R.O.

Skead, C.J. 1967. The Sunbirds of Southern Africa. Also the Sugarbirds, the White-eyes and the Spotted Creeper. Capetown.
Steyn, P. 1974. A confiding creeper. Bokmakierie 26(4): 80–83.

CREPUSCULAR HABITS: see under NOCTURNAL HABITS.

CRESCENT-CHEST: substantive name now regularly used for the 4 species of TAPACULO of the genus *Melanopareia*.

CREST: a tuft of feathers on the crown of the head, which in many species can be raised or lowered (see DISPLAY).

CRIMSON-WING: substantive name of *Cryptospiza* spp. (see ESTRILDID FINCH).

CRISSUM: the area round the vent, with the under tail coverts (see TAIL; TOPOGRAPHY).

CROCODILE-BIRD: name designating an African bird (or birds) said by Herodotus and Pliny to pick food (leeches, débris) from the gums of basking crocodiles, even entering the open mouth; usually identified with either the so-called Egyptian Plover *Pluvianus aegyptius* (see under COURSER), or the Spur-winged Plover *Vanellus* ('*Hoplopterus*') *spinosus* (see PLOVER), and perhaps applicable to both these species and to some others. The subject is controversial, because many observers who have had ample opportunities have never seen the birds feed from, still less enter, the crocodile's mouth and are accordingly sceptical. The number of positive modern records of any reliability is indeed so small that one may doubt whether this particular action of entering the mouth is frequent. It is not in dispute, however, that both the species named above

Snowy Egret *Egretta thula* with raised crest defending feeding territory. (*Photo: J.B. & S. Bottomley*).

commonly associate with basking crocodiles and feed close to them or on their ectoparasites (tsetse flies, etc.). This latter habit is also shown by the Common Sandpiper *Actitis hypoleucos* while in Africa during the northern winter—and has likewise been recorded from Borneo. Many other species fearlessly keep company with basking crocodiles, even sleeping beside them or standing on them. The Water Dikkop *Burhinus vermiculatus* goes further in apparently having a nesting association with the crocodile, laying its eggs at the same time (when the river is low) and often incubating them within a few feet of the brooding reptile (see THICKKNEE).

As in other circumstances the crocodile regularly preys on waterfowl, this mutual tolerance is remarkable; one recalls the different reactions of antelopes and the like to lions when the latter are respectively hunting and resting. It seems likely that the birds are of more value to the crocodile as sentinels, giving early warning of the approach of danger, than in removing parasites. To some of the birds the crocodile's parasites are food, and to the nesting Water Dikkop its proximity may provide some protection against egg-eating predators. With other species of birds the relationship seems to be casual. A.L.T.

Cott, H.B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. Trans. Zool. Soc. Lond. 29: 211–350.

Meinertzhagen, R. 1959. Pirates and Predators. Edinburgh.

CROMBEC: substantive name of *Sylvietta* spp. (for subfamily see WARBLER (1)). See photo NEST BUILDING.

CRONISM: term (*Kronismus* in German) proposed by Schüz for the actual or attempted swallowing by the parents of their own dead or sickly young.

Schüz, E. 1957. Der Verschlingen eigener Junger ('Kronismus') bei Vögeln und seine Bedeutung. Vogelwarte 19: 1–15.

CROP: also called 'ingluvies' (see ALIMENTARY SYSTEM; CROP MILK).

CROP MILK: a secretion of the oesophagus, resembling mammalian milk in its composition, produced by all pigeons (Columbiformes) and among other bird orders at least by the Greater Flamingo *Phoenicopterus ruber* and the Emperor Penguin *Aptenodytes forsteri*, with which they feed their young after hatching.

In pigeons and doves the milk is produced in the crop, a sac-like distension of the oesophagus (see ALIMENTARY SYSTEM) normally used for food storage. During the last few days of incubation the epithelial cells of the dorsal and lateral crop walls begin to enlarge and cells containing milk slough off. This process is under the control of the pituitary hormone prolactin (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM) and occurs in both sexes. For the first few days after hatching the nestlings are given only milk and it seems important that at this time the milk is not contaminated with other food. Only when the crop is empty are the milk cells sloughed off and regurgitated to the young at frequent intervals. Thereafter the young begin to receive whatever else the parents are collecting. In the domestic pigeon milk production continues for about 16 days. Unlike other granivorous birds, pigeons feed very little animal matter to their nestlings, so that the secretion of a crop milk rich in fat and protein ensures that the young receive adequate nutrition during the period of maximum growth.

In the Emperor Penguin the secretion of oesophageal milk by the male enables the chick to double in weight after hatching while receiving no other food. This is the more remarkable since the male has by that time undertaken all the incubation without feeding for over 2 months.

Greater Flamingoes do not regurgitate predigested food for their young and appear to feed them solely on their milk for up to 2 months after hatching. Between them the parents produce 200 ml of milk daily, enabling the chick to grow from 100 g at hatching to some 2–4 kg. For the first few weeks the milk is dark red, due partly to the presence of the pigment canthaxanthin but also to large numbers of red blood cells.

The composition of different crop milks is shown in the Table. Pigeons' milk contains, at least qualitatively, most of the amino acids essential to growing chickens (see NUTRITION). Pigeons' milk contains no carbohydrate, whereas penguin milk has an appreciable quantity. Flamingo milk has an unusually high fat content. P.J.J.

Comparative composition of crop milks of pigeons, Greater Flamingo and Emperor Penguin, expressed as percent of dry weight.

	Pigeon[1]	*Greater Flamingo*[2]	*Emperor Penguin*
Protein	58.4	32.5	59.3
Fat	35.1	65.3	28.3
Carbohydrate	—	0.8	7.8
Minerals	6.5	1.4	4.6

[1] Water content of milk 74%

[2] Water content of milk 73%

Lang, E.M. 1963. Flamingoes raise their young on a liquid containing blood. Experientia 19: 532–533.

Murton, R.K. & Westwood, N.J. 1977. Avian Breeding Cycles. Oxford.

Prévost, J. & Vilter, V. 1963. Histologie de la sécrétion oesophagienne du Manchot empereur. Proc. XIII Int. Orn. Congr.: 1085–1094.

CROSS: see HYBRID.

CROSSBILL: substantive name of *Loxia* spp. (see FINCH). See photo COURTSHIP FEEDING.

CROSS-FOSTERING: replacement of the eggs of one species by those of another (usually closely related), so that the young are reared by the 'wrong' parents.

CROTOPHAGINAE: see CUCKOO.

CROW (1): substantive name of many species of Corvidae (Passeriformes, suborder Oscines); in the plural, general term for the family, although also, in a more restricted sense, for the typical crows *Corvus* spp. Outside the typical genus, the most frequent substantive names are 'jay', and 'magpie' (varied to 'tree-pie' in one genus), while 'nutcracker', 'chough' and 'piapiac' are special names for one or two species in each case. Within *Corvus* 'raven' is applied to various large species, while 'rook' and 'jackdaw' are special names. The names 'crow' and 'jay' occur as misnomers for unrelated birds (see CROW (2) and JAY), while 'magpie' and 'chough' have other meanings in Australian ornithological usage (MAGPIE (1) and (2), and CHOUGH (1) and (2)).

It has been considered that the Corvidae were most closely related to the birds-of-paradise (Paradisaeidae), bell-magpies (Cracticidae), Old World orioles (Oriolidae) and the drongos (Dicruridae), but more recent studies of egg-white proteins suggest that their nearest relations are the shrikes Laniidae. The division into 2 subfamilies, the typical crows (Corvinae) and the jays and magpies (Garrulinae), is not now considered useful. There are some differences between authorities about the demarcation of both genera and species. Goodwin (1976) describes 23 genera and 113 species. The taxonomy and nomenclature followed here is that of Goodwin.

Characteristics. The crows, as a family, may represent the furthest stage so far reached in avian evolution; much in their behaviour suggests a highly developed mentality, and some species have a complex social organization. This is not to say that they show extreme specialization; on the contrary, they are characterized by great adaptability. They are certainly successful, as judged by the large number of species and the almost world-wide distribution.

They are large birds, by the standards of the Passeriformes (from 20–66 cm long), and they include the largest members of that order. The bill is stout, fairly long, and often with a small terminal hook. The nostrils are usually round, without an operculum, and shielded by bristles directed forwards. The legs and feet are robust, the tarsi are usually strongly scutellated in front and booted behind; in the choughs they are booted both in front and behind.

While the typical crows are either wholly black, including bill and legs, or black with some white, grey or brown, the jays and magpies often have bright colours, especially blues and greens; further, many of the jays and magpies have very long tails, and some of the jays are crested. The sexes are alike in plumage, or nearly so, and there is no marked seasonal change. Crows are mostly strong fliers.

Habitat. Apart from the two cliff-dwelling choughs *Pyrrhocorax*, the crows are found in woodlands of all types, though the *Corvus* species

Carrion Crow *Corvus corone*. (*C.J.F.C.*).

prefer open steppes, to which the landscapes modified by man, e.g. parkland, orchards, often approximate, and this assists their colonization by a number of species all over the world. The jays, on the whole, inhabit closed canopy woodland. A few species, e.g. Raven *Corvus corax* and Jackdaw *C. monedula*, occupy cliffs, quarries and even buildings.

Distribution. The family is almost cosmopolitan, but is most abundantly represented in temperate parts of the Northern Hemisphere. It is, however, unrepresented in New Zealand (apart from the introduced Rook *Corvus frugilegus*) and in most of the archipelagos of the Pacific Ocean; in South America the only representatives are jays.

The typical crows *Corvus*, a single genus, have an exceptionally wide distribution; they are absent from South America but are the only representatives of the family in Africa south of the Equator, in the Malagasy region and in Australia and Oceania. Both the choughs *Pyrrhocorax*, are Palearctic apart from an outlying colony of the Red-billed species *Pyrrhocorax pyrrhocorax* in Ethiopia. The nutcrackers *Nucifraga*, are Holarctic. The magpies are not necessarily a closely related group, those of the genus *Cissa* for example may be closer to the jays of the genus *Garrulus* than to the typical magpies of the genus *Pica*. Of the 5 genera now generally grouped as magpies, one has an Holarctic distribution, one is Oriental and Iberian and the remainder are all Asian, with several of the species confined to south-east Asian islands. Among the jays there are 8 New World genera and in South America they are the only representatives of the family; one genus is Holarctic, one is Palearctic. The ground jays of which there are 2 genera inhabit mainly high semi-desert areas in Asia. There are 3 monotypic genera whose relationship to other groups in the family is not clear, 2 are found in northern tropical Africa and one in south-east Asia.

Movements. Most members of the family are sedentary, but some may show weather movements, while a few perform regular migrations within the North Temperate Zone (see MIGRATION). Large scale autumnal movements of jays and nutcrackers are probably due to shortages of foods on which they are dependent and which are normally stored for winter and early spring use.

Food. Many of the species are practically omnivorous, taking both animal and vegetable food, and much feeding is done on open ground. Many have definitely predatory tendencies, some take the eggs and young of other birds; carrion is taken by some species, and some find their food among the jetsam of the sea or lake shore. Insects are taken, especially by the smaller species, and vegetable diet includes such items as acorns and the seeds of pine cones, and sometimes soft fruits. The birds are among those that hold food with the foot while tearing it with the bill. Some species, especially of jays, magpies and nutcrackers living in high latitudes or altitudes have the habit of hiding excess food for use in time of scarcity (see FEEDING HABITS; FOOD STORING).

Behaviour. Most, if not all, corvids are sociable, but there are different degrees of gregariousness among them, ranging from species like the Rook which nest in colonies and hold only a small territory immediately surrounding each nest, to those like the Carrion/Hooded Crow *Corvus corone* that maintain a large territory area throughout the year. In this species territorial integrity is vital to breeding success, because the most important predators on the eggs and young are other non-territory holding Carrion/Hooded Crows, but these are usually gregarious, living and feeding in a non-breeding flock. Many corvid species that nest in isolation, e.g. the Raven, use communal roosts under certain conditions. In several species additional birds, sometimes young of the previous season, are tolerated within the territory. This tolerance probably depends on the submissive behaviour of the additional birds and ranges from the 'helpers' of some of the New World jays, where several birds may assist with rearing the young and with territorial defence, to the 'third bird' which Carrion/Hooded Crows will allow within the territory outside the nesting season; these are males who give some assistance with territorial defence and may succeed to the territory if the holder is killed.

The sociability of corvids is most marked at special feeding sites such as rubbish dumps and during migration and at winter roosts. In the roosts the coming together at nightfall of birds from a wide area may facilitate the finding of food during the ensuing day's foraging. Among socially breeding species like the Rook and Jackdaw the territorial behaviour implies recognition of a number of individual territory holders and their mates, as these are not attacked in the vicinity of the territory, while total strangers are.

Territory serves a different purpose for the Nutcracker *Nucifraga caryocatactes*: it is not only the area within which they breed but also the area within which they store food in the late summer and autumn ready for the winter and early spring. They are dependent on these food caches as individuals and it may be because each bird remembers where its own food is stored, that the two nutcrackers appear to be the only corvid species in which the male takes a share in incubation, leaving the female free to visit her own food caches.

There are interspecific reactions between corvids, especially the typical crows. For example Rooks, Carrion/Hooded Crows and Jackdaws will mob a predator attacking or holding a member of these or related species. Again Jackdaws on a flight line to a winter roost may stop briefly to join a group of one of the other typical crow species on the ground (see TERRITORY; FOOD STORING).

Voice. Many of the calls are loud, and for the most part harsh and discordant. Nevertheless, some species have a not unmelodious subsong, or 'whisper-song' uttered by both sexes and audible only at very short range (see VOCALIZATION). Some show considerable powers of mimicry, both when wild and in captivity (e.g. Jay), although others are not known to do so in a wild state (e.g. Magpie) (see MIMICRY, VOCAL).

Breeding. The crows often breed colonially, but not necessarily so even in species that are markedly gregarious at other times. Some species pair for life. Courtship feeding is common, and the male continues to feed the female while she is sitting on the nest. Both sexes take part in building the nest. In almost all the species only the female incubates the eggs or broods the young, but the male helps to feed them and sometimes performs most of that task; food is brought in the throat. In some of the New World jays, help in feeding the young, and even in nest-building or in feeding the sitting female, may be given by non-breeding 'helpers', some of which are known to be immature.

The nest tends to be a bulky structure of coarse twigs, variously lined; it is usually open but in a very few species it is roofed over. It is placed in a tree or bush, or on a cliff or building or occasionally on the ground. The eggs number 2–4 in some tropical jays but in other species there may be up to 9 or more. The colour ranges from buff or cream to green or greenish-blue, and there is usually heavy blotching or spotting with brown or other colours and paler underlying markings. Incubation periods are recorded as 16–21 days. The young are hatched blind, helpless, and either naked or with sparse down. They may be fledged in 20 days, but in some of the larger species 5–6 weeks may be spent in the nest.

Typical crows. It is generally agreed that these are the most advanced members of the family; they have in fact been described as 'in many ways the most adaptable and highly evolved of all birds'.

They are nearly all large birds, none really small, and some are very large for passerines, ranging in size from the Raven (length 60–66 cm; wing 38–43.6 cm) to the Jackdaw (length 33–34.6 cm; wing 22.5–24.6 cm). The plumage is often entirely black, and with black bill and legs as well, but the feathers may show a metallic gloss, from purple to blue and bluish green. Some species have parts of the plumage brownish or grey, even white, but bright pigments are absent. They tend to be omnivorous and in part predatory. When feeding on the ground they walk, but they roost and nest on trees and cliffs, often in very inaccessible places. They are strong fliers, often indulging in aerobatics. They are intelligent and wary, and often highly gregarious. Many of their calls are loud and commonly harsh. R. Meinertzhagen placed all the typical crows in the genus *Corvus*, and this course has been followed by Amadon (1944) and by E.R. Blake and C. Vaurie, among others; such names as '*Coloeus*', '*Corvultur*' and '*Rhinocorax*' may therefore be relegated to the synonymy. Affinities within the genus are difficult to determine, and some of the decisions as to the validity of species may need revision.

The genus *Corvus* contains about 40 species and for the purpose of the present summary a geographical arrangement (ignoring slight overlaps of the boundaries of regions) is convenient.

Palearctic. The Rook is a rather distinctive representative, with the white bare skin of the face (in the adult), the relatively bland *caw*, and the highly social behaviour, including colonial nesting; the tall trees in which its 'rookeries' are built are often near human habitations. Similar in size is the Carrion/Hooded Crow, of harsher voice and more predatory habits, whose territorial requirements have already been referred to. It is at present usual to regard the all-black Carrion Crow and the partly brownish-grey Hooded Crow as conspecific—*C.c. corone* and 1 other race; *C.c. cornix* and 3 other races—because they replace each other geographically and interbreed freely where their ranges meet; but the intermediates are presumably selected against, as the main populations apparently remain pure (see HYBRIDIZATION, ZONE OF SECONDARY; SPECIATION; SPECIES). The Hooded Crow is a notable migrant, in huge daytime flocks, in northern Europe.

Smaller, and indeed small for the genus is the Jackdaw, with grey nape, generally nesting more or less colonially but nearly always in holes, a habit that is unusual in the genus; the site chosen may be in a tree, cliff, a building or in the ground. Larger and indeed the largest passerine species is the Raven, a bird now largely restricted to remote mountain areas but with a wide Holarctic range (extending also to Central America).

In the more easterly parts of the Palearctic Region the Jackdaw is replaced by *C. dauuricus*, sometimes called the Daurian Jackdaw, and there are 2 other members of the genus—the Jungle Crow *C. macrorhynchos* (also widespread in the Oriental Region) and the Collared Crow *C. torquatus*.

Nearctic (and Neotropical). In North America, in addition to the Raven, there is the widespread Common Crow *C. brachyrhynchos*, not unlike the Carrion Crow. Of more restricted distribution are the White-necked Raven *C. cryptoleucus*, the North-western Crow *C. caurinus*, and the Fish Crow *C. ossifragus*; the last is a shore-feeder of the Atlantic and Gulf coasts and some of the major river systems. In southern North America, Central America and the Caribbean the Raven ranges as far south as Nicaragua. The Sinaloan Crow *C. sinaloae* and the Mexican Crow *C. imparatus* are mainland species. The Cuban Crow *C. nasicus*, the Jamaican Crow *C. jamaicensis* and the Palm Crow *C. palmarum* are confined to islands.

Afrotropical (and Malagasy). The Pied Crow *C. albus* is a familiar bird throughout Africa south of the Sahara except in rain-forest and desert areas; and it is the only member of the family found in Madagascar. It is a large species, in which the glossy black plumage is relieved by white across the base of the hindneck and on the chest and upper belly. Also widespread in eastern and southern Africa, is the Black Crow (or Cape Rook) *C. capensis*, which lays eggs that are rather like the rare erythristic eggs of other crows; they have a buff, buffish white or pinkish ground colour, usually profusely spotted and marked with brown, brownish red or purplish grey.

The Brown-necked Raven *C. ruficollis*, of northern and north-eastern Africa (also south-eastern Asia), is sometimes treated as conspecific with *C. corax*. There are also the Fantailed Raven *C. rhipidurus* in north-eastern Africa and the Middle East, the White-necked Raven *C. albicollis* in East and South Africa, and the rather similar but larger Thick-billed Raven *C. crassirostris* in Ethiopia.

Oriental. The common crows of southern Asia are the widely distributed (also eastern Palearctic) Jungle Crow *C. macrorhynchos*, the House Crow *C. splendens* of India and adjacent countries, and the Slender-billed Crow *C. enca* distributed from Malaya to the Philippines. About 7 more species are spread through the islands of south-east Asia and the South Pacific, several restricted to particular islands. The most isolated of all is the Hawaiian Crow *C. tropicus*. Some of these species are apparently largely fruit-eating. The Long-billed Crow *C. validus* of the Moluccas has white irides, as have the Australian crows.

Australian. In Australia and Tasmania there is a group of related species all having white irides. They are the Australian Crow *C. orru* whose range extends north of Australia to New Guinea and the Moluccas and several other islands, the Little Crow *C. bennetti*, the Australian Raven *C. coronoides*, the Little Raven *C. mellori* and the Forest Raven *C. tasmanicus*. In New Zealand there are no indigenous crows, only the introduced Rook.

Choughs. The 2 species of *Pyrrhocorax* are birds of medium size for this family, with glossy black plumage. The red-billed *Pyrrhocorax pyrrhocorax* has a rather long decurved red bill and red legs. The Alpine Chough *P. graculus* has a longer tail, a much shorter and less curved yellow bill and orange to red legs, the depth of colour of both bill and legs varying considerably. They are both gregarious cliff-dwellers of strong acrobatic flight. The Chough still exists on the western coasts of the British Isles; it is almost absent from the Alps, but otherwise has a distribution roughly similar to that of the Alpine Chough. Both species inhabit the mountain areas from the Iberian Peninsula and the Atlas mountains eastwards to central Asia and China, but the Alpine Chough is found at higher altitudes and does not use maritime cliffs. Both species readily become tame when they are not molested; one of the Mount Everest expeditions recorded Alpine Choughs as in attendance at a camp at 8,100 m.

Nutcrackers. The Nutcracker is an inhabitant of coniferous forests in high latitudes and altitudes of the Palearctic Region. It is slightly larger than the Jay *Garrulus glandarius* and has chocolate brown plumage, boldly speckled with white; the size and profuseness of the white spots, the length of the tail and the length and thickness of the bill differ in different geographical races. The Nutcracker's most important foods are the seeds of *Pinus cembra* and allied species and hazel nuts. The habit of food storing, often in deep snow, is very well developed and the birds are dependent upon it (see FOOD STORING). Clark's Nutcracker *N. columbianus* inhabits corresponding country in western North America and has similar habits; it differs in appearance in having the plumage largely grey, with black-and-white wings and tail.

Magpies. The name 'magpie' has come to be applied to a number of species that are not pied at all but have some general resemblance to *Pica*, usually including the long tail.

The typical Magpie *Pica pica* is about 46 cm in length including its long graduated tail. The scapulars, underparts and the inner webs of the primaries are white, the rest black with green, blue, purple and bronze gloss. It is widely distributed in the Palearctic Region except in the treeless north. There are many geographical races within this area, varying a little in size and in the amount of white on the body and wings. The species is represented by the race *P.p. hudsonia* in North America where there is also the Yellow-billed Magpie *P. nuttalli*, generally considered to be a separate species.

In a monotypic genus, the Azure-winged Magpie *Cyanopica cyanus* is decidedly smaller than *Pica* but has the same general shape, with the long, graduated tail. The plumage is largely brownish-grey, with a deep black cap descending to the nape and with light blue wings and tail. The species is remarkable for its discontinuous distribution; it is found only at the extremes of the Palearctic Region, in the Iberian Peninsula in the west and in northern China, Mongolia, and Japan in the east. The Iberian population is subspecifically distinct from the group of races in the Far East, but the history of the distribution of the species as a whole is not known.

The magpies of the genus *Cissa* are about the same size as *Pica* but most of them have longer tails due to the very long central tail feathers. There are 8 species of the genus *Cissa*; Whitehead's Magpie *Cissa whiteheadi* is black and white with a comparatively short white-tipped tail; there are 4 blue and 3 green species in the genus. All live in southern Asia, mainly in the south-east and in islands as far east as Taiwan, Java and Borneo.

The genus *Crypsirina* contains 10 species also living in areas from India eastwards, some of them limited to a restricted island distribution. They are the 'tree-pies' and are less brilliantly coloured than *Cissa*, being mainly rufous-brown, and black with shades of grey; some have the tips of the central tail feathers widened to a racquet formation.

In Tenasserim, the Malay Peninsula, Sumatra and Borneo there is a monotypic genus *Platysmurus*. The single species is *Platysmurus leucopter-*

us, the Black Jay; a magpie-like black bird with a white wing patch and a comparatively short tail.

Typical jays. The Jay *Garrulus glandarius* is the original bearer of the common name. It is a medium-sized crow with pinkish-brown body plumage, white rump and wing patch, black tail, beautiful blue and black barred wing coverts, and a black-and-white erectile crest. It is essentially a woodland bird, feeding on acorns during much of the year but also taking quantities of caterpillars and other insects, on which the young are largely fed. It also takes the eggs and young of other birds in the nesting season. In winter and spring the adults subsist largely on acorns previously hidden. In the open it appears a heavy flier, but is agile among trees and its progression on the ground is by long hops. Its many races are widely distributed in the Palearctic Region, except the most northern parts and central Asia. It has 2 congeners, generally similar birds, the Lanceolated Jay *G. lanceolatus* in the Himalayas and the Purple or Lidth's Jay *G. lidthi* in the Ryukyu Islands.

The grey jays of the genus *Perisoreus* inhabit the northern coniferous forests of both Old and New Worlds; they are probably of Old World origin. The Siberian Jay *Perisoreus* (*'Cractes'*) *infaustus* is slightly smaller than *Garrulus glandarius* and of much less colourful plumage—mainly brown and grey, but bright rufous on the wing, rump, and sides of tail. It is a Palearctic species with a more northern range than *Garrulus*. It is replaced in Szechwan by *P. internigrans*. In northern America there is the similar Grey (or Canada) Jay *P. canadensis*, with a white forehead and black nape and lacking the reddish feathers.

American jays. There are over 30 species of American jays assigned to 8 genera. The Blue Jay *Cyanocitta cristata* is a familiar North American bird, distributed from southern Canada to the Gulf of Mexico. Its upper parts are bright blue, with white patches on wings and tail and it has a pointed crest. Its sole congener, Steller's Jay *C. stelleri*, ranges from Alaska to Nicaragua, mainly on the western side of the continent. The Scrub (or Florida) Jay *Aphelocoma coerulescens*, ranging from the north-western United States to Florida and Mexico, is predominantly deep blue and brownish above, with no white on the tail and no crest. It has 2 congeners, in Middle America.

The species of *Cyanolyca* (9), *Cyanocorax* (12), which includes the Green Jay *C. yncas* found from Texas to Peru, and *Cissilopha* (4) are all inhabitants of tropical America.

The Pinyon Jay *Gymnorhinus cyanocephalus*, sole member of its genus, has a breeding distribution restricted to mountain areas in the western United States. It is a stumpy bird with mainly blue-grey plumage, and is gregarious in its habits.

The Brown Jay *Psilorhinus morio* is a large jay living in Mexico and Central America; there are 2 colour phases, the lighter one having white-tipped outer tail feathers and lighter body colour, yellowish to cream on the underparts instead of brown. The 2 phases were at one time considered to be separate species. The 2 magpie-jay species *Calocitta formosa* and *C. colliei* live respectively from Mexico to Central America and in western Mexico and are considered to be conspecific by some authors. They differ in that *C. colliei* has a longer tail and black face, throat and upper breast; the forehead and crest are also black.

Ground jays. The group of ground or running jays, sometimes referred to as ground choughs, comprises 4 *Podoces* spp. and *Pseudopodoces humilis* in a monotypic genus. They live on the semi-arid plateaus of central Asia and are highly specialized members of the family. As the name implies, they are largely terrestrial and tend to run rather than take to the air. They are relatively small birds (20–25 cm long), fawn or pinkish fawn in colour except in one species which is silver grey, all have rather short glossy black and white wings and varying amounts of black and white especially on the head and tail; the legs are long in proportion. *Pseudopodoces* is the smallest of the group and looks more like one of the larks (Alaudidae) than a crow. It also departs from the family norm by nesting in crevices in walls or in rodent holes, and in having white eggs. The species of *Podoces* usually build nests in bushes, and they have spotted eggs.

Aberrant forms. There are 3 monotypic genera with affinities so obscure that their inclusion in the family at all has sometimes been doubted. They are quite unlike each other and are taken together here merely for convenience. It was only in 1938 that *Zavattariornis stresemanni*, sometimes called Stresemann's Bush-crow, was first described. It is confined to southern Ethiopia, where it inhabits the thorn bush and builds large domed nests. It is a relatively small crow (*c.* 30 cm long), mostly grey above, with blue-black wings and tail, and white below; a patch of bare skin round the eye is said to be blue in life.

The Piapiac *Ptilostomus afer* is a familiar bird in West Africa and eastwards to Uganda. It is smaller in body than a magpie *Pica* sp. and similarly has a long graduated tail; the legs and feet are notably strong. The plumage is glossy black, tinged with brown on wings and tail; the bill is reddish except at the tip while the bird is immature, but is wholly black in the adult. The birds are usually to be seen in small flocks, on the ground (feeding largely on insects) or in palm trees. They show but slight fear of man and are common about villages, often associating with sheep and goats, at times perching on their backs (as on those of large wild mammals, including elephants, in the limited parts of the range where such are common).

The Crested Jay *Platylophus galericulatus* has been classified with the shrikes Laniidae, and it is not certain that it should be considered a member of the Corvidae. It is about the size of a Blue Jay *Cyanocitta cristata*, dark olive brown and grey in colour with black face, throat and neck, and with a white crescent on each side of the neck; it has a long rather broad black crest and is found in tropical forests in Java, Sumatra, Borneo and the Malay Peninsula. C.J.F.C.

See photo ANTING; BROODING; CARE OF SICK, INJURED AND ORPHANED BIRDS; FOOD STORING; LOCOMOTION, TERRESTRIAL.

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CROW (2): name misapplied to a variety of birds that are not members of the Corvidae. Thus, 'Bald Crow' is sometimes used for the two species of *Picathartes* (see under BABBLER); 'John Crow' (also 'Carrion Crow') is a popular misnomer in America for species of Cathartidae (see VULTURE (2)), and 'Rain Crow' for the Great Lizard Cuckoo *Saurothera merlini* in the West Indies (see CUCKOO); 'Piping Crow' is an alternative substantive name in Australia for *Strepera* spp. (Cracticidae—see CURRAWONG), and 'Wattled Crow' in New Zealand for *Callaeas* spp. (Callaeidae—see WATTLEBIRD (2)). See also FRUITCROW (Cotingidae); KING-CROW (Dicruridae); PARADISE CROW (Paradisaeidae); and 3 items below.

CROWN: see TOPOGRAPHY.

CROWN-BIRD: alternative name of the Crowned Crane *Balearica pavonina* (see CRANE).

CROW-PHEASANT: name, also 'Griffin's Pheasant', applied in India to a species of coucal, *Centropus sinensis* (see CUCKOO).

CROW-SHRIKE: name sometimes applied to *Strepera* spp. (see CURRAWONG).

CROW-TIT: substantive name sometimes used for *Paradoxornis heudei* (see PARROTBILL).

CRURAL: pertaining to the leg, especially the tibiotarsus (see LEG).

CRYPTIC: term applied to coloration or other characters that, by providing concealment or disguise, afford protection against enemies (procryptic) or facilitate capture of prey (anticryptic);—see COLORATION, ADAPTIVE; NATURAL SELECTION. The opposite is PHANERIC.

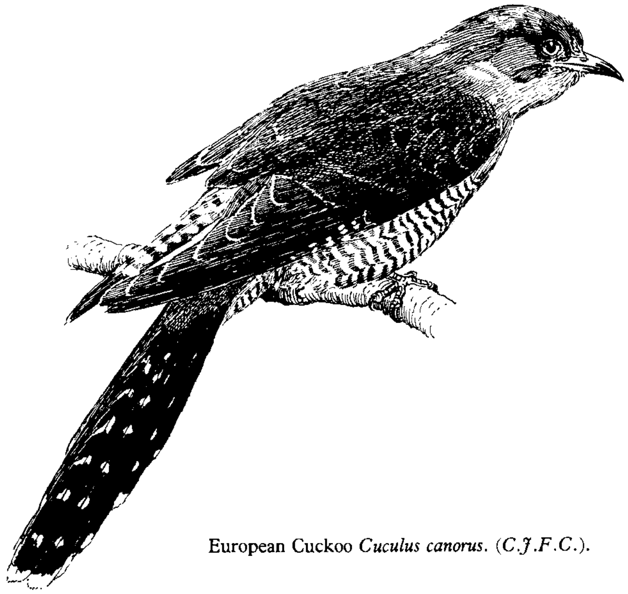
CRYPTIC SPECIES: alternative term (best abandoned, because of its ambiguity) for SIBLING SPECIES.

CRYPTOPTILE: term applied to the hypothetical early representatives of feathers in the remotest ancestry of birds; sometimes also to the first filaments appearing from the feather papillae in a young bird (see PLUMAGE).

CRYPTURI: see TINAMIFORMES.

CUBITAL: obsolescent alternative for 'secondary' in the terminology of wing feathers (see PLUMAGE; WING).

CUCKOO: substantive name of all species of Cuculidae (Cuculiformes); in the plural, general name for the family. Used without qualification in Britain, with equivalents in other languages in Europe,



European Cuckoo *Cuculus canorus*. (*C.J.F.C.*).

for *Cuculus canorus*. The common name in many European languages derives from the call of the European species. The family is large, with about 130 species in 34 genera. About 50 species lay their eggs in the nests of other species, which rear the young cuckoos (BROOD-PARASITISM). The other cuckoo species build a nest and rear their own young; a few are communal nesters.

Characteristics. Cuckoos vary considerably in size and appearance, but the species most often seen are slender, long-tailed, medium sized (20–30 cm) birds with two toes directed forward and two backward. In size the cuckoos vary from the small glossy cuckoos *Chrysococcyx*, which are about 15 cm long, to the coucals *Centropus*, the largest being nearly 90 cm. Most cuckoos have loose-webbed feathers and are variable in colour with most species being brown or grey, but some are all black, and others are brilliant greens, violets, or yellows. Many have brightly coloured bare areas of skin on the face, and some have a crest or long eye-lashes. Most have a slender straight or decurved bill not unlike other insect-eating birds, but some have a laterally compressed bill with a high arch. Most cuckoos have short legs, but the large terrestrial cuckoos are long-legged.

The closest relatives to the cuckoos are probably the turacos (Musophagidae). Aside from this, the relationships of cuckoos to other groups of birds are not known. The current systematic arrangement of cuckoos is based largely on breeding biology and geographic distribution, rather than on details of the feather tracts and moult and on skeletal and muscle anatomy. Within several subfamilies the anatomy varies among the species, and sometimes cuckoos within a subfamily are more different from each other than from cuckoos placed in different groups.

The subfamily Cuculinae, the brood-parasitic cuckoos of the Old World, includes the Cuckoo *Cuculus canorus*. Twelve other species occur in this genus, ranging through Europe, Asia, Africa, and Australia. Common species in other areas include the glossy cuckoos *Chrysococcyx*, the Koel *Eudynamis scolopaceus* of India, China, New Guinea, and parts of Australia, and the crested cuckoos *Clamator* of Africa, India, and the Mediterranean region.

The subfamily Phaenicophaeinae includes the typical nest-building cuckoos of the Old and New Worlds. They are slender, short-legged, insect-eating birds with long, graduated tails. In tropical Asia and the Malaysian region these cuckoos are often called 'malkohas'. The Red-faced Malkoha *Phaenicophaeus pyrrhocephalus* of Ceylon and part of southern India is probably the rarest of the cuckoos, and the continuing encroachment upon its primary forest habitat threatens its existence. In the New World the Phaenicophaeinae have developed the most diverse forms on the islands of the Caribbean, with the large lizard-eating cuckoos *Saurothera* of the Greater Antilles and the more widespread *Piaya* squirrel cuckoos resembling the Old World malkohas. The genus *Coccyzus* of the New World is the most successful in number of species.

The subfamily Crotophaginae includes the anis (*Crotophaga*, 3 species) and the Guira Cuckoo *Guira guira* of the New World. These are group-living cuckoos with group territories. Sometimes several pairs have nests within a group territory, and sometimes they have communal nests. They are short-winged, the bill is laterally compressed and deep, and the tail has only 8 feathers (10 in the other cuckoos).

The subfamily Neomorphinae includes several long-legged, terrestrial cuckoos, mainly of the New World. The Greater Roadrunner *Geococcyx californianus* is a familiar bird of scrub deserts in south-western North America. Roadrunners seldom fly except to a display perch, and they run in pursuit of lizards or in a scramble for cover. Hand-raised roadrunners have been followed all day on foot as they walked through the desert scrub. The brood-parasitic cuckoos of the New World, the Striped Cuckoo *Tapera naevia*, the Pheasant Cuckoo *Dromococcyx phasianellus*, and the Pavonine Cuckoo *D. pavoninus*, are associated with the nesting cuckoos in this group by their roadrunner-like appearance.

The subfamily Couinae includes 10 species of *Coua* on Madagascar. These are long-legged, pigeon-sized cuckoos often with bright colours of plumage and naked skin on the head. One of these, *C. delalandei*, is probably now extinct.

The subfamily Centropodinae includes about 26 species of coucals *Centropus* in the Old World, mainly in Africa and south-east Asia. They are terrestrial cuckoos with a long, straight hind claw, and they build a covered nest.

Habitat. Most cuckoos are birds of forest and woodland, often living in dense thickets where they are difficult to observe. Some live in open woodland, such as the Yellow-billed Cuckoo *Coccyzus americanus* of North America. Others live in open country with only scattered trees or shrubs, such as the South American Guira Cuckoo or the parasitic African Didric Cuckoo *Chrysococcyx caprius*. The Greater Roadrunner lives in desert scrub. A few coucals of the Old World tropics live in wet grassland and marshes.

Distribution. As a group, cuckoos are cosmopolitan with species on all tropical and temperate continents and on many islands. The species are most numerous in the tropics. Many genera are restricted to certain parts of the world. Three genera are known only from New Guinea (*Rhamphomantis*, *Caliechthrus*, and *Microdynamis*, all brood-parasites), and 2 only from the Philippines (*Dasylophus* and *Lepidogrammus*). The New World ground-cuckoos *Neomorphus*, found in tropical forest from Nicaragua south through Peru, Bolivia, and Brazil, are large terrestrial cuckoos. It is uncertain how many species are involved. Only one kind lives in any one region, but the kinds are morphologically distinct and may comprise several species. They are apparently isolated from each other by large rivers, especially in the Amazon basin. On the other hand some cuckoos are widespread; the typical cuckoos *Cuculus* have species in Europe, Asia, Africa, Madagascar, and Australia, and the genus *Coccyzus* occurs throughout the New World, including most Caribbean islands and the Galapagos Islands. The Caribbean islands have many distinct local races of the Mangrove Cuckoo *Coccyzus minor*. Islands near New Guinea have distinct species of the largest of the coucals *Centropus*. Records of strayed migrant North American *Coccyzus* in Europe and of Palearctic *Cuculus* in North America suggest the ability of these widespread birds to invade new regions.

Movements. Cuckoos that breed in temperate habitats usually migrate to warmer areas for the winter. They generally migrate by night, though they also move by day along the East African coast and they fly on to the coast of Britain by day. Several species migrate long distances. The Cuckoo of northern Europe and Asia migrates to Africa, apparently with non-stop flights of 3,000 km or more. Many then move further across the tropics into the temperate-zone woods of southern Africa. Cuckoos from the Iberian Peninsula winter in West Africa north of the Equator. The Shining Cuckoo *Chrysococcyx lucidus* of New Zealand migrates northward over 3,000 km of land and ocean to the Solomon Islands. A few cuckoos of temperate areas in southern Africa remain during the entire year, but their quiet ways in the non-breeding season make them difficult to find. Most cuckoos of temperate southern Africa migrate to north of the Equator. Some Indian birds of one of the same species, the Jacobin Cuckoo *Clamator jacobinus*, cross to east-central Africa for the winter.

Food. Cuckoos are mainly insectivorous. Many are specialists on caterpillars, particularly noxious-tasting hairy kinds that other birds seldom take. Cuckoos bite one end, mince the insect back and forth in the bill, and shake it vigorously at one end until the gut and its toxic contents come free. They beat both hairy and smooth caterpillars against a branch. Hairs are usually swallowed along with the rest of the caterpillar. Local seasonal outbreaks of eastern tent caterpillars in North America are often associated with an influx of Black-billed *Coccyzus erythrophthalmus* and Yellow-billed Cuckoos which then nest in the infested woods and feed the caterpillars to their young. Other insects taken by cuckoos include grasshoppers, mantids and locusts, including some large, brightly-coloured, apparently noxious species. Larger cuckoos such as the lizard cuckoos, roadrunners, and coucals take both insects and small vertebrates, including lizards and snakes. Coucals and some female parasitic cuckoos take the eggs and nestlings of other birds. The ground-cuckoos *Neomorphus* of tropical forests in the New World often feed on insects flushed by swarms of army ants, which they follow, and sometimes they follow peccaries, which may flush insects. The Old World ground-cuckoos *Carpococcyx* also feed on insects but appear not to have been described feeding with ant swarms. Two species of anis *Crotophaga* of the American tropics feed on grasshoppers and associate in flocks in pastures with feeding cattle. The couas *Coua* of Madagascar take some fruit but rear their young on large insects and centipedes. The Channel-billed Cuckoo *Scythrops novaehollandiae* and the Koel also feed largely on fruit; the young of these brood-parasites are fed mainly insects by their foster parents.

Behaviour. Most cuckoos are solitary and shy, remaining alone and quiet most of the year except when they breed. In the breeding season the males sing and defend a territory. The anis and the Guira Cuckoo are however highly social birds that live in flocks throughout the year. Smooth-billed Ani *Crotophaga ani* flocks defend a territory from other flocks throughout the year. From 8 to 25 birds may live in a flock. They often nest more or less communally, with more than one pair in the flock breeding, and more than one female sometimes using a nest. Non-breeding adults as well as the breeding pairs help to feed the young.

Voice. Cuckoos are noisy in the breeding season. The most often heard birds of African woodlands in the rainy season are cuckoos and doves. The details of songs vary among the species, but many cuckoos have series of *coos* or *kuks* on the same pitch or changing pitches. The parasitic glossy cuckoos *Chrysococcyx* of the Old World and the parasitic New World Striped Cuckoo *Tapera naevia* have whistled calls. The biggest known repertoire is that of the Greater Roadrunner; it includes dove-like coos, a bark, a whine, a whirr, a growl, and a vigorous bill clacking. The male European Cuckoo alone gives the familiar *cu-koo*; and the song of most cuckoo species is given only by the male. The female may have a distinct call, such as the bubbling sound or a growl in several species of the parasitic *Cuculus*. Young parasitic cuckoos sometimes sound like the young of their foster species, and young of the Yellow-billed Cuckoo sound like a hissing snake. Some parasitic cuckoos call both day and night and have earned local names such as 'brain-fever birds' for their monotonous repetition. Cuckoos also sing in the rainy season when they nest, sometimes just before a rainstorm, earning the name 'rain bird' for various species in the Caribbean, Africa, the Australasian Region, and Asia.

Breeding. Courtship behaviour of most cuckoos includes the feeding of the female by the male during the egg-laying period. Most nesting species of cuckoos build a simple platform nest of sticks in bushes or trees or on the ground in wooded country. Eggs are laid at intervals of 2–3 days. The eggs of most nesting cuckoos are uniform in colour, often glossy bluish or whitish. The incubation period is short (10 days), and incubation may begin with the first egg. The period to fledging is also short and the young grow rapidly from the helpless hatchling covered with a stiff hair-like down to the feathered fledglings in 6–7 days. Clutch size varies considerably; the Black-billed Cuckoo lays 2–6 eggs, one every 2 days. When it lays a large clutch of 5 eggs, the last egg may be laid the same day that the first laid egg hatches, and the last egg laid may not have time to hatch by the time the first-hatched young has fledged. Both male and female of this species help feed the young.

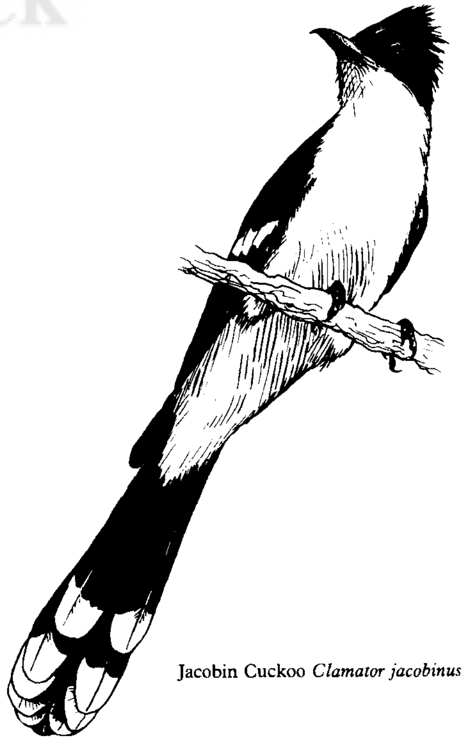
Most tropical nesting cuckoos have small clutches of 2–3 eggs, but anis may lay up to 7 eggs, and huge composite 'clutches' (up to 29 eggs have been recorded) result from several females laying in the same nest. In the communal nests of the anis the bluish eggs have a distinct whitish chalky layer on the surface. The socially dominant pair does most of the breeding in the group.

Breeding of the coucals differs from other cuckoos in that the nest is domed with a side entrance. In some species the female is larger than the male. The polyandrous female may have two or more mates, each with a different nest. The parental roles of the male and female are not well known.

In the parasitic cuckoos the female lays in the nest of another species, nearly always a song-bird, which then behaves as host or foster parent, incubating the egg and feeding the young. In some species the egg closely matches the egg of the host. The resemblance is an adaptation to parasitism; the eggs that most closely match the host eggs are more likely to be accepted by the incubating host. A few parasitic cuckoos have different kinds of egg, one female laying eggs of one colour and pattern, another laying another kind of egg. Eggs are usually laid in the nest of a host with similar eggs. The European Cuckoo *Cuculus canorus* has local populations each with several different morphs of eggs, some spotted and others of uniform colour. The female often removes and eats an egg of the host while she is investigating the host nests before laying her own egg. She lays her egg after holding it in her oviduct for a day, thus putting the embryo a day ahead of a fresh host egg in development. Eggs of parasitic cuckoos usually hatch before the eggs of the host, though not in a shorter time than in nesting cuckoos of the same size. When it hatches, the young European Cuckoo shoves the host eggs or chicks out of the nest. Thereafter it receives all the food brought to the nest by the foster parents, and may remain in or near the nest for up to 4 weeks. Evicting behaviour has also been seen in a few other species of *Cuculus* and in some glossy cuckoos *Chrysococcyx*. The New World Striped Cuckoo *Tapera naevia* upon hatching kills any other young birds in the nest, using a sharp hook at the tip of its bill, an adaptation otherwise known only in some honeyguides. In some other parasitic cuckoos, such as the Great Spotted Cuckoo *Clamator glandarius*, the young grow up together with the foster siblings.

The plumage of the young resembles the plumage of the host young in some cuckoos that grow up with them. The young of the Koel *Eudynamis scolopaceus* in India are dark, like their young crow nest-mates. Young Koels in Australia are pale; here they parasitize paler hosts and not crows. The juvenile plumage of the Drongo Cuckoo *Surniculus lugubris* in southern Asia is black with small white spots, much like the juvenile plumage of the local drongos. The significance of this resemblance is not known; Drongo Cuckoos parasitize small babblers not drongos, at least in Malaya. In the Philippine Islands the juvenile plumage of *S.* (*lugubris*) *velutinus* is a uniform rufous, much like the local Rufous Paradise Flycatcher *Terpsiphone cinnamomea.* Field studies are needed on these cuckoos.

No apparent pairs are formed by most parasitic cuckoos. Males sing and advertise themselves on a territory, but a male may mate with more than one female, and a female may mate with more than one male. A female lays her eggs in the territories of several males, and several females (often known by their distinctive eggs) may lay in the territory of the same male. In most species the female alone finds the nest, usually by watching the hosts as they are building, and lays after flying to the nest while it is unattended. The male and female of the Great Spotted Cuckoo and of the Jacobin Cuckoo associate more closely in pairs and work together to parasitize a nest. The male flies near the nest, the host chases



Jacobin Cuckoo *Clamator jacobinus.* (*K.P.*).

him off, and the female then slips quickly into the unattended nest to lay.

Parasitic cuckoos lay in a series, or 'clutch', an egg every other day, for 3 to 5 eggs, then rest for a few days until the next series. If host nests are unusually abundant, either in nature or in a field experiment, then the cuckoo may continue to lay on the alternate-day schedule for a few weeks.

The eggs of parasitic cuckoos are smaller in relation to the female's body size than are the eggs of nesting cuckoos. As the cuckoo foster species are usually much smaller birds than the cuckoos, the small eggs allow a female to parasitize a number of nests of the foster species. Small egg size and the success of females in tracking several nests allow many eggs to be laid in a season. Females of several species of parasitic cuckoos in Africa as well as the Cuckoo in Europe commonly lay as many as 20–24 eggs in a season.

Population structure. Certain colour patterns of mimetic cuckoo eggs are found over a wide region, while others are local. Because more than one kind of European Cuckoo egg occurs in some areas, it has been suggested that there may be several races living together but each mating only within its own race. This suggestion was made to explain why egg mimicry and polymorphism do not break down in areas where more than one kind of egg pattern occurs. Each egg race, or 'gens', would then breed true, behaving much like a biological species. In fact there appears to be no difference in the voice or other behaviour of cuckoos living in such mixed populations. The egg mimicry may instead be maintained by a sex-linked gene complex, with mother passing on to daughter her genetic code for egg colour and pattern. Cuckoos resemble other birds in that the female, and not the male as in mammals, carries the odd sex chromosome (female heterogamy). At the present time it seems likely that a sex-linked polymorphism, and not a splitting of local populations into non-interbreeding races or 'gentes', explains the variation in egg colour.

Some parasitic cuckoos are polymorphic in plumage. European populations of the Cuckoo include grey birds and brown birds; similar polymorphisms are known for a few other species in the genus *Cuculus*. Females alone are variable in these cuckoos. A possible explanation of plumage polymorphism is that the less common form is less likely to be recognized by the local hosts, and so is more likely to lay in a host nest.

Cuckoos tend to return to breed in the same general area where they were born, but not to exactly the same location. Most recoveries in a later breeding season of Cuckoos ringed in Europe as nestlings have been found 20–100 km from the site of birth. This is about the same distance as in the nesting Black-billed and Yellow-billed Cuckoos . A Cuckoo may be attracted to a habitat or to a host species like the one it grew up with, but we have no direct evidence on the nature of development of host recognition and host specialization in the Cuckoos.

See also under BROOD-PARASITISM. See photo BROOD-PARASITISM.

R.B.P.

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Payne, R.B. 1974. The evolution of clutch size and reproductive rates in parasitic cuckoos. Evolution 28: 169–181.

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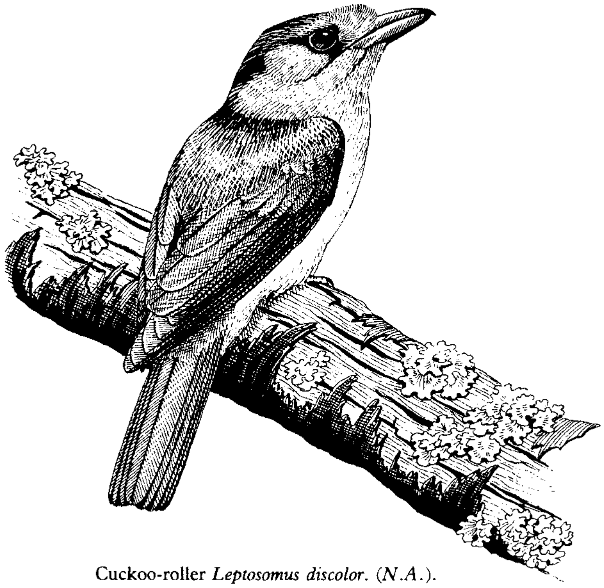
CUCKOO-FALCON: *Aviceda cuculoides* of tropical Africa and allies, 'falcon' being a misnomer (see HAWK).

CUCKOO-ROLLER (or COUROL): the names used for *Leptosomus discolor*, the single species in the family Leptosomatidae (Coraciiformes), perhaps correctly placed in a different superfamily from the GROUND-ROLLERS and ROLLERS.

Characteristics. The species is confined to Madagascar and the Comoro Islands. It may represent a first invasion of Madagascar by primitive roller stock (contrast with the ground-rollers). There are 3 subspecies (one endemic to Anjouan, another to neighbouring Grand Comoro). Excluding the last, it is *c.* 43 cm long, with a stoutish bill (broad at the base), long ample wings, a moderately long tail and very short legs. There is a pair of powder-down patches, one on each side of the rump. The greyish bloom characteristic of the plumage may be due to this powder-down. The feathers of the lores face forward and upward to conceal the base of the bill. There is also a short crest, adding to the apparent size of the large head.



Cuckoo-roller *Leptosomus discolor*. (*N.A.*).

The sexes differ conspicuously in colour. The adult male has the upperparts, except the hindneck, slaty, with iridescent green or copper, depending on the incidence of light; the underparts and hindneck ashy grey. The female and young male have the upperparts dark brown, with the crown and hindneck barred black and rufous; the underparts pale rufous, boldly spotted with black. The Grand Comoro form is only *c.* 38 cm long, the female with the tail bright chestnut-red instead of dark brown.

Habitat. Evergreen forest or virtually any type of woodland.

Distribution. Throughout Madagascar (including the dry southwest) and on all 4 Comoro Islands.

Populations. Not known to be anywhere endangered, but numbers must be diminishing everywhere, through habitat destruction. Those in the limited Comoro environments require special attention.

Movements. There is no satisfactory evidence of any regular movement.

Food. Large insects (including hairy caterpillars) and chameleons.

Behaviour. Usually solitary, occasionally in small parties; tame and confiding. Often circles with slow wing-beats over forest or woodland, frequently calling; or likewise when perched on a conspicuous stub at the top of a tree, the bird leaning forward with its throat puffed out.

Voice. The most usual call is an arresting, beautiful, loud *kwiii-yu, kwi-yu, kwi-yu, kwi*, the second and third notes not so long drawn-out, nor so loud, as the first; the fourth (final) note the shortest and least loud.

Breeding. The eggs are whitish tinged green, laid in a natural cavity in a tree. The clutch-size in Madagascar can be up to 5, although a cavity in the Comoros contained only 2 young. Incubation may be entirely by the female, but she is fed by the male, and he assists in the feeding of the young, which are covered in long white down. (A.L.R.) C.W.B.

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Cracraft, J. 1971. The relationships and evolution of the rollers: families Coraciidae, Brachypteraciidae, and Leptosomatidae. Auk 88: 723–752.

Forbes-Watson, A.D. 1967. Observations at a nest of the Cuckoo-roller *Leptosomus discolor*. Ibis 109: 425–430.

Forbes-Watson, A.D. 1969. Notes on birds observed in the Comoros on behalf of the Smithsonian Institution. Atoll Res. Bull. 128: 23 pp.

CUCKOO-SHRIKE: substantive name of some species of Campephagidae (Passeriformes, suborder Oscines); in the plural, general term for the family (also known as caterpillar-birds). They have nothing to do with either cuckoos (Cuculidae) or shrikes (Laniidae). Various other substantive names are applied to different species without much consistency, some being compounds including the word 'shrike', e.g. 'grey-birds', 'trillers', 'caterpillar-shrikes', 'flycatcher-shrikes', 'wood-shrikes' (also used for Prionopidae), 'Cicada-bird', and 'Pied Shrike'.

The name 'cuckoo' perhaps derives from the grey coloration, sometimes conspicuously barred, and the name 'shrike' from the strong notched bill.

The family includes 70 species in 2 distinct groups: the colourful and lively minivets in the genus *Pericrocotus* and the rather drab and dull-coloured cuckoo-shrikes in 8 other genera; 3 of these (*Pteropodocys*, *Campochaera*, and *Chlamydochaera*) are monotypic; the remaining 5 are *Tephrodornis*, *Hemipus*, *Campephaga* (including '*Lobotos*'), *Lalage*, and *Coracina* (including '*Edolisoma*').

Characteristics. The minivets *Pericrocotus* spp. are a distinctive group, the size of wagtails *Motacilla* spp. and with a moderately long and graduated tail. In most species the male is a striking black and red, whereas the female is yellow or orange and black or grey. The cuckoo-shrikes of the other 8 genera vary in size from that of sparrows *Passer* spp. to that of pigeons *Columba* spp. (*c.* 14–40 cm) and the prevailing colours are light and dark grey, more rarely black and white. The wings are rather long and pointed, and the tail is moderately long and round; rictal bristles are well developed and in many species partially conceal the nostrils. The sexes differ in depth of colouring, the female being a pale and washed-out version of the male. The young often have a white nestling plumage, exchanged for a plumage resembling that of the female at the post-juvenile moult.

A notable peculiarity is that, in most species, the feathers of the back and rump are thickly matted, partially erectile, and equipped with rigid pointed shafts. These spine-like feathers are easily shed, and according to Gilliard, it is possible that they act as a mechanism of defence, as in the trogons and pigeons. The White-winged Triller *Lalage sueurii* of Australia is the only member of the family known to have 2 moults yearly; the normal postnuptial moult in the autumn produces an eclipse plumage, which in the male (but not in the female) differs strikingly from the breeding plumage.

Habitat. All the cuckoo-shrikes except one are arboreal, although some, e.g. the Pied Triller *Lalage nigra* of Malaysia, often drop down to the ground for a few moments when feeding. In central Australia however, the Ground Cuckoo-shrike *Pteropodocys maxima* frequents treeless plains, perches on fence posts, flies after insects like a swallow, and runs strongly on the ground unlike any other member of the family. A few species are restricted to the true forest, but the rest are more typical of the forest edge, secondary growth, gardens, and coastal vegetation. The minivets are birds of the tree-tops.

Distribution. The cuckoo-shrikes are an Old World and mainly tropical family, ranging from Africa across southern Asia and Malaysia to Australia and the western Pacific.

Several species of the genus *Campephaga* are inhabitants of Africa. For example, the *Campephaga phoenica* subspecies ranges from Senegal and the Sudan to Cape Province. The Wattled Cuckoo-shrike *C.* ('*Lobotos*') *lobata*, with the aberrant character, in the male, of a yellow wattle near the gape under each dark red eye, has a limited range in West Africa, and is little known. The Pygmy Triller (or Pied Shrike) *Hemipus picatus* occurs in India, and the Black-breasted Triller *Chlamydochaera jefferyi* is a montane species in Borneo with a restricted distribution from Mt. Kinabalu to Mt. Dulit.

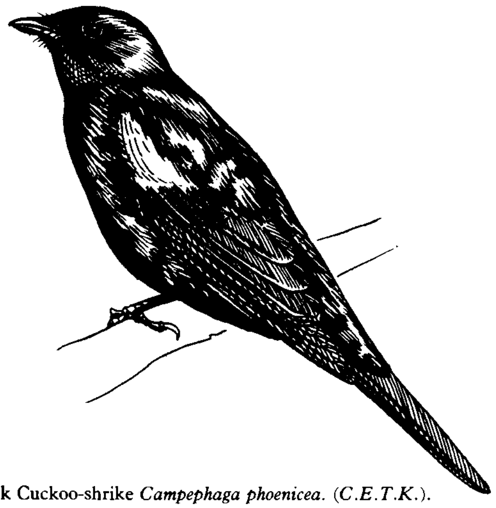
The minivets are absent from Africa and Australia but extend up into the far eastern Palearctic Region (eastern Siberia, China, Japan, the Ryukyus).

Movements. The only long-range migrant in the family is *Pericrocotus brevirostris* which migrates from the far eastern Palearctic Region to winter in the Oriental Region. Some species move locally, especially in Australia.

Food. The family is mainly insectivorous, but caterpillars, especially hairy ones, and some fruit are taken. The Black-breasted Triller is reported to feed only on fruit. The Pygmy Triller catches flying insects after the manner of flycatchers.

Behaviour. Minivets are gregarious in winter, collecting in flocks of a dozen or more individuals. Their bright tones harmonize well with the Burmese scene, where they are among the most characteristic birds. A feature of the montane forests, from the Himalaya to Borneo, is the mixed parties of birds, usually including babblers, warblers, flycatchers and others, with one or two species of cuckoo-shrikes or minivet.

Voice. The cuckoo-shrikes mostly have loud call-notes, either whistles or rather disagreeable squawks; the call of the Black Cuckoo-shrike is described as a soft double whistle. Minivet flocks communicate with soft and musical call-notes.



Black Cuckoo-shrike *Campephaga phoenicea*. (*C.E.T.K.*).

Breeding. In the courtship display of some of the large cuckoo-shrikes, the male lifts each wing alternately, without opening the feathers, perhaps half a dozen times, calling vigorously while doing so. The performance is repeated at intervals, and is a most distinctive field character.

Both sexes build the nest, but in many species only the female incubates. The nest is usually placed high up in the fork of a tree, or simply on a horizontal branch, and is difficult to see from below. It is a shallow little cup of fine twigs, roots and grasses, or moss and lichen, usually lined. The minivets build a shallow but massive little cup of fine twigs and roots, often matted with cobwebs and studded with lichens so that it resembles the twig on which it is placed. The clutch usually consists of 2–5 eggs (but 1 egg only in the Cicada-bird *Coracina tenuirostris*), usually pale green when fresh but apt to fade if exposed to light, marked with brown, grey or purple; the eggs of some minivets are white or greyish in ground colour.

Knowledge of breeding by cuckoo-shrikes of the genera *Coracina* and *Campephaga* is scanty. In general, however, development stages of all seem to be protracted, with incubation for *c.* 3 weeks and a nestling period of similar or greater length. The share of the sexes in building, incubation and tending the young evidently varies. B.E.S.

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Marchant, S. 1979. Nesting of the Cicadabird *Coracina tenuirostris*. Ibis 121: 80–84.

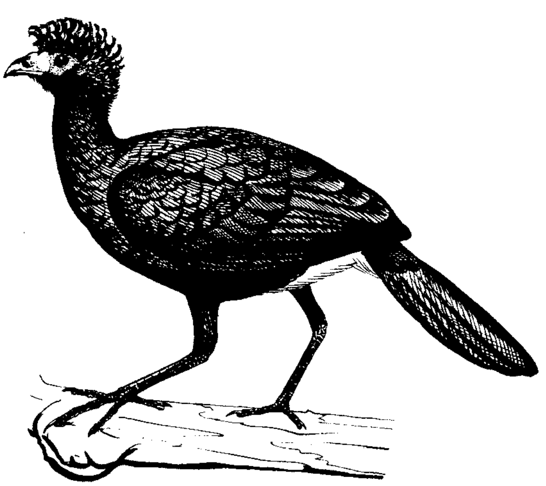
Peters, J.L., Mayr, E. & Deignan, H.G. 1960. Family Campephagidae. *In* Mayr, E. & Greenway, J.C., Jr. (eds). Check-list of Birds of the World vol. 9. Cambridge, Mass.

CUCKOO'S LEADER; CUCKOO'S MATE: popular name, in Britain, for the Wryneck *Jynx torquilla* (see under WOODPECKER). It refers to the approximately simultaneous appearance in spring of this summer visitor and the Cuckoo *Cuculus canorus*.

CUCULI; CUCULIDAE: see below.

CUCULIFORMES: an order, alternatively 'Cuculi', comprising 2 suborders: Musophagae, Cuculi; 2 families: Musophagidae (TURACO), Cuculidae (CUCKOO). They comprise mainly arboreal birds with short legs and rounded wings. The largest number of species occur in the tropics; those living in temperate and cold climates are migrants with long, pointed wings. The fourth toe can move sideways in turacos and backwards in cuckoos (zygodactylous foot). Anatomical characters and outward appearance of the birds are often reminiscent of gallinaceous birds and relationship has been suggested by several authors, but the systematic position of the order is still unclear. The cuckoos are especially notable for their breeding strategies, which range from normal parental care to various forms of social breeding and nest parasitism (see BROOD-PARASITISM).

CULMEN: the dorsal ridge of the upper mandible, from forehead to tip (see BILL).



Black Curassow *Crax alector*. (*C.E.T.K.*).

CURASSOW: substantive name of the big species (*Crax, Mitu, Nothocrax* and *Pauxi*) of the Cracidae (Galliformes); in the plural, serving as a general term for the family, other members of which are called guans (*Penelope*), piping-guans (*Pipile*) and chachalacas (*Ortalis*). The family is restricted to the warmer zones of the New World and is considered to be the most primitive group of living gallinaceous birds. In South America the curassows largely take the place of the Phasianidae which are very poorly represented and from which the curassows stand phylogenetically well apart; there is no hybridization between the 2 families.

Characteristics. In size curassows vary from 75–112 cm in length. Most true curassows (*Crax, Mitu, Nothocrax*) are conspicuously crested with curved feathers. In most genera the sexes are alike, but *Crax* is sexually dimorphic. They can be sexed by cloacal examination (adult males have a copulatory organ), or sometimes by the colour of the iris; e.g. in *Penelope obscura* the iris of the male is red, that of the female dark brown, whereas the contrary is true for *Crax blumenbachii*. The wings are short and round, and markedly concave. The bill is heavy and bent, frequently with a shiny coloured cere. Most true curassows (*Crax, Mitu*) have the base of the bill enlarged; *Pauxi* is adorned with a large helmet; *Oreophasis*, a guan, with a horn on the forehead. The legs are long and strong, the toes are heavy and fairly long and have bent claws.

Habit. The curassows are the most arboreal Galliformes. They usually stay in trees, either in the forest or at its edge. They run with great agility along the branches, jumping up and up until they reach the tree-top, whence they take off, half gliding, half fluttering.

Distribution and systematic characteristics. The range of the family extends from the southern United States to northern Argentina. There are 10 genera (2 of which *Mitu* and *Pauxi* are sometimes included in *Crax*) and 44 species. The status of many forms, whether species or races, is in doubt, especially when their distribution is allopatric, which is very common. There exist several monophyletic groups which can be combined into superspecies.

There are 14 species of true curassows. The Great Curassow *Crax rubra*, weighing approximately 4,800 g, ranges from Mexico to Ecuador; the male is black with a greenish or bluish sheen above, white on belly and sides, and has stiff, narrow crest-feathers strongly recurved at the tips, and the base of the bill ornamented with a large turgid yellow knob which increases in size during courtship; the plumage of the female is brown. The Red-billed Curassow *Crax blumenbachii* is a member of the same superspecies; it lives in south-eastern Brazil where it is endangered by deforestation and hunting. In the Amazonian Razor-billed Curassow *Mitu mitu tuberosa* the bill-adornment is not soft but consists of a hard, narrow brilliant red frontal comb. The plumage is black with a steel blue sheen, brown on the belly; birds of both sexes weigh about 3,500 g; the species is still relatively common in Amazonia. Recently, after a space of 300 years, the race of Razor-billed Curassow *Mitu mitu mitu* from north-eastern Brazil was rediscovered, a last remnant living in small forest pockets in Alagoas; it can be saved from extinction only by breeding in captivity.

In the Helmeted Curassow *Pauxi pauxi* both sexes have a solid fig-shaped casque on the base of the bill; the bluish-grey colour of this casque contrasts with the red of the bill itself; the bird is about 1 m long, weighs about 3,600 g and inhabits the mountain forests of Venezuela.

There are 12 species of guans, called 'jacu', 'camata', 'pava', etc. most of them similar in appearance, greenish olive to brown. The sexes are alike except that sometimes the colour of the iris is different in male and female; there is bare skin round the eyes and on the upper part of the neck, and the naked throat forms a conspicuous wattle, being yellowish red, strikingly visible while the bird is calling. A big species of guan such as *Penelope purpurascens* (Mexico to Ecuador) weighs about 1,900 g. *Penelope superciliaris* from Brazil weighs only 850 g.

There are 3 species and several subspecies of piping-guans, *Pipile* (also called *Aburria*) spp., known as 'cujubi', 'jacutinga' etc. They are all similar in colour, black with white spots on breast and wings and a white crest; the outer primaries are sharply attenuated (see under Behaviour below). The naked throat is shiny blue and red with a long wattle; the weight of *Pipile pipile cumanensis* is about 1,200 g. One species, *Pipile jacutinga*, from south-eastern Brazil (down to Misiones), which was still extremely common 50 years ago (e.g. in Santa Catarina), is now near extinction.

There are 9 species of chachalacas *Ortalis* spp. called 'aracua' in Brazil, an onomatopoeic name like 'chachalaca'. The Plain Chachalaca *Ortalis vetula* has, like other chachalacas, a bare bright red throat with a strip of feathers down its centre. The upper parts of the plumage are dark olive brown, the lower parts lighter, and the tail is greenish black, white tipped on the sides; the bird is 50 cm long and weighs about 550 g. It ranges from Texas and Mexico to Nicaragua.

Food. Curassows do not scratch for food as much as other gallinaceous birds, although they often come down to the ground to feed on fallen fruits and flowers. They like to feed on buds and tender leaves, and occasionally on small animals such as insects and frogs. They store food in the crop (*Crax, Mitu*) or in the greatly expandable oesophagus (*Ortalis, Penelope*). The larger species and the piping-guans have a muscular stomach. Stones of fruits pass through the alimentary tract whole or are spat out, but the larger species grind up hard seeds.

Voice. The voice is raucous (*Ortalis, Penelope*), whistling (*Pipile*) or booming with a strange muffled quality (*Crax, Mitu, Nothocrax*). In many species the voice is amplified and modified in pitch by means of an extended, looped trachea, the curve sometimes reaching to the abdomen. These modifications which resemble those in cranes, swans and the Capercaillie *Tetrao urogallus* may be present in both sexes (*Penelope*) or only in the males (*Ortalis, Crax, Nothocrax*). A system of air-chambers in the neck may also serve as a voice amplifier (*Crax*).

Behaviour. During the nesting season some species produce a loud noise with the wings, some guans wing-drumming, all piping-guans wing-whirring very strongly. To do this they fly from one treetop to another, a display that is difficult to see because the birds perform only very early in the morning, late in the evening or in moonlight.

Breeding. The Cracidae build their nests of dry twigs and leaves loosely woven together; the nest is quite small in relation to the size of the birds; the nest cup is at times relined with fresh material. The nest is placed a few metres high in trees, sometimes in branches overhanging water or even quite near the ground. A few species nest on the ground (e.g. *Penelopina nigra* of Mexico). Occasionally the nest of another bird is used as a base for building. The clutch consists of 2–3, rarely 4 eggs. These are large, white, with a rough shell (*Ortalis, Crax*) or smooth (*Penelope*). Incubation lasts 22 (*Ortalis*), 29 (*Crax*) or 34 (*Pauxi*) days. The young are hatched with well developed primaries and secondaries. They are led out of the nest by the female on their first day and hide in the branches. They are able to fly after 3 or 4 days, and they soon do not hesitate to take off from the end of a branch to fly to a neighbouring tree, following the female or both parents. The parents present food in their bills to the young and this is mostly of animal origin. The colouring of the chicks is light brown and black; at times a striped pattern appears. The bigger species do not breed until 2 years old.

Parents and offspring keep together for some months. Later they join with others to form flocks of 10–20 birds until the next breeding season. In *Crax*, *Pipile* and *Penelope* the same individuals appear to pair in succeeding years, thus forming continuous monogamous relationships. Chachalacas (*Ortalis*) are partly polygamous and form nesting colonies; males co-operate at times in nest building. Parental care varies with species, but little is known about it. In some curassows (*Crax*) the male takes part in feeding the young. The question of sex ratio has not been sufficiently clarified; a ratio of 1 : 1 has been noted in several species of *Penelope* and *Ortalis*, but females predominate in some *Crax* spp. Curassows have now been bred successfully in captivity. H.S.

Delacour, J. & Amadon, D. 1973. Curassows and Related Birds. New York.
Schäfer, E. 1953. Estudio bio-ecológico comparativo sobre algunos Cracidae de Norte y Centro de Venezuela. Biol. Soc. Venez. Cienc. Nat. 15: 30–63.
Vaurie, C. 1968. Taxonomy of the Cracidae. Bull. Am. Mus. Nat. Hist. 138,4.
Vuilleumier, F. 1965. Relationships within the Cracidae. Bull. Mus. Comp. Zool. 134,1.

CURLEW: substantive name of *Numenius* spp.; used without qualification in Britain, for *N. arquata* (see under SANDPIPER). See photo VOCALIZATION.

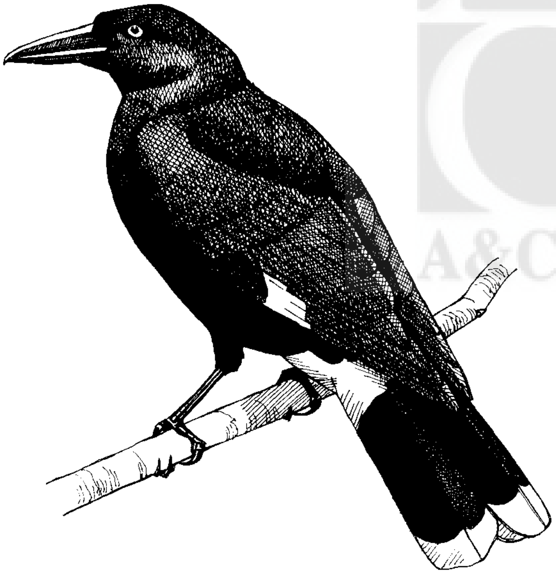
CURLEW, BEACH: name used in Australia for *Burhinus neglectus* (see THICKKNEE).

CURLEW, BUSH: name sometimes applied to the Stone-curlew *Burhinus magnirostris* of Australia and New Guinea (see THICKKNEE).

CURLEW, STONE: see STONE-CURLEW; THICKKNEE.

CURRAWONG: substantive name of the species of *Strepera*, family Cracticidae (Passeriformes, suborder Oscines).

Characteristics. Currawongs (also called bell-magpies or crow-shrikes) are large birds, about 50 cm in length, having a long tenth primary, tarsi almost completely sheathed in scales arranged in a kind of boot, and the bill long and straight with a sharp, slightly hooked point. The plumage is black, grey and white. Six species used to be recognized, but recently they have been grouped into 3, the Pied *graculina*, the Black *fuliginosa* and the Grey *versicolor*. A peculiarity of the *versicolor* group is the number of isolated forms and the tendency to an inconsistency in plumage characters where some forms have come secondarily into contact. Thus, there are currawongs with greyish plumage and white wing patches, and others which are black and white or greyish-brown and white, in varying degrees; but no clear-cut colour characters that separate the 2 groups.



Pied Currawong *Strepera graculina*. (*N.W.C.*).

Habitat. The birds frequent all types of forest and woodland from coastal rain-forest to montane woodlands and inland mallee woodlands.

Distribution. The Pied Currawong occurs in eastern Australia and Lord Howe Island, the Black is confined to Tasmania and the Grey occurs throughout Australia and Tasmania. The Grey has probably invaded Tasmania twice, the earlier immigration leading to the evolution of the Black Currawong and the later to one not yet fully differentiated from its mainland ancestor, although its plumage is already much darker.

Populations. There is no information about the density at which currawongs occur, nor about the rate of recruitment into the population. Numbers appear to be more or less stable at present and those of the Pied Currawong have been estimated to exceed a million (Readshaw 1968a).

Movements. Only the Pied Currawong undertakes recognizable movements. In winter, when breeding is over, the species forms large flocks which move extensively about south-eastern Australia harvesting phasmatids and other large insects that sometimes develop into plagues in the *Eucalyptus* forest (Readshaw 1968b).

Food. Currawongs feed on large insects, many of which they take on the ground. They will also eat small vertebrates and have no hesitation in taking arboreal insects when they are abundant. They will take orchard fruits and various wild berries.

Behaviour. During the spring and summer breeding season territories are strongly defended, mainly by pairs. Territorial boundaries are maintained during the non-breeding season, but at much lower intensity. Only Pied Currawongs form large winter flocks.

Voice. The Grey Currawong's calls are bell-like, but vary across their range. The Black and Pied Currawongs have different variations of a rollicking *currawong* call, from which the genus gets its name.

Breeding. The currawongs all build a large stick nest, usually placed high in a tree-fork and lined with bark fibre. The clutch varies from 2–4, but there is no information about the length of incubation or nestling periods. Nests of the Pied Currawong are sometimes parasitized by the Channel-billed Cuckoo *Scythrops novaehollandiae*. The fledged young of the Grey Currawong continue to be fed by their parents for some months, possibly until the next breeding season. S.J.J.F.D.

Readshaw, J.L. (1968a). Estimates of the size of winter flocks of the Pied Currawong, *Strepera graculina* (Shaw), from mark-recapture data—a new approach. Aust. J. Zool. 16: 27–35.
Readshaw, J.L. (1968b). The distribution, abundance and seasonal movements of the Pied Currawong *Strepera graculina* (Shaw), an important bird predator of Phasmatidae in Eastern Australia. Aust. J. Zool. 16: 37–47.

CURSORIAL: adapted to running (see EARLY EVOLUTION OF BIRDS; LOCOMOTION, TERRESTRIAL).

CURSORIINAE: see COURSER.

CUSHAT: popular name (with several variants) in Britain for the Wood-pigeon *Columba palumbus* (see PIGEON).

CUTICLE, EGGSHELL: see EGG; EGGSHELL, ULTRASTRUCTURE OF.

CUT-THROAT: *Amadina fasciata* (see ESTRILDID FINCH).

CYCLARHINAE: see under VIREONIDAE; PEPPER-SHRIKE.

CYGNET: special term for a young SWAN.

CYPSELI: name formerly used for the order APODIFORMES; SWIFT.

D

DABCHICK: alternative name for certain of the smaller Podicipedidae (see GREBE).

DACELONINAE: see KINGFISHER.

DACNIS: generic name used as substantive name of *Dacnis* spp. (see HONEYCREEPER(1)).

DAMBO: an environment, consisting of grassy land that seasonally becomes marsh, characteristic of parts of tropical Africa.

DAPTRIINAE: see FALCON.

African Darter *Anhinga rufa*. (*J.B.*).

DARTER: substantive name (alternatively 'Snake-bird' or 'Water-turkey') of Old World species of Anhingidae (Pelecaniformes, sub-order Pelecani); in the plural, general term for the family. The substantive name of the New World species is anhinga; in the plural, alternative general term for the family, which includes 4 allopatric forms that are treated as 1–4 species in 1 or 2 genera, subgenera or superspecies. Several other forms that have been described as subspecies are of doubtful taxonomic validity. Some authors place the darters in a subfamily Anhinginae of the cormorants Phalacrocoracidae.

Characteristics. Darters are medium to large in size (0.8–1.0 m long). The bill is of moderate length, spike-shaped with the distal halves of the cutting edges finely serrated. The head is slender with about the same circumference as the long G-shaped neck, with its peculiar articulation of the vertebrae and single carotid artery (2 in the cormorants). The short legs are set far back and the feet are totipalmate. The wings are long and the tail very long. Although they take off from water with difficulty, darters are excellent flyers, gliding and soaring like flying crosses. Outer webs of the central tail feathers have prominent transverse corrugations. There are age, sex and species differences in the amount and pattern of black, white, grey, brown and silver in the plumage. New World adult males have a black erectile crest on the nape, while Old World adults have instead a prominent white stripe on the side of the head and upper neck. In Old and New World adults the scapular coverts are extremely elongated and lanceolate with white or silver stripes. Bare part colours of the head, legs and feet vary individually and include black, brown, pink, red, orange, yellow, green and blue.

Habitat and distribution. Darters frequent tropical, sub-tropical and temperate regions where there are sheltered inland and marine waters with no waves, and wooded shores where they can perch in the trees. *Anhinga anhinga* occurs in the New World and there are several morphological differences that suggest that it is at least specifically and possibly generically distinct from the 3 Old World darters. All 4 forms differ from each other in their adult breeding plumage patterns. *A. rufa* occurs in Africa south of the Sahara, Madagascar and Asia Minor; *A. melanogaster* is found in southern Asia including Indonesia and the Philippines; and *A. novaehollandiae* occurs in Australia and New Guinea. A skin found in 1874 nailed to a shed wall on the west coast is the only New Zealand record. There have been errors in the specific name even in recent publications, when the Old World forms are lumped together as a single species. The order of priority is *melanogaster* 1769, *rufa* 1802 and *novaehollandiae* 1847.

Movements and feeding. Movements are mainly in response to weather-induced shortages in the availability of food. Darters feed mainly on fish and insects. Often they swim with the body under and the head and neck above water and thus appear like a swimming snake. From this posture they slowly submerge to stalk fish which they spear in the flank, with the bill slightly open. The rapid heron-like forward movement of the head under water is facilitated by highly modified hinges between the 7th, 8th and 9th cervical vertebrae. The fish is commonly brought to the surface, tossed in the air, caught in the bill and swallowed head-foremost. Plumage modifications for the reduction of buoyancy are similar to those of cormorants (see CORMORANT; SWIMMING AND DIVING). The bill is also used as a pair of forceps to pick insects off the water surface.

Communications. Clicking and rattling sounds are made away from the nesting area, where, when breeding, darters make several cawing and hissing calls with individual, sexual, age and species differences. They have no alarm call, but react to those of other birds. Visual signals are complex and are similar to those of gannets, cormorants, pelicans and herons.

Breeding. Darters nest in colonies often with other kinds of water-birds. The male selects the nest site, and the female builds the nest often overhanging water in the fork of a tree, initially with green and later with dry twigs gathered mainly by the male. The pair take turns guarding the nest and its contents, with nest relief occurring at least 3 times a day. The average clutch size is 4. The parents use their webbed feet to warm the eggs, and their body shade to keep them cool. Chicks are naked when hatched after about 4 weeks' incubation. Within 2 days they are covered with white or pale buff down, soon to turn darker brown above. Chicks squeal for food with a closed bill and beg silently for water with an open bill. Very small chicks take fluid from their parents' upper bill as in pelicans and not from the lower bill as in cormorants and gannets. When larger, they take solid bits of food from their parents' throats. They leave the nest after about 5 weeks and fledge when about 7 weeks old. Parents feed their chicks for some time after fledging. G.F. van T.

Harrison, C.J.O. 1978. Osteological differences in the leg bones of two forms of *Anhinga*. Emu 78: 230–231.

Owre, O.T. 1967. Adaptations for locomotion and feeding in the Anhinga and the Double-crested Cormorant. Orn. Monogr. 6.

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DARWINISM: see EVOLUTION.

DARWIN'S FINCHES: (alternative Galapagos Finches) general term for the Geospizinae, usually classified as a subfamily of the Fringillidae (Passeriformes, suborder Oscines). Opinions differ on the exact number of species and genera. 14 species are generally placed in 6 genera; *Geospiza* (ground finches), *Camarhynchus* (tree finches), *Cactospiza* (woodpecker and mangrove finches), *Platyspiza* (vegetarian finch), *Certhidea* (warbler finch) and *Pinaroloxias* (Cocos Island finch).

All the finches are found on the Galapagos archipelago which straddles the Equator 1,000 km west of Ecuador, except *Pinaroloxias inornata* which is on Cocos Island about 700 km north-east of Galapagos. These islands have been formed by volcanic activity in the last 5 million years and have never been connected to the mainland. Since all Darwin's finches are more similar to each other in anatomical and behavioural

Medium Ground Finch *Geospiza fortis* landing on land iguana in Galapagos. (*Photo: F. Pölking*).

characteristics than to any living species on the central or South American mainland, they are believed to be the product of a single over-water colonization followed by repeated evolutionary divergence and speciation on the different islands. They are of general importance for two reasons. First, they contributed to the development of Darwin's theory of evolution by natural selection. Second, they provide an unusually clear example of allopatric speciation and adaptive radiation.

Characteristics and song. The finches are 10–15 cm in length and weigh 8–40 g. There are plumage differences between genera, most noticeably among males. Females vary from streaked brown to olive. Immature males resemble females, but older males may develop a fully black plumage (*Geospiza* and *Pinaroloxias*), a black head and upper breast only (*Camarhynchus* and *Platyspiza*) or no black feathers at all (*Cactospiza* and *Certhidea*). Song is more differentiated. No two species have the same song. Populations of the same species on different islands sing different songs. There are frequently two or three song types within a population, but it is rare for an individual (male) to sing more than one type. There is territorial advertising song; also a song described as a hiss or a whistle, that occurs often in courtship when the males are stimulated by the presence of females.

Habitat. Ground finches occur mainly at low altitudes in arid zone vegetation. Tree finches occur mainly at higher altitudes in more mesic vegetation.

Populations and movements. Up to 10 species occur together on the central islands of the Galapagos group. Populations appear to be limited by food in the dry season. In a drought year population sizes may fall to about 10–20% of initial numbers. Short-eared Owls *Asio flammeus*, hawks *Buteo galapagoensis*, herons *Butorides striatus*, *Nyctanassa violacea*, and egret *Casmerodius alba* prey on finches, mainly on nestlings and fledglings. Altitudinal movements of the seed-eating finches occur, and inter-island movement is a recurrent, occasional phenomenon. In recent times only one population is known to have gone extinct. Human activities on Isla Santa Cruz were probably responsible for the disappearance of *G. difficilis*. In the last century, after Darwin's visit in 1835, *G. magnirostris* became extinct on Islas San Cristóbal and Floreana.

Food and beaks. Darwin's finches have adaptively differentiated in beak form. Beak size and shape is clearly related to diet, most conspicuously to that in the cool–dry season (June to December) when food is generally scarce. *Certhidea* (warbler finch) has a fine beak with which it feeds on small insects and spiders. The beaks of some of the ground finches (*Geospiza*) have a steep profile which makes them suitable for cracking seeds, and the largest species in the genus (*magnirostris*) cracks much harder and larger seeds than does the smallest (*fuliginosa*). *Camarhynchus psittacula* has a powerful blunt beak, used for extracting insects and termites from wood by bark-ripping and twig-breaking, while the tit-like *C. parvulus* has a smaller beak of similar shape which it uses to take smaller insects from the surfaces of twigs and leaves. The bullfinch-like beak of *Platyspiza* is used to feed, as in the European Bullfinch *Pyrrhula pyrrhula*, on buds, as well as on leaves. The long and slightly decurved bills of *G. scandens* and *G. conirostris* (on Isla Genovesa) are used to probe into *Opuntia* flowers for nectar.

Two feeding habits are unusual. The 2 species in the genus *Cactospiza* break off a twig or leaf petiole, grip it in the beak and use it by probing to excavate insect larvae and termites beneath bark and in cavities in branches. *Cactospiza pallidus* also uses *Opuntia* cactus spines to this end. On Isla Wolf and Darwin only, *G. difficilis* individuals draw blood from moulting boobies *Sula* by pecking at the developing feathers at the base of the tail; then they drink it.

Some populations are unusually variable in beak dimensions. The significance of this variation is not fully understood, but it is known that the smallest and largest members of some populations have somewhat different diets.

Behaviour. All species are territorial, and monogamy is the rule. They exhibit similar courtship postures and movements. Males build several nests and display at either their own or other nests, even those of other species, to attract a female. The female chooses a nest and lines it.

Breeding. All species build nests with domed roofs and side entrances, in cactus bushes and trees in the branches and twigs. They lay up to 6 (average 4) white eggs with orange or brown spots or streaks, and have similar incubation (*c.* 12 days) and nestling periods (13–15 days). Hybridization occurs, even intergenerically, but is apparently very rare.

P.R.G.

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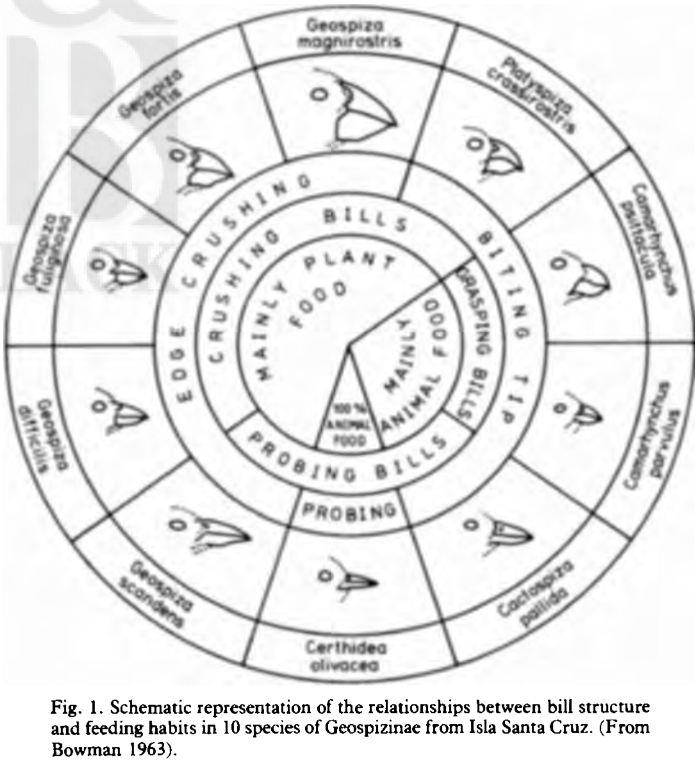

Fig. 1. Schematic representation of the relationships between bill structure and feeding habits in 10 species of Geospizinae from Isla Santa Cruz. (From Bowman 1963).

DAW: popular abbreviation of JACKDAW (see CROW (1)).

DAWN CHORUS: name given to burst of spring song from many species in a more or less fixed order, beginning before and continuing after local dawn, then dying almost abruptly away; for its function, see under ROOSTING. There is a lesser peak of song at dusk.

DAYAL-BIRD: alternative name (variously spelt), in India, of the Magpie Robin *Copsychus saularis* (see THRUSH).

DEATH-RATE: see AGE; ECOLOGY.

DECOMPOSED: apart from its ordinary meaning, a rather ambiguous term sometimes applied to feathers, e.g. ornamental plumes, of which the vanes are incoherent because the barbules on adjacent barbs do not engage.

DECOY: derived from Dutch words 'eende' meaning ducks and 'kooi' meaning cage or trap, a duck decoy being a device constructed on the edge of a lake, or round a pond specially dug for the purpose, in which wild ducks *Anas* spp. etc. are caught. Typically the device is set in a woodland and consists of a pond of 0.5–1.5 ha, from which radiate 4 to 8 'pipes'—curved tapering ditches, each covered by a tapering tunnel of netting stretched over semicircular hoops. The pipes may be 50–70 m long, 5–8 m wide at the mouth and the hoops at the mouth 2–5 m above the water. The success of the system depends on the mobbing behaviour of ducks when confronted with a predator. By using a trained dog which the ducks will follow, the decoyman entices them into the pipe. Along the outside of the curve is a range of 2 m high screens in an overlapping pattern; these work on the principle of a sunblind, hiding the decoyman from the birds on the pond but allowing him to be seen by those in the pipe. In between these high screens, and making in plan a zig-zag pattern, are screens about 50 cm high known as 'dog-leaps'.

On many quite small decoy ponds a thousand, sometimes several thousand, ducks may be resting during the day. Selecting the best pipe for the wind direction, the decoyman peeps through a tiny slit in one of the screens near the mouth of the pipe. If the ducks are suitably placed he signals to the dog, which then jumps over the dog-leap, runs round the screen *away* from the ducks and returns to its master over the next dog-leap. Immediately, the ducks start to swim towards the pipe, apparently drawn partly by bravado and partly by curiosity. The process is repeated round the next screen, and the next; watching through each successive 'peep hole' the decoyman gradually works the dog up the pipe, the ducks following often only a few metres behind. When as many as possible have been drawn in (it may be only one or two, or it may be 70) the decoyman or a colleague runs silently by a screened path to the mouth of the pipe and appears suddenly to the ducks in the pipe. He is in the outermost gap in the screens, known as the 'show place'. The retreat of the ducks to the open pond appears to be cut off and they try to escape by flying farther up the ever narrowing pipe. The decoyman follows, constantly in their sight through the gaps in the screens, until he drives the birds into the detachable 'tunnel net' at the end. Meanwhile the remaining birds on the pond have seen nothing but the dog and are therefore undisturbed. Such catches may be made several times in a day.

The device was perfected in Holland in the late 16th century. More than 200 decoys were built in England, although only a handful now remain and are used for ringing and research. Some of those in Holland still send thousands of ducks to market each year; in 1956 it was estimated that some 300,000 ducks were caught in the 100 remaining Dutch decoys. The first and only decoy in the New World was built at the Delta Waterfowl Research Station in Manitoba, Canada, in 1949.

There are many variants on the method described above. Cats and ferrets have been successfully used instead of dogs, and also stuffed foxes and stuffed stoats. In certain decoys tame ducks are trained to come for food, offered either in conjunction with the appearance of the dog or by itself to the accompaniment of a soft whistle. These decoy ducks lead their wild fellows but do not react to the appearance of the decoyman and so are not caught. Tame ducks used in a similar way to entice their fellows to destruction in wildfowling (or 'duck hunting' as it is called in North America) are frequently described as 'decoy ducks' or 'decoys', and the word also includes dummy birds used to attract wild ones within gunshot. From this usage the word 'decoy' has been further extended to human deceptions. P.S.

DEFAECATION: see DROPPINGS.

DEFINITION: in taxonomy, see under DESCRIPTION.

DEFINITIVE PLUMAGE: the adult plumage finally assumed by species which show differing plumages previously (see PLUMAGE).

DELTOID: see MUSCULATURE.

DEME: term (used more by botanists than by zoologists) for a local population that can in some way be considered separately from other populations of the same species. The deme has no status in nomenclature, and the term may thus be useful in the discussion of what is often an essentially fluid situation, wherein adherence to rigid concepts of taxonomy would obscure the reality (see SUBSPECIES; SYSTEMATICS).

DEMOISELLE: see CRANE.

DENDROCOLAPTIDAE: see under PASSERIFORMES, suborder Deutero-Oscines; WOODCREEPER.

DENDROCYGNINI: see DUCK.

DENSITY: see AGGRESSION; COLONIALITY; FLOCKING; TERRITORY.

DENSITY COMPENSATION: compensatory increase in abundance of a species in the absence of competing species with which, elsewhere, it coexists (or compensatory decrease in the reverse situation, though the term is less often used in this sense).

Density compensation has been reported most commonly from islands colonized by one species but not by its competitors. It presumably happens because food or other important limiting resources are more abundant when not being used by the competitors. Density compensation has been reported for several bird populations on islands supporting reduced numbers of potential competitors, but it is by no means a universal phenomenon.

DENSITY DEPENDENCE: see ECOLOGY (Population dynamics).

DENTARY: a paired bone of the lower jaw (see SKULL).

DERMIS: the inner layer of the SKIN.

DERTRUM: term sometimes applied to the tip or hook (if any) of the upper mandible (see BILL).

DESCENDENT MOULT: term applied to moult of primary feathers, in which sequential loss of adjacent feathers proceeds from the innermost to the outermost feather (see MOULT).

DESCRIPTION: term used in taxonomy for a statement of the observed taxonomic characters of a specimen or a taxon. A 'definition' or 'diagnosis' is a statement only of the distinguishing characters of a taxon.

DESERT BIRDS: see ADAPTATIONS, ENVIRONMENTAL.

DESIGNATION: term used in taxonomy for the express act of an author in fixing the type specimen or type species of a taxon, or in stating a type locality (see NOMENCLATURE; TYPE LOCALITY; TYPE SPECIES; TYPE SPECIMEN).

DESMOGNATHOUS: see PALATE.

DETERMINATE LAYERS: species in which the number of eggs laid in a clutch cannot be altered by the addition or removal of eggs during laying (see LAYING).

DEUTERO-OSCINES: one of the two suborders of PASSERIFORMES, a name introduced by Voous 1977 (Ibis 119: 224).

DEVELOPMENT, EMBRYONIC: from fertilization of the egg-cell (ovum) to emergence of the young bird from the shell (see EGG; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; GROWTH; HATCHING).

Embryonic processes in birds are most often studied using the domestic hen *Gallus gallus* since the eggs are easy to obtain, but it is likely that all birds develop in essentially the same manner. However, the time of incubation may vary from as little as 11 days to as much as 2 months, and the level of maturity at hatching may also vary (see YOUNG BIRD).

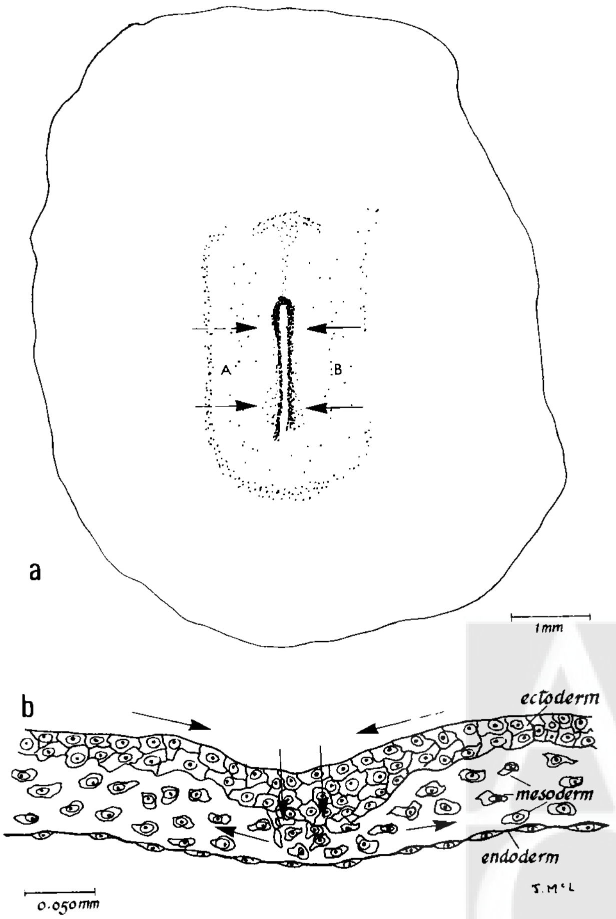

Fig. 1(a). The embryo lies at the surface of the yolk, and the yolk always rotates so that the embryo comes to lie uppermost. After a few hours of incubation, the chick embryo lies in the centre of an expanding disc of cells. The surface cells are flowing in the direction of the arrows towards the midline, where they sink down through the ectoderm. This midline marks where the backbone will form.

(b). A slice through the embryo between the points (A) and (B) shows how the cells migrate out towards the sides again, forming the mesoderm which lies between the ectoderm and the endoderm.

Development up to fertilization. Cells normally contain 2 complete copies of the genetic information used in making the adult. In the ovary, however, a 'meiotic' cell division occurs so that each germ cell contains only one copy of the genetic information. This genetic information, carried on molecules of DNA, is localized in the 'pronucleus'. The germ cells, now known as 'oocytes', then grow very slowly inside follicles in the ovary (reaching about 6 mm in diameter in the domestic hen), then they pause. When external and internal conditions are appropriate, a few of the oocytes will suddenly begin to increase enormously in size, reaching 40 mm in diameter in the domestic hen within about 9 days. This increase in size is caused by the cells of the follicle wall secreting particles of yellow yolk into the oocyte through the transparent membrane (known as the vitelline membrane) which surrounds it. The pronucleus remains at the periphery of the germ cell. Release of the oocyte occurs when the follicle ruptures along a predetermined band, and the oocyte then enters the upper part of the oviduct.

Fertilization. Sperm from the male, which like the oocytes contains only one copy of the genetic information, may be stored in the oviduct after mating and used to fertilize a number of eggs. Several sperm may enter the female oocyte, but only one will fuse with the pronucleus, restoring the number of complete sets of genetic information to 2 and enabling further development to proceed. It is, however, sometimes possible for development to begin without fertilization, and in some birds, notably turkeys *Meleagris*, full development can occur, giving rise to a chick carrying genetic information only from the mother—a parthenogenetic or virgin birth (see PARTHENOGENESIS).

Development up to laying. The fertilized egg continues to move down the oviduct, propelled by contractions of the oviduct wall. The upper part of the oviduct is lined with various glands which secrete the albumen or egg white, and the membranes which wrap round the egg, while the shell itself is secreted in the lower part of the oviduct, which is known as the uterus. The egg spends about 24 hours in the oviduct, and is normally laid as soon as it is completed. All this time cell division is taking place, so that when the egg is laid the embryo is composed of several thousand cells. The volume of the yolk is so enormous that the whole egg cannot be partitioned by the early cell divisions; instead the embryo lies as a small circular patch of cells at the periphery. Development can now pause for a short period without harm to the embryo until the parent begins incubation, which may be some days later if there are several eggs in the clutch.

The first days of incubation. The yolk is surrounded by the transparent vitelline membrane. The disc of cells which will give rise to the embryo lies inside this membrane, and the periphery of the disc adheres to it. Even by the time the egg is laid, the embryonic disc has separated into two layers with a space between them and, in the hours after laying, the cells of the upper layer begin to flow towards the mid-line of the disc (see Fig. 1a and b). There they pour through into the underlying space and begin to spread out again towards the edges. The embryo now consists of three layers: the uppermost is called the ectoderm, and will give rise to the skin, the nervous system, and the brain: the middle layer is called the mesoderm, and gives rise to muscles, bones, cartilage, tendons, as well as to some internal organs such as the heart and kidneys: and the lower layer, which lies next to the yolk and is known as the endoderm, gives rise to the lining of the gut, the stomach, the liver, and the lungs. The line through which the cells migrated to the inside marks out the main body axis and, beginning at the end which corresponds to the head, the ectoderm begins to form itself into a tube (see Fig. 2a and b). This, called the neural tube in the embryo, will become the spinal cord in the adult, and the main nerves will grow out from it. The first part to form also begins to bulge in various places to give a complex secondary structure; and this fore-part of the neural tube will form the brain.

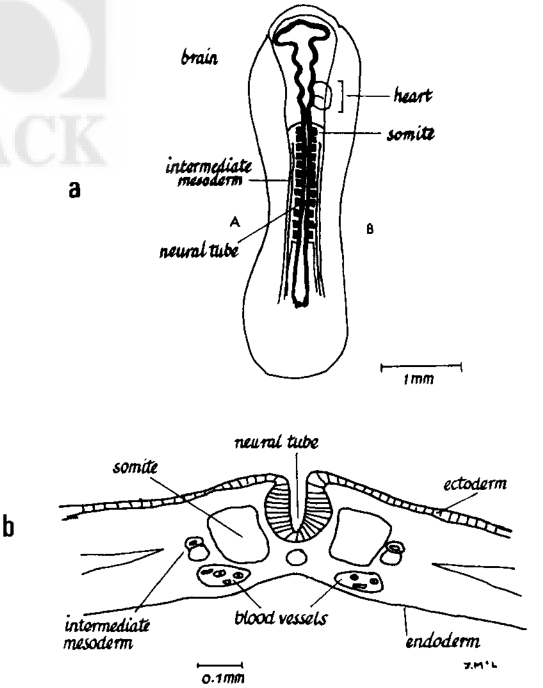

Fig. 2(a). After 48 hours of incubation, the ectoderm has rolled up to form the neural tube at the midline, and at the head end this has begun to form the complex structure of the brain. The mesoderm has formed the somites, the heart, and the intermediate mesoderm.

(b). A slice through points (A) and (B), in (a), reveals how the neural tube is sinking into the mesoderm.

While this is happening in the ectoderm, complex things are also happening in the mesoderm. On either side of the neural tube, which has sunk down from the ectoderm, pairs of small square condensations appear, beginning at the head end. These are called the somites (Fig. 2a and b). Part of each somite will grow round the neural tube to meet its neighbour on the other side, turning into cartilage as it does so. This cartilage is later replaced by bone in the same pattern, and becomes the vertebrae surrounding the neural tube. Other parts of the somite turn into muscle, and cells move out from these into the rest of the mesoderm to give rise to the skeletal muscles of the body. On either side of the somite rows the intermediate mesoderm is beginning to form tiny tubules which carry out the functions of primitive kidneys, filtering out waste materials.

Near the head end, where no somites form, a thickening appears in the mesoderm on each side of the embryo, and gradually these cells arrange themselves into a pair of tubes. These move towards the mid-line, under the neural tube, and fuse to form a single tube, which soon begins to twitch, and then to beat, revealing itself as the heart (Fig. 2a and b).

The endodermal tissues such as gut and lungs are not formed till later in development than the mesodermal tissues, since their functions in the adult are carried out by other structures in the embryo.

Extra-embryonic membranes. The developing embryo has 4 major concerns: air, food, waste disposal and something to sit on. It meets these problems by a set of remarkable structures which operate only in the embryo, and are discarded or resorbed at hatching. After hatching, of course, quite separate ways of meeting these needs are employed. It is convenient to deal with the problems facing the embryo in reverse order. Figure 3 is a guide through the rather complicated relationships of the various membranes.

Mechanical support. The membranes on either side of the embryo rise up, come together, and fuse, so that the embryo is trapped in a small space which subsequently becomes filled with fluid. This corresponds in function to the amniotic fluid of mammals, and is known by the same name (Fig. 3b).

Waste disposal. The waste products of metabolism (mainly uric acid in the chick embryo) are poisonous. The embryonic kidney tubules therefore pour them into an impermeable bag, called the allantois, emerging from the tail end of the gut. The allantois grows out into a space formed by a split in the mesoderm outside the embryo proper. It gets bigger and bigger with time as the yolk is used up, and eventually is left behind in the shell when the chick hatches.

Nutrient supply. The embryo is surrounded by a rich nutrient supply in the yolk. At first the embryo is so small and flat that enough nutrient material for its needs can diffuse into it, but this will only work over short distances, and the embryo soon becomes too large. At this point the *extra-embryonic circulation* takes over. As described above, the margin of the embryonic disc adheres to the underside of the vitelline membrane surrounding the yolk. The edge cells begin to migrate outwards, and the cells behind them divide to keep pace, so that the embryonic disc begins to expand. The mesoderm splits into two layers with a gap between them: the upper layer, together with the ectoderm, is called the chorion, and the lower, together with the endoderm, is called the yolk sac (Fig. 3). Little red spots begin to appear in the yolk sac; these are composed of differentiating red blood cells. Short lengths of tubule begin to appear in the yolk sac also, and link up to form a network of vessels which finally connect to the heart, which is already beating. Blood is carried in a set pattern out from the embryo proper through the thin-walled extra-embryonic yolk sac, where it can pick up nutrients from the yolk over which it passes. To aid in nutrient collection, the yolk sac is also thrown into folds, which increase its surface area. Then the blood is gathered in a blood vessel which runs in a circle just behind the advancing edge of cells, and flows back through veins to the heart, whence it is pumped through the embryo. The extra-embryonic vascular circulation is resorbed back into the gut round about the time of hatching.

Embryonic respiration. At about 5 days of incubation, the allantois fuses with the overlying chorion, and the combination 'chorio-allantoic' membrane rapidly grows round the inside of the shell. The allantois starts off as a bag-shaped structure which contains the poisonous waste products, so the inside surface of the bag must be impermeable. The outside of the bag, however, is covered with thin-walled blood vessels, and these are now pressed against the inside of the shell. The chorio-allantoic membrane now acts as a 'lung': oxygen diffuses through the shell into the blood vessels, and carbon dioxide diffuses out of the blood vessels and out through the shell. When the embryo begins to breathe the air in the air-space just before hatching, the chorio-allantoic membrane detaches and gets left behind in the shell.

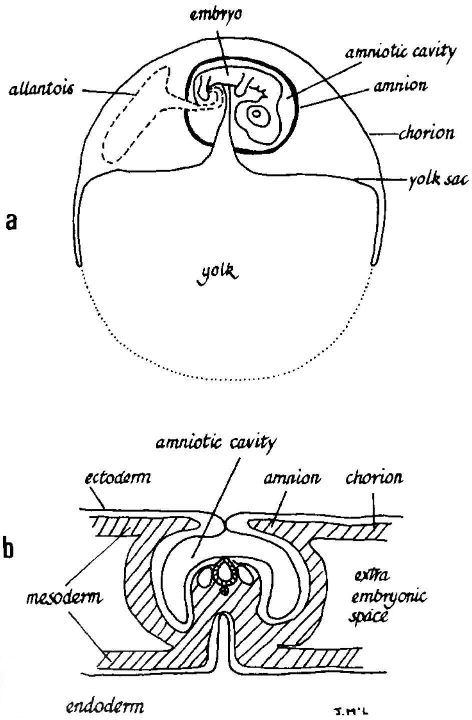

Fig. 3(a). A diagram of the relationships of the extra-embryonic membranes, looking at the embryo from the side.
(b). A stage a few days after that shown in Fig. 3(a).

Formation of the limbs. Once the plan of the body axis is established by 2 days of incubation, the *Gallus* embryo begins to roll over on to one side and rise up off the yolk. It is at first largely tubular but, after between 60 and 72 hours of incubation, 2 pairs of bulges begin to grow out from the flanks. By 3 days of incubation, these are distinct buds (see Fig. 4); and their growth continues as they give rise to the limbs. Cartilage begins to condense visibly in the centre of the limb buds at 5 days of incubation, and forms recognizable elements almost immediately: by 10 days of incubation, a tiny model of the limb can be seen, perfect

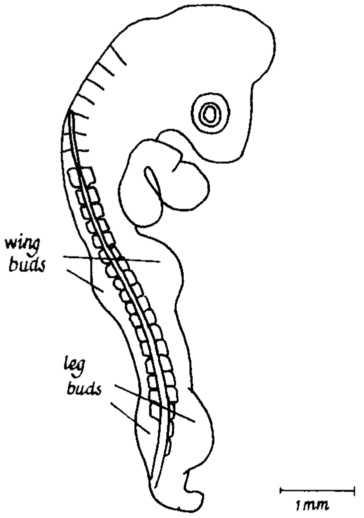

Fig. 4. Outline of the embryo at 3.5 days of incubation, showing the limb buds growing out from the flanks.

in all its details except size (see Fig. 6a). The cartilage elements are easiest to see; but muscles, blood vessels, tendons, and nerves are also present in the same pattern as the adult. At about this time, the cartilage begins to be replaced by bone, and this will continue throughout the growth up to and after hatching. It is not known why the embryo has to form a cartilage model of each bony element in advance of bone formation.

Formation of the internal organs. The splitting of the mesoderm described above takes place inside the body of the embryo as well as outside. It is the uppermost of these two layers which contributes mesoderm to the limbs. The lower gives rise to some of the internal organs. The development of the sexual organs is particularly curious. Twin ridges arise from the mesoderm on either side of the main axis but down towards the tail. These are invaded by cells from the extra-embryonic mesoderm from beyond the head. These primordial germ cells will eventually turn into the eggs or sperm. Depending on the sex of the animal, the mesodermal ridges, up to now identical in both sexes, will develop either into testes or ovaries. If the animal is female, only the left ovary will continue to develop, and it will move over towards the mid-line. This may be an adaptation for flight: two ovaries both full of maturing oocytes are probably just too heavy to carry.

Formation of gut and lungs. As the yolk sac becomes smaller and smaller, the endoderm begins to grow round it and take on the appearance and position of the normal gut. Up towards the head, a small hollow bud appears as an outgrowth from each side of the gut, and these continue to grow and branch until they are clearly recognizable as the rudiments of the lungs. These become functional before hatching, when the chick sticks its beak into the air-space, and this means that the chorio-allantoic membrane becomes redundant, and can be left behind on hatching.

Formation of feathers. At about 8 days of incubation in the domestic hen, dense condensations begin to form in the mesoderm of the back just under the ectoderm. One line forms first above the spine, and then others form on either side of this, covering the gaps in the preceding line so that eventually a hexagonal pattern develops. The mesodermal condensation begins to expand, raising a little lump covered by ectoderm, which will eventually grow into a long thin finger shape. Inside the ectodermal covering the mesoderm differentiates into a central barb with pairs of strands growing out round the inside of the finger, but not meeting on the opposite surface. Finally the ectoderm splits, and the fully formed feather uncurls. See also FEATHER.

Mechanisms of development. Development is still one of the great unsolved mysteries of biology, but some clues are frequently gained by experiments carried out directly on the developing avian embryo. Since the embryo cannot feel pain until the sensory nervous system has developed, operations can be carried out without causing distress to the embryo or to the experimenter. Some examples are given below.

Development of the heart. The heart develops from the fusion of paired structures arising from the mesoderm. If this fusion is prevented by the insertion of a small barrier, then each of the structures will form a functioning heart by itself. This may be a fail-safe mechanism which corrects for defects arising on one side of the embryo. If the heart is removed from an early embryo, and dissociated to single cells which are then cultured separately in glass or plastic dishes filled with nutrient fluid, then each individual cell can be seen to contract and expand rhythmically on its own. If two such cells come in contact, the rhythm of the slower changes to that of the faster almost immediately, and this will continue as more and more cells come in contact with the original group so that the whole clump is expanding and contracting synchronously. This indicates that the beating of the heart is due to a basic property of its cells.

Development of the limb. Limbs develop from buds which grow out from the flank. These are composed of mesoderm covered with a layer of ectoderm which is mostly one cell thick, but at the tip of the limb is pushed up into a ridge which is several cells thick—the Apical Ectodermal Ridge (AER) (see Fig. 5a). If this is cut off, the limb which develops from the bud is truncated at a level which depends on the time at which the AER was removed: if it is removed early in bud development, then nothing beyond the elbow may develop; if it is removed slightly later, then the limb may be truncated at the wrist; and later still, it may be truncated in the middle of the digits. This indicates that the parts of the limb are laid down in sequence, rather than being formed at once, then gradually expanding. If an AER is grafted on to the flank of a young embryo just at the time when the limb buds are beginning to grow out, then it will induce an extra limb to grow out. Together these experiments show that the AER is necessary for limb outgrowth. However, it is believed that a small piece of tissue on the edge of the wing bud nearest the tail (see Fig. 5b) acts with the AER to give the actual form of the limb, for if it is removed and grafted to the opposite edge of another limb bud, then the limb which forms is reduplicated in the head to tail axis (Fig. 6b). This phenomenon probably underlies the development of all vertebrate limbs, because if the corresponding region is removed from the developing embryos of a whole variety of animals, including the mouse *Mus* and the tortoise *Testudo*, and grafted to the chick limb bud in the same way, they are all capable of bringing about such a reduplication. The extra parts are always characteristic of the chick, not the donor. Such experiments on limb formation are of vital importance in understanding how limb defects, such as those brought about by Thalidomide, are caused.

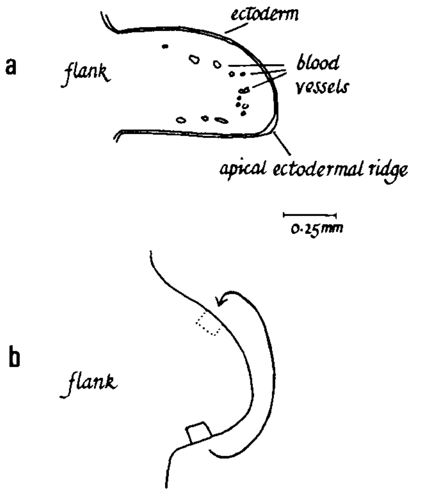

Fig. 5(a). A section through a wing bud after 4 days of incubation, showing the apical ectodermal ridge at the distal tip. Note that there are no blood vessels in the core of the limb where the cartilage is going to form.

(b). A small piece of tissue may be removed from the posterior edge and grafted to the anterior edge of a wing after 4 days of incubation. The result of this operation is shown in Fig. 6(b). The converse experiment (anterior tissue to posterior) has no effect.

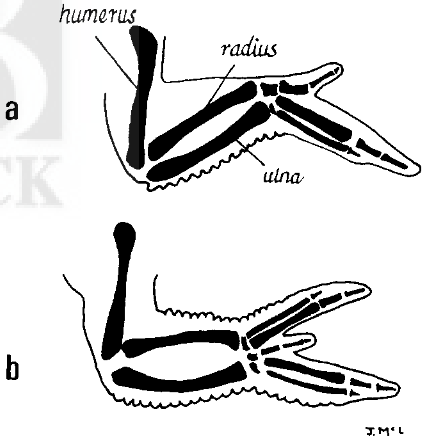

Fig. 6(a). A normal wing bud after 10 days of incubation. The cartilage elements have been stained dark and the remaining tissue made transparent. The form of the wing is very much that of the adult—apart from scale.

(b). 10-day limb after the operation shown in Fig. 5(b). The limb has reduplicated in the anterior-posterior axis from the elbow onwards.

Development of the feather germs. The feather germs develop as mesodermal outgrowths covered with ectoderm, not unlike limb buds, though smaller. However, here it can be shown that the ectoderm does not bring about the outgrowth. A small square of skin containing both ectoderm and mesoderm can be removed from the embryo, just before the feather germs form, and grown in a dish. The ectoderm can be removed, rotated through 90° and replaced. When the feather germs appear, they do so in the pattern characteristic of the mesoderm rather than the ectoderm. On the leg, scales form rather than feathers, and again, the mesoderm controls where they form. If a piece of back ectoderm is rotated and replaced on leg mesoderm, feathers form, but they do so with a distribution characteristic of scales. Curiously, however, if Vitamin A is applied to the developing embryo, feathers rather than scales form on the legs, and this is reminiscent of the owls, which naturally have feathers rather than scales in this position.

The colour of feathers depends in part on pigment cells which move out through the body from the neural tube. They seem capable of recognizing where they are and of going to the right place—even if they are placed in the wrong animal. So pigment cells from the 'Barred' variety of chicken if placed in the embryo of the 'White Leghorn' will migrate to the appropriate places and give a barred pattern. Similarly, if a piece of skin from a Robin *Erithacus rubecula* embryo is placed in an embryonic chicken wing, then the pigment cells will migrate out and take up their normal distribution, so that the resulting animal has a wing coloured grey and buff like that of a robin. J.C.McL.

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Embryonic thermoregulation. The first distinctive step towards independent regulation of body temperature appears in the domestic fowl on day 7, when thyroid iodine is first produced, and by day 10 chicken embryos are able to produce thyroxine and TSH, two thyroid hormones implicated in temperature regulation. Thyroid activity increases sharply on day 15 and by the following day the chick is able to breathe. The developing embryo initially meets its oxygen requirements by simple diffusion but a circulatory system is already detectable in the domestic fowl after 48 hours. Haemoglobin synthesis can be detected midway through the second day of incubation and the concentration of erythrocytes increases linearly thereafter until hatching. These cells tend to form earlier in precocial species than in altricial species. Heart rate increases between day 4 and day 10 but then decreases slightly as the growing heart is able to cope with a larger volume of blood on each stroke. The oxygen affinity of the blood increases between days 14 and 17, thus contributing further to the embryo's ability to metabolize oxygen.

In altricial species oxygen consumption increases exponentially throughout the incubation period but in precocial species this increase ceases about two-thirds of the way through, thereafter remaining relatively constant.

Oxygen consumption in embryos of different species measured shortly before hatching, i.e. in full-term embryos, is a power function of egg weight according to the equation

$$m = 18.5\,W^{0.730}$$

where m is heat reduction (Kcal/day) and W is fresh egg weight (g). This equation thus describes a double logarithmic regression line, which is parallel to but below the Aschoff–Pohl regressions for adult metabolism on body weight (see METABOLISM). This means that full-term eggs have metabolic intensities about one-third of those prevailing in adults of the same body weight.

The initial energy requirements of the embryo are met by carbohydrate metabolism and once the liver has differentiated by about day 6–7 it can synthesize and store glycogen. Most carbohydrate is however drawn from the yolk sac membrane. Embryonic metabolism in domestic fowl embryos increases steeply after day 14 and this is fuelled largely by lipids; about 80% of the lipids in the egg are consumed during this period.

In a number of species eggs are neglected by the parents when the adults have difficulty finding food. Thus Fork-tailed Storm Petrels *Oceanodroma furcata* may absent themselves from their eggs for as long as 28 days and European Swifts *Apus apus* similarly allow their eggs to chill during wet and rainy weather. Their embryos show a number of special physiological adaptations to enforced neglect. Metabolism decreases, with metabolic rates in the Fork-tailed Storm Petrel, for example, increasing daily at only one-third the rate of increase of Japanese Quail *Coturnix japonica* eggs of similar size and taking 50 days for normal incubation (instead of the 21 days expected for a typical egg of that size). The embryos have particularly large stores of embryonic fat to fuel this slow development. Such adaptation is more costly than the normal development patterns but does accommodate to the need to 'switch off' metabolism at times when parental duties are not possible. In such conditions the embryo can continue to develop at temperatures as low as 30°C; if cooled further, e.g. to 10°C, the incubation period is simply prolonged by the corresponding amount. R.J.O'C.

DEVELOPMENT OF BEHAVIOUR: see BEHAVIOUR, DEVELOPMENT OF.

DEVELOPMENT, POST-EMBRYONIC: see GROWTH.

DEVIL BIRD: see SWIFT.

DIABLOTIN: name used in the West Indies for the Black-capped Petrel *Pterodroma hasitata* (see PETREL), and also (Trinidad) for *Steatornis caripensis* (see OILBIRD).

DIACROMYODIAN: see SYRINX.

DIAGNOSIS: in taxonomy, see under DESCRIPTION.

DIAL-BIRD: see DAYAL-BIRD; THRUSH.

DIAMOND-BIRD: alternative substantive name of *Pardalotus* spp. (see PARDALOTE; FLOWERPECKER).

DIAPHRAGM: a system of membranes partially dividing the thoraco-abdominal cavity, so that the lungs and cervical air-sacs occupy one chamber and the majority of the air-sacs another, while the heart and abdominal viscera are in the remaining space (see RESPIRATORY SYSTEM). This arrangement in birds contrasts with the complete and more muscular transverse partition between the thoracic and abdominal cavities in mammals.

DIASTATAXIS: see PLUMAGE; WING.

DICAEIDAE: a family of the PASSERIFORMES, suborder Oscines (see FLOWERPECKER).

DICHROMATIC: having two distinct types of coloration; used with reference either to the two sexes or to two colour MORPHS of a species ('dimorphic' being a loose equivalent, more often used but strictly applying to differences of form).

DICKCISSEL: *Spiza americana* (see CARDINAL-GROSBEAK).

DICRURIDAE: a family of the PASSERIFORMES, suborder Oscines (see DRONGO).

DIDUNCULINAE: see PIGEON.

DIENCEPHALON: part of the forebrain (see NERVOUS SYSTEM).

DIGESTION: see ALIMENTARY SYSTEM; GRIT; NUTRITION; PELLET.

DIGIT: a 'finger' or toe (see LEG; SKELETON, POST-CRANIAL; WING). Primary feathers borne on the wing digits are sometimes called 'digitals'.

DIKKOP: see THICKKNEE.

DIMORPHISM: see POLYMORPHISM; SEXUAL DIMORPHISM.

DINORNITHIDAE: extinct family of STRUTHIONIFORMES; MOA.

DIOCH: substantive name of *Quelea* spp. (see WEAVER).

DIOMEDEIDAE: see under PROCELLARIIFORMES; PETREL.

DIPPER: substantive name of the 4 members of the family Cinclidae (Passeriformes, suborder Oscines); is used without qualification in Britain for *Cinclus cinclus*.

Characteristics. The dippers as a group provide an excellent example of the adaptability of a typical passerine bird to an unusual environment without any very obvious modifications. It would hardly be suspected from a cursory examination of a dipper, even in the hand, that it is a water bird. Its size (*c.* 17–20 cm) and shape are approximately those of the Starling *Sturnus vulgaris*, although the plumage differs in colour and also in being soft and very dense in texture. The flight, too, resembles that of a starling. Whereas most water birds have feet modified in some way for swimming, dippers have feet of the kind normal for a perching bird. When swimming on the surface, the feet of a dipper have to be moved very rapidly indeed because they present only slight resistance to the water. Under water a dipper can walk on the bottom, but it uses its wings for swimming.

Like many other birds, dippers have a third eyelid or nictitating membrane. The dipper's membrane is unusual in being conspicuously white and this shows clearly when the dipper does its characteristic bobbing motion, and at the same time draws the white membranes across the eyes so that the bird appears to blink. When underwater, the third eyelid can be used to clean the eyes and keep them free from particles of matter in suspension.

Habitats. Typically swift-flowing streams or rivers which are cascading down from higher ground. This means that there are usually plenty of boulders and rocks on which dippers can perch beside the water. It also follows that dippers generally frequent hilly or mountainous terrain. But they may occupy stretches of slow-flowing rivers where man has created 'rapids' artificially, e.g. water mills.

Distribution. Mountainous regions of Eurasia, western North America, Central America, and western South America. Like the wrens, it is probable that the dippers originated in tropical America and then spread northwards, first to North America and then westwards to Asia and Europe. They do not occur on the eastern side of North America even where the country is mountainous.

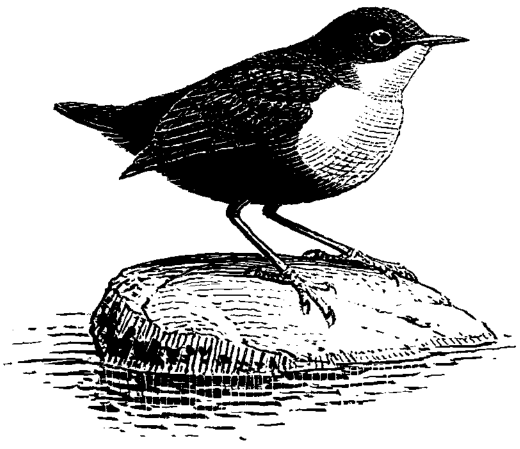
In the Andes there are several races of the White-capped Dipper *C. leucocephalus*. The North American species *C. mexicanus* is found only on the western side of that continent and the Dipper *C. cinclus* is discontinuously distributed in suitable habitats across Asia and Europe with a foothold in north-west Africa. The Brown Dipper *C. pallasii*, a sombre bird, chocolate-brown all over, inhabits mountainous parts of Asia eastwards to Japan. In the Himalayas, where the distribution of *C. cinclus* overlaps *C. pallasii*, the latter tends to frequent the lower levels from the foothills upwards, the former mostly from 2,000 m, and both species may reach heights of over 4,000 m.

Populations. Dippers are stricly limited by their habitat requirements. An average of 4–6 territories per 10 km of river is typical of British rivers (Marchant and Hyde 1980).

Movements. Dippers' movements are largely dictated by the severity of the weather. In montane populations there is some altitudinal shift with the seasons to escape the rigours of the higher regions in winter. In the colder northernmost part of the range, there is a movement south in winter. Apart from these movements, dippers are non-migratory.

Food. The diet consists of many kinds of small water creatures living in fast-flowing streams and rivers. The list of prey includes caddis-fly and dragon-fly larvae, small aquatic molluscs and crustaceans, worms, tadpoles and very small fish. When feeding, a Dipper will often wade into shallow water and snap up underwater creatures within reach. For feeding in deeper water a Dipper will wade further out and dive to the bottom, propelled downwards with powerful beats of its wings. Sometimes a Dipper will plunge off a stone or even from flight into the water and dive below. It can rise straight out of the water after a dive and fly off. In a remarkable film by J.W. Jones of a wild Dipper taken through the glass side of a fish-hatchery tank, the bird is seen swimming with a sustained effort of the wings to keep down; it only took ova which were exposed and made no attempt to uncover those which were buried in the usual way. Like many other birds, dippers eject pellets of indigestible material through the mouth.

Behaviour. Dippers cannot be described as sociable birds. They typically are well spaced out along the watercourses they inhabit. Pairs hold territories of several hundred metres. In one respect Dippers might seem to be sociable: they may roost communally. Up to a couple of dozen may use a roost under a bridge, but the main advantage appears to be that of shelter, especially from the wind (Shaw 1979).



Dipper *Cinclus cinclus*. (*D.W.*).

The Dipper has a display which resembles that of the Robin *Erithacus rubecula*. In both species two birds may face each other with beaks pointing straight upwards so that in the case of the Dipper the white bib is made as conspicuous as possible, just as in the Robin the red breast is prominently displayed. When a pair meet after being separated for a while they often face each other and posture in this way. The sexes are similar in both Dipper and Robin, and there are times when the females sing.

Voice. The call-note of the Dipper is a strident *zit*, *zit*, which may be given from a boulder or in flight. The song resembles that of a Wren *Troglodytes troglodytes* in being loud and penetrating, and like the call-note it can be heard above the roar of a cascading torrent.

Breeding. Nesting dippers require sites close to water. Usually there is water immediately below the nest. A typical natural nest site is in a steep bank overhanging the river, but man-made sites are often provided by recesses in bridges, or in walls that face a river. Sometimes a nest is close to or even under a waterfall, so that it is constantly wetted by spray. The domed nest is composed mainly of moss with a lining of dead grass and a few dead leaves. The clutch of 4 or 5 white eggs is laid early compared with most birds; in Britain it is usually in April, but sometimes earlier. Incubation is 16 days, fledging 20–24 days. The young disperse soon after leaving the nest. A second brood is sometimes reared. H.G.H.

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DIPTEROCARP FOREST: rain forest of south-east Asia, almost entirely lowland, dominated by trees of the family Dipterocarpaceae.

DIRECT HEAD SCRATCHING: see COMFORT BEHAVIOUR.

DIRECTION, SENSE OF: see NAVIGATION.

DISCRIMINANT FUNCTION: see BIOSTATISTICS.

DISEASE: may be defined as a departure from the normal state of health. Many injurious agents enter the body or may be produced in the body and bring about disease. Such agents include micro-organisms, parasites and poisonous substances. Deficiencies of food substances such as vitamins and minerals also cause disease, as do metabolic disorders and degenerative processes. All these conditions may cause biochemical changes in cells, leading to structural alterations which may be microscopic or macroscopic in nature. Such alterations in cells and tissues are called lesions.

Lesions are sometimes specific for the cause, e.g. inclusion bodies in certain viral diseases, but usually several different causes may produce very similar changes and effects. The primary cause of disease may act locally or be widespread through the body. Frequently primary lesions have a secondary action elsewhere in the body.

Disease occurs in domestic, free-living and captive birds. Some types of disease are more often associated with particular environmental conditions or with particular groups of birds. Much is known of the diseases of domestic poultry and of birds kept in captivity in zoological gardens, but relatively little collected information is available on the diseases of free-living wild birds.

The part played by disease in regulating populations of wild birds is not yet clear but in general it appears that numbers are controlled primarily by food supply and that disease is one of several factors of secondary importance (see ECOLOGY).

In some cases food shortage and disease may act together, since dense populations help the spread of disease and also reduce the available food. Climatic factors are also often linked to food supply and disease. The bird's resistance to disease may be lowered by poor nutrition or by sudden changes in temperature; thus abnormal heat or abnormal cold may cause heavy losses either directly or by predisposing to infectious disease or to the production of toxic substances (see later). Sustained wet and cold weather is liable to bring on pulmonary disease, a common source of trouble in young birds, especially of the nidifugous species, the main change being one of acute congestion and oedema of the lungs. It is probable that the poor heat-regulating mechanism of the young chick is also a factor in the development of this syndrome of 'chilling' (see HEAT REGULATION).

Wet weather, on the other hand, may increase food supply by allowing birds to catch more worms and molluscs. This, however, may be a disadvantage in that such animals act as intermediate hosts for many parasites and thus a well-fed nestling may receive a pathogenic burden of parasites such as the massive infection with trematodes sometimes seen in waders (Charadriidae) and gulls (Laridae). Periods of drought, conversely, increase the concentration of birds at drinking and bathing places and thus facilitate the spread of infectious diseases such as salmonellosis. A similar situation sometimes arises when birds are attracted in large numbers to confined supplies of food and water in times of severe winter weather, for example at garden feeding centres.

Diseases caused by pathogenic micro-organisms, fungi, bacteria, rickettsiae and viruses are known as the infectious diseases; when diseases are spread by contact, either direct or indirect, they are termed contagious diseases. Illnesses and death may also be caused by toxic substances, which may be produced by micro-organisms or by man in the wide range of chemicals which are used in industry, agriculture and horticulture, in particular the various pesticides and herbicides (see TOXIC CHEMICALS).

Emphasis will be placed here on some of the more important diseases of free-living wild birds; detailed reference to diseases in domestic birds should be sought in the standard textbooks of poultry disease.

Bacterial and fungal diseases:

Aspergillosis. This disease is due to infection with a mould, usually *Aspergillus fumigatus*, which is commonly present in decaying vegetable matter. Infection occurs when the bird inhales or ingests the spores of the fungus, producing lesions chiefly in the lungs and the air sacs. The pulmonary lesions vary in size from 1 or 2 mm to nodules several centimetres across: the air sacs may be converted into thick-walled sacs with caseous, necrotic (pus) centres; in some instances the air sac lining is covered by a greenish-blue mould. Sometimes the disease is widespread in the body, and many organs, including the brain, may be affected. Aspergillosis has been recorded in many species of birds, and occasionally occurs in large outbreaks with heavy mortality. Waterfowl and game-birds are particularly susceptible, especially when kept in a semi-wild state. The disease is also frequently seen in penguins kept in captivity. It is sometimes associated with other conditions such as salmonellosis and in cases occurring in captive exotic species stress and malnutrition play important parts in initiating infection.

Thrush, also called Candidiasis, Moniliasis and 'sour crop', is a mycotic infection of the digestive tract of birds. Thrush is most often seen in chickens, pigeons, geese, turkeys, pheasants, quail, grouse, and psittacine birds. The cause is a fungus, *Candida albicans*, and in young birds serious losses may occur in aviaries and bird gardens.

Ringworm or favus is caused by a fungus *Trichophyton gallinae*. It occurs chiefly in chickens and turkeys, but is also seen in pigeons and small passerines. Infection occurs chiefly about the head. There is partial or complete feather loss and the head may be covered with scales and sometimes scabs.

Avian cholera. This acute septicaemic disease is caused by a bacterium *Pasteurella multocida*. Most, if not all, species of birds are susceptible. The disease may occur in enzootic form with a high death rate, but more often sporadic cases occur. Exceptionally, very large outbreaks with large-scale mortality occur in waterfowl on migration or at their wintering grounds. As with many other diseases stress factors are important in initiating outbreaks. The chief lesions are multiple small haemorrhages on the body surfaces and, usually, small foci of necrosis in the liver.

Erysipelas. This disease, an acute septicaemia, caused by *Erysipelothrix rhusiopathiae* a Gram-positive bacillus, affects many species of animals both domestic and free-living. The organism can live for long periods in the soil. A wide range of avian species is susceptible and disease due to this organism is of economic consequence in bird parks, zoological gardens and especially domestic animals.

Listeriosis. Several forms of this disease, caused by the bacterium *Listeria monocytogenes*, occur in birds and mammals throughout the world. The avian disease is sometimes septicaemic in nature but its principal importance is that infected birds constitute reservoirs of infection for other animals.

Salmonellosis. Infections of birds with *Salmonella* bacteria are common and create important problems in the poultry industry. Wild birds sometimes harbour the organisms and may show lesions at post mortem examination. Both acute septicaemic and chronic forms of the disease are encountered. Usually the liver and spleen show lesions in the form of grey or white nodules scattered through the substance of the organ; there may be translucent nodules in the lungs. *Sal. typhi-murium* is the species most often isolated from wild birds. The organisms are excreted in the droppings, which thus serve as further sources of infection. It is not unusual for a build-up of infection to occur around drinking places and artificial feeding areas such as bird tables in gardens. Outbreaks have been recorded in Greenfinches *Carduelis chloris* and House Sparrows *Passer domesticus* under such circumstances. Salmonellosis sometimes occurs in epidemic form in gulls, probably as a result of their scavenging propensities.

Tuberculosis. The avian type of *Mycobacterium tuberculosis* is a common cause of the disease in birds, which become infected by ingestion of the organism. Affected birds frequently excrete the bacilli in vast quantities and so spread the infection. The incidence of the disease is variable and is higher in some species than in others, but all birds are susceptible. One survey of gulls revealed a 10.3% infection amongst 97 examined and in another survey approximately 4% of Woodpigeons *Columba palumbus* were affected. Avian predators become infected from their prey. The disease affects many organs and most commonly produces lesions in the liver, spleen and gut. The tuberculous lesions are nodular, white and cheesy in consistence, varying a good deal in size. Parrots are susceptible to the human type of tubercle bacillus as well as to the avian one.

Yersiniosis. This disease, also known as pseudo-tuberculosis, is frequently encountered in birds and mammals. It is due to the bacterium *Yersinia* (*Pasteurella*) *pseudo-tuberculosis* and occurs both as a sporadic and as an epizootic disease. Major outbreaks occur in Canaries *Serinus canaria* and other caged songbirds, and the disease has been reported in at least 12 orders of birds in many areas of the world. Stress factors are important in the development of outbreaks. Characteristic lesions, yellowish-white in colour and approximately 1–2 mm in diameter, occur in the liver and spleen, although in many acute cases only septicaemic lesions may be present.

Mycoplasmosis. Many serotypes of mycoplasmas have been isolated from birds; in particular raptors and psittacines may be infected. Some of the mycoplasmas cause disease of economic importance in domestic poultry. *Mycoplasma gallisepticum* occurs in chickens *Gallus gallus*, turkeys *Meleagris gallopavo*, pheasants, Chukar Partridge *Alectoris chukar* and Bobwhite Quail *Colinus virginianus*, as well as in other species, in all of which it produces a chronic respiratory disease, one form of which is coryza. *Mycoplasma synoviae* is responsible for infectious conditions of the joints and tendon sheaths of birds.

Coryza. This term is applied to infections of the upper respiratory tract of birds. It is a condition with many similarities to the human common cold. Some forms are infectious and occur most frequently in domestic poultry and game birds. The usual causes are the bacterium *Haemophilus gallinarum* and *Mycoplasma* spp., but several agents produce identical clinical signs and mixed infections are common. It is also associated with specific diseases such as Ornithosis and Newcastle Disease. Affected birds have discharges from the eyes and nostrils and the infraorbital sinus is frequently over-filled with mucus and purulent exudates. This disease may become chronic and extend to the air sacs.

Botulism. An anaerobic bacterial organism *Clostridium botulinum* produces a powerful exotoxin that is responsible for a serious and fatal form of food poisoning in man and animals. Various types of the organism occur; type C most often affects birds. The importance of botulism in birds is illustrated by the fact that millions of waterfowl die from it each year throughout the world. The toxin is formed when the anaerobic organism multiplies in water containing decaying vegetation, dead fish and, in particular, large quantities of dead insect matter on which birds feed. Outbreaks occur most often during the summer months when prolonged spells of fine weather with resulting high temperatures, low water levels, oxygen depletion and alkalinity of the water lead to rapid bacterial multiplication and hence the production of large quantities of toxin. Ducks are so often affected that the condition is termed 'duck sickness'. The disease is not, however, confined to waterfowl and birds of at least 21 families are known to have been affected. Extensive and severe outbreaks of botulism have been recorded in many parts of the world on game bird farms, especially pheasant rearing units. Intoxication and death follow the ingestion of blowfly larvae, *Calliphora* spp., which contain the toxin. Botulinum toxin may be carried through the larval and pupal stages to the adult insect. Major outbreaks sometimes occur in gulls which have fed on contaminated refuse dumps and many shore birds may be killed feeding in toxin-contaminated tidal estuaries.

It seems probable that spores of *Cl. botulinum* can be transferred on the plumage, the feet and via the excreta of birds. Mud samples from lakes, rivers, mud flats, etc. sometimes show a high incidence of several types of the organism and thus when environmental conditions become suitable, explosive outbreaks of the disease may occur.

Botulin toxin produces its effects on the nervous system, the chief clinical feature being a flaccid paralysis preventing the birds from flying; often the neck is held to one side, hence the term 'limber neck' used in this disease. Leg paralysis is also a common sign. Birds die from respiratory failure or from drowning.

Psittacosis or Ornithosis. Sometimes called Chlamydiosis, since it is caused by *Chlamydia psittaci*, this disease is a systemic, contagious, serious disease of birds and mammals. In the parrot family it is usually referred to as Psittacosis and the same condition in non-psittacines is termed Ornithosis. The disease has a world-wide distribution and has been identified in at least 17 orders of birds. Numerous strains of the organism have been found in many species, varying greatly in their pathogenicity and virulence. The disease is often endemic in wild populations and susceptibility is a function chiefly of age and species. Psittacines, ducks, geese, gulls, petrels and pigeons are perhaps most frequently affected, but over 140 species have been found to be infected. Infection often occurs at the nestling stage and severe disease may be precipitated by stress factors.

In birds there are no characteristic clinical signs and at autopsy an enlarged spleen may be the only lesion. Some avian cases may have necrotic foci in the liver and spleen and there may be fibrinous deposits on the pericardium and liver.

Viral diseases:

Arboviruses. These have recently been designated togaviruses. In general this group of viruses produce little clinical disease in birds but they are of importance in that they may cause encephalitis in man and other mammals, birds acting as reservoirs of infection. Mosquitoes, mites and ticks are the biological vectors and birds are infected usually at the nestling stage.

Avian leucosis complex. A complex group of diseases characterized by abnormal production of white blood cells and consequent changes in the organs and tissues. As a result of multiplication of the stem cells of the blood, tumour-like swellings are produced. These diseases are of great importance in domestic fowls and similar conditions have been recorded from game birds and owls.

Avian pox. This viral disease has been reported in at least 60 species of birds from 20 families. Several strains of the virus occur with different degrees of specificity. The strains affecting small passerines appear to be more host-specific than others. The disease usually presents in one of two forms. The common type is a cutaneous infection involving chiefly the head region but also the feet and legs; less frequently there is infection of the mucous membranes of the upper respiratory and digestive tracts. The other, internal, form was at one time called 'avian diphtheria'. The disease is usually mild in character, but young birds may suffer severe mortality and large numbers of roosting birds are often involved at one time, e.g. outbreaks have been seen in roosts of House Sparrows and Tree Sparrows *Passer montanus*. The disease is common in domestic gallinaceous birds and wild populations. In Canaries kept in bird rooms and aviaries there may be extensive, severe outbreaks with high mortality.

Herpesvirus infections. Several herpesviruses infect birds. One affecting homing pigeons *Columba livia* and other members of the Columbidae causes a serious disease which is characterized by, amongst other things, intranuclear inclusion bodies in the cells of the liver. Similar viruses occur in other species and the disease they produce is sometimes called '*inclusion body disease of raptors*' since it has been recorded in several species of falcons and owls. Affected birds have focal necrosis of liver cells and also parts of the reticulo-endothelial system. Herpesviruses have been recovered from psittacine birds with Pacheco's parrot disease.

In the domestic fowl a herpesvirus is responsible for an important respiratory disease known as *infectious laryngotracheitis*.

Marek's disease. This is one of the most common lympho-proliferative diseases of the domestic fowl and it is also recorded in several other species of bird. The cause is a herpesvirus which produces an infiltration of nerves, viscera, gonads and other tissues by mononuclear cells. It is of major importance in the poultry industry.

Duck plague. Also known as *duck virus enteritis* this is a serious, acute, contagious and often fatal herpesvirus infection of domestic ducks, geese and swans. Present also in free-living waterfowl, it probably has a world-wide distribution. The disease is apparently density-dependent and is more liable to occur under stress conditions. The disease is principally one affecting ducks and is characterized by high mortality. There are multiple haemorrhages throughout the body and diphtheritic membranes on the oesophagus and elsewhere. Many types of cells are attacked by the virus and undergo necrosis.

Myxoviruses and Para-myxoviruses. Members of this large group of viruses are responsible for serious epidemics amongst birds and mammals. In addition they are important in that some of these viruses which occur in wildlife populations may be progenitors of some human pandemic strains. Examples include:

Influenza A viruses, isolated from feral and domestic ducks, terns, gulls, shearwaters (Procellariidae), guillemots (Alcidae) and from a variety of cage birds from India and S.E. Asia. Also viral antibodies, indicating previous infections, have been found in the blood of many species of migratory birds. These influenza viruses in free-ranging birds have been suggested as the source of viruses responsible for outbreaks of disease in domestic livestock. It is apparent that diverse influenza A viruses circulate in waterfowl outside their breeding areas and along their migratory routes.

Fowl plague is a good example of a highly pathogenic member of the myxoviruses. The disease spreads rapidly in poultry and results in a high mortality. 'Fowl Pest' is the term used to embrace both this condition and Newcastle disease.

Newcastle disease, caused by a world-wide multistrain paramyxovirus, is one of the most serious diseases of the domestic fowl. The disease also occurs in representatives of most orders of birds. The various strains affect the central nervous system, the respiratory tract and the digestive system. Acute, chronic and symptomless forms of the disease occur. One major outbreak in the USA, which resulted in the deaths of millions of birds, was traced back to the importation of psittacine birds.

Quail disease. Several enzootic diseases occur in quail and there is sometimes confusion over what is meant by quail disease. *Quail bronchitis*, a fatal disease due to an adenovirus, occurs in the Bobwhite on game farms. The main lesions are confined to the respiratory tract. A more widespread and serious disease is *Ulcerative enteritis of quail*, also called quail disease, a bacterial disease caused by *Clostridium colinum*, which attacks many species of quail as well as, amongst other species, Ruffed Grouse *Bonasa umbellus*, Grey Partridge *Perdix perdix*, Pheasant *Phasianus colchicus*, and young domestic chicken and turkey poults. There may be 100% mortality in some outbreaks. At autopsy there is usually a severe haemorrhagic enteritis, sometimes with extensive ulceration of the gut lining.

Puffinosis. This is a viral disease affecting seabirds. First described in Manx Shearwaters *Puffinus puffinus*, it produces lesions on the webs and sometimes the eyes in these birds as well as in several species of gulls and in the Oystercatcher *Haematopus ostralegus* and Fulmar *Fulmarus glacialis.* There is evidence that the virus persists in Trombiculid mites.

Protozoal infections. Many protozoa parasitize birds, but few of them are pathogenic. They are to be found in many tissues of the body. Genera of the suborder Haemosporina are important pathogens, e.g. *Plasmodium* spp. which cause avian as well as human malaria, the parasites being transmitted by mosquitoes and undergoing complicated life cycles, the details of which differ in man and birds. The parasitized erythrocytes (red cells) break down at intervals, causing the symptoms and producing anaemia. *Plasmodium gallinaceum* produces a high mortality in domestic fowls. It is believed that the junglefowl is its natural host.

Blood parasites of the genus *Haemoproteus*, transmitted by louse-flies (Hippoboscidae) and midges (Ceratopogonidae), are common in many species of birds and occasionally cause disease. *Leucocytozoon* spp. occur in the white blood cells of birds as well as in the red cells. They are common in wild birds and also cause disease in many species of domestic birds. Leucocytozoon species are transmitted by blackflies *Simulium*. *Besnoitia* spp., sporozoan parasites, cause outbreaks of disease in Knots *Calidris canutus*, and probably other birds, with death following injury to blood vessels of the intestines.

Lankesterellosis is caused by *Lankesterella* spp. which parasitize lymphocytes and monocytes of birds. They are transmitted chiefly by mites.

Parasites of the order Eucoccidiorida, which includes the coccidia, are of importance in domestic poultry. They are responsible for the disease *Coccidiosis*. The infective oocyst is ingested by a bird and a multiplication cycle then occurs in the parasitized tissue, which is usually the intestine. Serious damage to the gut cells results in disease and death. See also ENDOPARASITE and ECTOPARASITE.

Non-infectious conditions: examples include:

Amyloidosis. A disease with multiple causes seen in a wide variety of birds principally in zoological gardens. Most susceptible of all are some species of waterfowl, but many wading birds, which do not adapt well to an artificial environment, such as Common Snipe *Gallinago gallinago*, sandpiper spp. (Scolopacidae) and Oystercatcher, may also have a high incidence. Amyloidosis is often associated also with chronic diseases like tuberculosis and aspergillosis. It is recognized by the deposition of amyloid material in tissues such as the liver and spleen and consequent malfunctioning of these organs.

Deficiency diseases. Lack or imbalance of amino-acids, proteins, carbohydrates, fats, minerals, water, and vitamins may lead to disease and death. Common signs of a deficiency disease include retarded or stunted growth, poor feathering, certain bone conditions and poor reproduction. Much is known of this group of diseases in domestic birds but little of the nutritional requirements of wild birds in nature. Young Mallard *Anas platyrhynchos* are sometimes affected with a disease characterized by lack of head feathers, and this appears to be due to a deficiency of vitamins of the B complex. Deficiencies of thiamine (Vitamin B_1) have been recognized in several species of captive raptors and lack of Vitamin A together with mineral insufficiency may also occur in these birds if they are fed an all-meat diet. Vitamin D_3 deficiency resulting in rickets occurs in captive birds deprived of adequate sunlight and on diets supplemented by Vitamin D only. Bone abnormalities occur in the Cape Vulture *Gyps coprotheres* due to lack of calcium in the diet when there is a shortage of carrion; this may be a factor in the decline of the species in South Africa.

Gout. A metabolic disorder characterized by the deposition of uric acid and urates in the tissues of the body. The disease is caused by an impaired blood clearance of uric acid due to kidney disease or metabolic dysfunction. It probably occurs in all birds but is most often seen in domestic poultry and aviary-kept falcons, eagles, hawks and owls. It appears to be uncommon in free-living wild birds.

Disorders of the female reproductive system. These are not uncommon, and cause considerable economic loss in the domestic poultry industry. One survey indicated an incidence of 8.9% in 88 species of 6 orders of birds. The most frequent abnormality is obstruction of the oviduct and ectopic ovulation.

Disorders of the cardiovascular system. Spontaneous arterial disease is seen in aviary kept birds and also occurs in free-living wild birds, but its real incidence is unknown. The frequency of occurrence of vascular degenerative disease varies amongst the different avian orders; arteriosclerosis, atherosclerosis, arteritis, arteriopathy, aneurysms and amyloidosis have all been described.

Tumours. Neoplasms (malignant new growths) are common in birds, and may arise from any organ or tissue. Some of them are of viral origin, and in domestic poultry an intensive study has been made of their properties and characters. One viral-induced tumour is a squamous cell papilloma which appears to be specific for Chaffinches *Fringilla coelebs*. It results in warty growths on the legs and claws. The Budgerigar *Melopsittacus undulatus* is particularly susceptible to neoplasia and incidences as high as 24.2% have been recorded.

Poisons. Many poisonous substances cause disease in birds. Some are biological toxins such as *Clos. botulinum* toxin (see above). Another is saxitoxin, produced by dinoflagellates. Saxitoxin causes paralytic 'shellfish poisoning', the outbreaks being associated with 'water-bloom' or a RED TIDE. Under certain suitable conditions there may be an over-production of flagellates and ciliates in the sea, some of which produce a potent neurotoxin which is picked up by filter-feeding molluscs and by sand eels *Ammodytes* spp. Saxitoxin is thus accumulated during the development of food chains and when cockles *Cardium*, mussels *Mytilus*, sand eels, scallops *Pecten* or queens *Chlamys* are eaten by man or birds, poisoning ensues. Terns, Shag *Phalacrocorax aristotelis* and Eider *Somateria mollissima* are the most commonly affected birds. There are differences in susceptibility to saxitoxin between the various avian species.

Chemical poisons affecting birds include the metals lead and mercury, many insecticides, herbicides and pesticides. *Lead poisoning* is a common and serious disease chiefly seen in waterfowl, usually resulting from the ingestion of lead pellets or lead fishing weights. Lead is a cumulative poison and is slowly absorbed from the tissues. Mortality due to lead on some migration routes and in areas which have been shot over for many years may be high; in some localities it is estimated to be from 5–10% of wildfowl using the area. The chief signs are loss of weight, lethargy and, in the later stages, muscle paralysis. *Mercury poisoning* usually results from the ingestion of seeds dressed with fungicides and from contamination of rivers and estuaries with effluents containing the metal. Mercury is another cumulative poison and may be present in many organisms. High levels may develop in seed- and fish-eating birds and in their predators with fatal results.

Pesticides may have serious and long-lasting effects on birds, species at the end of food chains being the most susceptible. The pesticides of greatest significance appear to be the organochlorine compounds, DDT and its analogues aldrin, dieldrin, heptachlor and heptachlor epoxide. The reported effects of these compounds include paralysis, delayed breeding, infertile eggs, reduced eggshell thickness and adult and embryonic mortality. A.R.J.

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DISPERSAL: term used in general sense to describe non-breeding movements of birds away from areas of high density. So, for example, departure on a daily or seasonal basis from a roost or breeding colony to visit feeding sites may be referred to as dispersal.

More particularly, the term describes the movement of an individual from its birthplace to a breeding locality or between a series of breeding localities, and may be divided into two categories. Natal dispersal is the movement an animal makes from its site or group of birth to the site or group where it reproduces or would have reproduced if it had survived and found a mate. This can be distinguished from breeding dispersal, which is the movement of an animal, which has reproduced, between successive breeding groups or sites. When successful reproduction follows dispersal the movement can be described as effective. To facilitate comparisons between species, dispersal should be measured in terms of the spatial dispersion of individuals within a species and not in terms of distance.

Species differences. Some species show high levels of dispersal within all age groups. They are usually referred to as nomadic (see MIGRATION; NOMADISM). Examples include seed-eaters (e.g. Crossbill *Loxia curvirostra*, Nutcracker *Nucifraga caryocatactes*) and rodent predators (e.g. Snowy Owl *Nyctea scandiaca*, Rough-legged Buzzard *Buteo lagopus*) of Arctic regions which are subject to periodic fluctuations in their food supply. Species which inhabit arid areas with unpredictable rainfall (e.g. honeyeaters in Australia) may also have periods of nomadism, settling to breed where the food supply becomes locally abundant. Birds of this type frequently undergo periodic irruptions to areas outside their normal breeding range (see IRRUPTION).

Many species of birds exhibit relatively low levels of natal and breeding dispersal and the distributions are heavily skewed towards the point of origin. Examples range from the colonially breeding albatrosses (Diomedeidae), gulls and terns to numerous passerines such as the Great Tit *Parus major*, Pied Flycatcher *Ficedula hypoleuca* and Song Sparrow *Zonotrichia melodia*. Such species can be described as philopatric.

Age differences. Although many species are philopatric, only a proportion of individuals of any species is faithful to one locality. Almost invariably natal dispersal is much more widespread than breeding dispersal. Thus juvenile Great Tits, on average, move 4–7 territory widths from birth to breeding site whereas adults return to within one territory's width of their previous breeding site (Greenwood *et al* 1979). This age difference in dispersal is shown by many other species. There may also be a tendency for breeding birds to become more philopatric with age. Such site tenacity is usually assumed to have arisen from the advantages which individuals may gain from increasing familiarity with an area (e.g. locations of feeding sites and predators).

Sex differences. Sex differences in dispersal occur in a taxonomically wide range of philopatric species. Female-biased dispersal has been reported in the majority for both natal and breeding dispersal (see Table). Thus, amongst adult Pied Flycatchers in a Scandinavian population, 93% of males but only 37% of females returned each year to their first nesting locality: 61% of females nested in a different place each year (von Haartman 1949). Striking examples of sex differences in natal dispersal occur in certain species of communal breeders (e.g. babblers *Turdoides* spp., Florida Scrub Jay *Aphelocoma coerulescens*). Male jays normally remain within their territory of birth throughout life whereas the majority of females breed elsewhere. Female-biased dispersal occurs in species where males defend resources (e.g. territory) in order to attract females. Exceptions to this prevalent pattern of female-biased dispersal occur in one family, the Anatidae. For example, in the Lesser Snow Goose *Anser caerulescens* males return to the females' natal colony to breed. Male-biased dispersal occurs in species where males are primarily concerned with guarding and defending their mates and not resources (Greenwood 1980) (see MATING SYSTEM).

PREDOMINANT DISPERSING SEX

	NATAL			BREEDING		
	Male	Female	Both	Male	Female	Both
Species	3	21	6	3	25	1
Families	1	11	5	1	14	1

Table of sex differences in natal and breeding dispersal of birds. The number of species and families of birds with female biased and male biased dispersal and those in which males and females disperse equally. The data are from a wide range of passerine and non-passerine groups (from Greenwood 1980).

Causes. There are a number of factors which cause dispersal. Marked changes in the distribution of food resources accentuate dispersal. In more stable habitats, population density is a major influence on dispersal. Some individuals may be prevented from breeding in their natal area and forced to disperse. They are often the socially subordinate, younger and weaker members of the population. In the Song Sparrow the dispersal of juveniles is probably a consequence of many of the adults re-establishing their old territories. Subordinate birds are excluded from optimal breeding habitats in the Red Grouse *Lagopus lagopus*, whilst in several species of passerines offspring from second broods may disperse further than those from first broods.

Density and aggressive interactions mediated through density are not the only factors to influence dispersal. In many cases birds, particularly adult females, will change to a new nesting site following an unsuccessful breeding attempt. Amongst juveniles of species which are highly philopatric, those which select a breeding locality too near to their birthplace may increase the chance of mating with a close relative. It is known from a number of laboratory studies that the reproductive success of individuals which inbreed is lower than that of animals which mate with a non-relative. In natural populations, close inbreeding has been reported in the Great Tit, Yellow-eyed Penguin *Megadyptes antipodes*, Song Sparrow and Acorn Woodpecker *Melanerpes formicivorus*. In the one study where it was possible to measure the reproductive costs of inbreeding, nestling mortality of Great Tits was nearly twice as high among inbreeding pairs as among outbreeding pairs. The sex difference in natal dispersal close to the birth site in sedentary species may have evolved as a means of minimizing the chances of mating with a close relative and thereby avoiding the detrimental effects of inbreeding.

Consequences. Dispersal can have substantial effects on the genetic structure of populations. Since dispersal is a prerequisite for gene flow, widespread movement may disrupt local adaptations. Limited dispersal or philopatry may lead to the genetic differentiation of neighbouring groups. Genetic differences between neighbouring populations of the White-crowned Sparrow *Zonotrichia leucophrys* are associated with differences in song. The dialects may act as a barrier to movement between the two groups (Baker and Mewaldt 1978) (see VOCALIZATION). Philopatry of individuals to their natal group or area also provides conditions which facilitate the evolution of cooperation between close relatives. For example, in some communal breeders, e.g. Florida Scrub Jay, young males help their parents to rear offspring in the territory of their birth. Eventually they may secure a territory adjacent to the parental one or inherit the natal site on the death of their father. Male philopatry is clearly correlated with the evolution of this type of patrilineal social organization (Greenwood 1980). P.J.G.

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DISPERSION: the state of spatial separation between individuals of a flock, colony, or population. Dispersion changes in time due to the processes of DISPERSAL from which term it should be distinguished (see AGGRESSION; ECOLOGY; FLOCKING; TERRITORY).

DISPLACEMENT ACTIVITY: term describing movements which appear to the observer to be out of context or to occur in a situation in which they seem irrelevant. Thus a gull in a dispute with a territorial neighbour may suddenly start to pull at grass, a component of nest building behaviour. In a similar situation, fighting Red Burmese Junglefowl *Gallus gallus* frequently peck at food on the ground without ingesting it, while a Chaffinch *Fringilla coelebs* mobbing an owl will often wipe its beak on a perch in an apparently irrelevant grooming movement. Much has been written about why behaviour patterns occur out of context but it is important to realize that labelling such an occurrence as a displacement activity is in no way an explanation: it simply indicates a phenomenon that has to be explained (Tinbergen 1952). It is because it explains nothing that the term has tended to fall from use in recent years.

The most commonly proposed theory for the causation of displacement activities is that they occur when the animal is thwarted or in a state of motivational conflict. Unable to perform the behaviour pattern or patterns of highest priority, the animal carries out an alternative, less relevant, behaviour. Conflict was originally seen as between drives or instincts, the dammed up energy from which was thought to 'spark-over' and activate another system (Tinbergen). Thus a fighting bird in a conflict between aggression and escape might suddenly show grooming behaviour without any stimuli appropriate to grooming being present. This view has been modified by subsequent research. Because behaviour (see BEHAVIOUR, HISTORY OF) cannot be thought of as caused by discrete and easily separated drives, it has become more usual to refer to conflict as being between tendencies or between motor patterns which are incompatible. Displacement activities have also been found to be affected by stimuli relevant to themselves: for example, a bird in a conflict situation will show more grooming if its plumage is wet (C.H.F. Rowell). Rather than being motivated by one of the conflicting systems, it has been proposed that displacement activities occur because of a phenomenon known as disinhibition: when the conflicting tendencies suppress one another this removes their inhibition on other activities so that the behaviour next in priority is able to appear (McFarland 1966).

Although still influential and attractive (Baerends 1975), the conflict theory for the causation of displacement activities is open to the objection that it could too easily explain anything. It is easy to postulate conflicting tendencies, but not easy to measure or observe them; furthermore, in cases where displacement activities have become ritualized as displays (see below) it can be argued that the original conflict may no longer exist, making the idea even more difficult to disprove. In any case, given the heterogeneous nature of displacement activities, it is essential that alternative possibilities are borne in mind. One of these is that the preceding behaviour pattern may cause the displacement activity directly: for example, an energetic display may lead to dishevelment of the plumage and thus to grooming. Alternatively, the posture of the bird may be such as to bring it into contact with the appropriate external stimulus for the activity so that it is elicited in the normal manner even though apparently out of context. Beak-wiping as a bird turns round on a perch may be an example of this, in which case it is not necessary to propose that it occurs because approach and avoidance are in equilibrium.

Words such as 'brief', 'incomplete', 'hurried' or 'frantic' are often applied to displacement activities. These suggest that, even though stimuli for that behaviour pattern may be present, the performance is not having its usual function. Where conflict is involved, this may be because the conflict is resolved rapidly and inhibition on the displacement activity is re-established before its usual goal is achieved. It has, however, been suggested that displacement activities may have important functions additional to those normally served by the same behaviour patterns performed in context. Lowering of arousal, the achievement of a shift in motivation and the reduction in alarm of a fighting bird are three possible effects for which there is some evidence. Thus displacement activities may, in some circumstances, have motivational effects which are beneficial to the animal showing them.

Whatever their original causation and function, there is no doubt that displacement activities have been a rich source of movements which have subsequently evolved into social signals (see DISPLAY; RITUALIZATION). In courtship behaviour striking examples are the preening of an enlarged wing feather by male Mandarin Ducks *Aix galericulata* and the beak wiping of male estrildine finches which is, in some species, reduced to little more than a nod as they approach the female. Ritualization has led such behaviour patterns to become highly stereotyped and clearly recognizable as signals. In the process, they have lost their original functions: signals derived from preening movements have, for example, no further use in feather maintenance. Analysis of the contexts in which these displays occur suggests that the messages they signal often indicate ambivalence: this may be taken as evidence for an underlying conflict or, more simply and descriptively, as indicating that the animal may do one of two things (e.g. escape or attack) depending on the response shown by its partner. P.J.B.S.

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DISPLAY: term denoting movements that have become specialized in the course of evolution to serve as 'signals' in social communication. Although it is usually restricted to visual signals, many primarily visual signals are associated with characteristic calls; and visual and auditory signals may both have a display function. The discussion here is primarily concerned with visual signals.

Functional aspects. Display movements can be roughly classified according to the context in which they appear.

Fulmars *Fulmarus glacialis* displaying. Note distension of neck of left-hand bird. (*Photo: B. Zonfrillo*).

Threat. These movements are used in encounters with rivals, and indicate the potential aggressiveness of the displaying individual. They can be seen as signals used in negotiation between rivals. Two common types are the 'head forward', in which the body is horizontal and directed towards the rival, and the 'head up', where the bill is pointed upwards and the breast directed towards the opponent. Some species have a repertoire of several different threat postures.

Submissive. These are used between rivals or mates and serve to reduce the aggressiveness of the bird to which the display is directed. Amongst passerines a common submissive posture consists of perching slightly crouched, with the head withdrawn and the body feathers raised. Thus a subordinate bird in a dominance hierarchy will display in this way to a superior, and a receptive female may adopt such a posture at pair formation (see DOMINANCE (2); PAIR FORMATION).

Begging. These are used primarily by juveniles begging for food from their parents, and also in COURTSHIP FEEDING.

Sexual. These are used between mates or potential mates; they serve a variety of functions such as pair formation, maintenance of the pair-bond, reduction of mutual aggressiveness, synchronization of reproductive rhythms, and facilitation of COPULATION.

Greeting and nest-relief. This category overlaps the two previous ones. It

Grey-headed Albatrosses *Diomedea chrysostoma* courtship display. (*Photo: British Antarctic Survey*).

consists of displays given when two individuals meet after a temporary separation, and thus occurs in the contexts of parent/young and male/female relations. These displays probably function in reducing aggression.

Social. These are without obvious sexual or aggressive significance, and are important, for instance, in flock integration (see FLOCKING).

Anti-predator. This includes a number of displays given to predators—for instance, the 'mobbing' displays given by passerines and others to predators, and distraction displays (see DISTRACTION BEHAVIOUR).

Such a classification according to content is useful for many purposes. However, it is important to note that many displays occur in more than one context. In such cases it is useful to distinguish between the 'message', or features of the sender common to all the situations in which the display is given, and the 'meaning', which includes contextual factors that also contribute to the response of the recipient. Thus tyrannid flycatchers have a 'locomotory hesitance vocalization' given in a number of situations in which locomotion is inhibited, but the response of the recipient varies with the nature of the caller (e.g. juvenile, intruding male, etc.) and the context (e.g. position in territory) (Smith 1977).

Although displays function as social signals, this does not necessarily imply an immediate response by the partner. Thus the importance of submissive and greeting displays lies not so much in evoking a response as in inhibiting the aggressiveness of the partner. Further, many courtship displays occur at intervals during periods of maintenance activities, and although they may have long-term stimulatory or pacificatory effects they often seem to produce no immediate changes in the situation.

Smew *Mergus albellus* male and female (on left) courtship display. (*Photo: Y. Shibnev*).

Causation. In nearly all cases that have been analyzed, display movements are associated with tendencies to behave in incompatible ways and are then spoken of as involving an internal 'conflict' between the two or more types of behaviour. In some cases it is profitable to regard the conflict as concerned with incompatible patterns of behaviour: for instance the tail-flicks of many passerine birds occur in situations in which causal factors for flight and for staying put are both present. In other cases there is evidence that the conflict involves higher level 'tendencies'. With aggressive displays, tendencies to attack and flee from the rival are involved. In courtship display, a sexual tendency is involved in addition—although the meaning of 'sexual' here is to be interpreted rather broadly, as many courtship displays are only distantly related to copulation—and sometimes also tendencies to nest-build, preen, etc. In mobbing, the tendencies are to investigate, to attack, and to flee; and in distraction display, conflicting tendencies to show parental behaviour, to attack, and to flee may be involved.

When any one of these tendencies is present alone, the behaviour is simple—e.g. pure attack, escape, or sexual behaviour may be shown. When two or more incompatible tendencies are present, various types of ambivalent behaviour may occur (see AMBIVALENCE), and some instances of this have been specialized in evolution for a communicatory function and thus may be designated as displays. Most species have a large repertoire of display movements, and each is associated with a particular range of strengths and relative strengths of the conflicting tendencies. Thus, where there are several threat postures, each is associated with different values of attacking and fleeing tendencies. Similarly, as the absolute and relative values of the male's tendencies to attack, to flee from, and to behave sexually towards the female change throughout the reproductive season, there are correlated changes in the courtship displays. Often particular components of a display (e.g. crouching, wing raising) are associated primarily with one of the conflicting tendencies; the nature of the display then indicates the motivation. Thus, although the displays of any one species usually fall into a number of fairly distinct types, each type shows considerable variability and there may be intermediates between them.

There are some exceptions to this general rule that display movements are associated with conflicting tendencies. Thus the various components of the soliciting posture of most female passerines all fluctuate together; although the female may change over suddenly from soliciting to aggressive or fleeing behaviour, it may be that the posture itself is purely sexual. Similarly, although the begging displays of young birds may contain aggressive or fleeing components, these may not be essential to the display.

Ontogeny. Display movements characteristic of the species normally appear in individuals on the first occasion that the relevant circumstances arise. Furthermore, the response to display movements made by other individuals is also usually appropriate on the first occasion it arises (see BEHAVIOUR, DEVELOPMENT OF).

Evolution. Display movements are usually characteristic of the species, and are more similar in closely related species than in distantly related ones. The comparative study of display can thus provide evidence about phylogenetic relationships between species. Alternatively, by comparing the displays of species of known phylogenetic relationship, it is possible to form hypotheses about the evolution of the displays.

So far, three evolutionary sources of display movements have been recognized—intention movements (e.g. intention movements of attack, escape, nest building, etc.); displacement activities (used here in the sense of a heterogeneous category of activities appearing in contexts in which they appear to be functionally irrelevant); and redirection activities (see DISPLACEMENT ACTIVITY; REDIRECTION). In addition, displays of one type may be evolved from displays originally used in another context—e.g. courtship feeding from parent/juvenile behaviour, or sexual from aggressive behaviour. In evolution the display movements have been ritualized—i.e. they have become more adapted for a signal function. The changes involved in RITUALIZATION have resulted in the movement becoming more conspicuous and more different from other signal movements of the same species and from signal movements of other species. They consist in:

(*a*) Changes in the form of the movement itself (e.g. changes in the intensity or co-ordination of the components).

(*b*) Changes in the relations between the associated internal and external causal factors and the movement; important here is the development of 'typical intensity', whereby a movement of constant form is given over a wider range of causal factors than that

Little Egret *Egretta garzetta* defensive display. (*Photo: E.J. Hosking*).

which evoked it initially. In this way variability of the movement is reduced and it becomes more efficient as a signal.

(*c*) The development of conspicuous structures that are shown off by the display movement. Since homologous movements in related species often show off different structures, it would seem that the movements must be evolved first and the structures later; but there has undoubtedly been much interaction.

(*d*) Recombination of single displays into various rigid sequences.

In general, the threat and anti-predator displays of related species are more similar than are the courtship displays; and the early courtship displays, functioning in pair formation, diverge more than those used in copulation. This is to be expected on the view that the early pair-forming displays are important in promoting reproductive isolation. There may even be some selective advantage in similarity of the aggressive and anti-predator displays to those of related species. The degree of differentiation between the courtship displays of closely related species renders these displays useful as taxonomic characters, and they have been so used with effect in a number of groups (e.g. Anatidae).

It is not possible here to attempt any description of the variety of display types to be found amongst birds. Often the displays are extremely elaborate—as in the manakins, bowerbirds, or birds-of-paradise, or in those sexually monomorphic species that have intricate reciprocal ceremonies between the mates (e.g. Great Crested Grebe *Podiceps cristatus*)—see articles on the groups named. To what extent the principles discussed in the preceding paragraphs, which have been derived from the study of relatively simple cases, can be applied to these highly ritualized and elaborate cases remains to be seen. R.A.H.

See photos AGGRESSION; COPULATION; LEK.

Cactus Wrens *Campylorhynchus brunneicapillus* courtship display. (*Photo: R. Pop*).

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DISTAL: furthest from the centre of the body or from the point of attachment (e.g. of a limb); opposite of PROXIMAL.

DISTRACTION BEHAVIOUR: general term for those active parental anti-predator strategies which aim to deflect a predator or to divert its attention from eggs or young. The terminology of the behaviour is still confused, but attempts to establish elaborate classifications and to substitute synonyms for long-accepted names have not been generally welcomed.

Distraction behaviour includes: (1) stratagems in the form of distraction–lure displays etc; (2) distraction-threats; (3) demonstration; and (4) diverting attacks. They reach their most developed form in ground-nesting birds such as waders (Charadrii). In distraction displays a parent bird presents stimuli to the predator that elicit and direct its prey-seizing responses (distraction-lure display) or alarm it (distraction-threat display). Though the two have been confused, and do intergrade in some species, the functional distinction is clear, the one aiming to induce approach, the other withdrawal. Such displays are species-characteristic in form and type, and are often highly ritualized.

1. Distraction-lure displays and other stratagems are often accompanied by calls serving to attract attention and function as 'tricks' or 'ruses' for deceiving the predator, especially ground predators hunting opportunistically by sight. In addition to a crouching run away from the predator, distraction-lure displays comprise (a) the small-mammal type ('rodent-run', 'rat-trick') in which the resemblance to a scurrying beast may be most realistic, including squealing cries, and (b) the disablement or incapacity type ('injury-feigning', 'broken-wing trick', 'exhausted-bird posture') in which the bird appears to be vulnerable in some way, even acting as if mortally wounded or like a helpless chick; the small-mammal type and the mobile forms of the disablement type are typically performed as the bird retreats from the predator, the stationary forms of the disablement type often with the back to it, though some species may turn and face it at a safe distance. In waders, distraction-lure displays are most likely to occur when the young are most vulnerable: at hatching or when seized by a predator (especially if the young call). Other stratagems of waders include the 'fly-away trick'; ground-pecking (mock or real feeding or the picking up of nest material); mock or real side-throwing of small stones and other 'busy-bird ruses'; pseudo-sleeping; mock-brooding; decoy-brooding; and distraction flights. Special flights round or away from the predator—often in the form of 'impeded-flight' with slow or flicking wing-beats—may serve to draw attention to the bird and its subsequent behaviour on the ground.

New Zealand Dotterel *Charadrius obscurus* distracting predator from nest. (*Photo: G. Moon*).

2. **Distraction-threat displays** involve the spreading of the wings, tail or both in a bold, alarming fashion, sometimes suddenly in a 'flash-' or 'shock-display'. In waders and some other ground-nesting birds, distraction-threat displays may be performed while advancing towards the predator as closely as the bird dares, or from a stationary defensive position over eggs or young, and may lead to attack or to distraction-lure display.

3. **Demonstration** consists of loud and persistent calling from a perch, on the ground, or in the air. The bird often makes itself conspicuous, especially in flight as it 'scolds' the predator while circling; it may also approach aggressively on the ground or more usually in the case of large birds, e.g. Oystercatcher *Haematopus ostralegus*, Avocet *Recurvirostra avosetta*, in mock attack-flight, the bird typically swerving off without striking. Demonstration is akin to MOBBING, especially when performed by 2 or more birds together (see also DISPLAY).

4. **Diverting attacks** tend to follow demonstration, e.g. at the climax of attack-flights, the bird striking the predator with wings, legs or bill. Such an attack may develop in other situations, e.g. from nest-protecting display, the bird fluttering into the face of the predator or pecking it.

See photo HEAT REGULATION. K.E.L.S.

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DISTRACTION DISPLAY: see DISTRACTION BEHAVIOUR; PARENTAL CARE.

DISTRESS CALLS: loud vocalizations emitted by birds when caught by a predator, a mist-net, or held in the hand. The calls have a harsh, tonal quality and contain a wide range of frequencies. They thus differ from alarm calls given when a predator is merely sighted. Their function may be to startle the predator into releasing his prey. Some distress calls attract conspecifics who mob the predator, but others have the opposite effect and have been broadcast in an attempt to disperse unwanted flocks of birds.

DISTRIBUTION, FREQUENCY: see BIOSTATISTICS.

DISTRIBUTION, GEOGRAPHICAL: the distribution of species or other categories considered in broad terms of range. Since local abundance and local distribution within the limits of the range depend on ecological factors (see ECOLOGY), the range may be limited by the same factors, such as climate or its effect on habitats, habitat availability, or presence of competitors, predators, or prey. Ecology and ZOOGEOGRAPHY thus have broadly overlapping interests. The range boundaries may, however, also be set by evolutionary history, plate tectonics (continental drift), effective dispersal barriers, or the different dispersal abilities of species.

Zoogeographical studies address themselves to various aspects of geographical distribution. The time scale examined may vary from a static 'snap-shot' view of the present distribution to millions of years, and the geographical focus of interest may range from global distribution to distribution on islands or to dynamics of a portion of the range boundary. In addition, the emphasis may be qualitative or quantitative.

In terms of scientific research and the philosophy of science, a distinction can be made between descriptive, analytic, and predictive zoogeography. The descriptive view records facts of distribution, past or present. Analytic zoogeography attempts to relate results of descriptive studies to various causes, ecological or historical. Predictive zoogeography uses theoretical, often mathematically formulated, models in order to derive predictions on patterns of geographical distribution. In recent years, analytic and predictive aspects of zoogeography have developed rapidly, and, at the same time, quantitative approaches and population biology have been increasingly used in order to understand distribution patterns.

Breeding and non-breeding ranges. The breeding range often differs from the non-breeding range because of seasonal migrations or other movements (see MIGRATION). Distribution maps normally take seasonal movements into account. Mapping breeding distributions has progressed far, and detailed range maps are now available for the breeding bird faunas of many countries. For example, the ranges of all bird species breeding in the British Isles have been mapped using a grid of 10 km squares, with several symbols indicating various degrees of certainty of breeding (see ATLAS). The non-breeding range of many temperate-zone species is in the Tropics, where bird distributions are often inadequately known.

The range of a species is usually presented in a qualitative map showing whether the species is present in an area or not. Exact breeding localities of rare species or species breeding in readily found colonies (e.g. seabirds) have also been mapped. Quantitative distribution maps are difficult to obtain because of methodological problems involved in censusing large regions. Since density may vary by several orders of magnitude within the limits of the range, quantitative maps (published, e.g., for many North American and Finnish birds) nevertheless tend to show gradients in average density correctly. Ranges are dynamic (see RANGE CHANGES). Spectacular expansions in the European avifauna include that of the Collared Dove *Streptopelia decaocto* and of the Serin *Serinus serinus*. In Northern Europe, faunistic information shows that Denmark, Norway, Sweden and Finland were colonized by an average of 2.8 species per decade and country in 1850–1970; several species, such as the Lapwing *Vanellus vanellus*, the Black-headed Gull *Larus ridibundus*, or the Scarlet Rosefinch *Carpodacus erythrinus* have expanded there dramatically. On the other hand, many ranges shrink rapidly. Examples include the abrupt decrease and finally the extinction of the once widespread and abundant Passenger Pigeon *Ectopistes migratorius* in North America in the 19th century, or the increased patchiness and contraction of the Western European ranges of the Great Bustard *Otis tarda* or the White Stork *Ciconia ciconia* in recent decades.

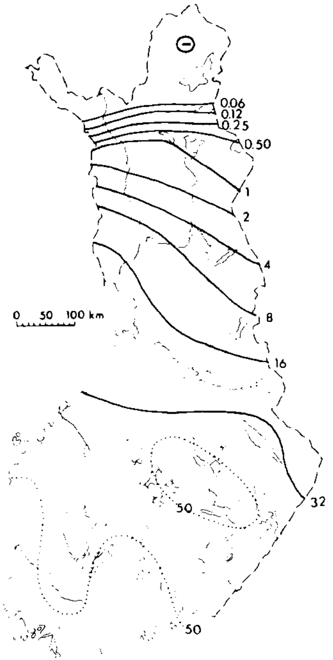
Quantitative data are helpful in understanding dynamic aspects of geographical distribution. The expansion of the Scarlet Rosefinch in Finland was rapid from the 1940s to the 1970s, and it was observed in population ecological studies that increased numbers of Scarlet Rosefinches started breeding in open bushy habitats created by man. The breeding success in this new habitat was observed to be unusually high, and quantitative estimates on the concomitant population increase—the Finnish population increased approximately 30-fold in 30 years—fitted extremely well with observations on the increased breeding success. Thus habitat changes in the Finnish breeding range of the species are a sufficient explanation for the expansion, and no changes in the poorly studied non-breeding range of the species need to be invoked. But in many species changes occurring in the non-breeding range are probably responsible for the changes that can be observed in the expansion or contraction of the breeding range, and vice versa.

Dynamic aspects are relevant also in historical zoogeography. For example, the Old World vultures (see VULTURE (1)) are presently confined to Europe, Africa and Asia, but Tertiary and Quaternary fossils are known from North America, and the place of origin of this taxon may be either the New World or the Old World. No decision can be made on the place of origin of the New World vultures (Cathartidae), either, for Eocene and Oligocene fossils have been found also in Europe, even though the family is presently strictly American.

Kinds of species boundaries. Populations on the periphery of the species range define the species boundary. Regulation of these populations may differ greatly from the regulation of central populations; for example, some peripheral populations may perish without a constant influx of immigrants, but there must also exist populations producing a surplus of emigrants. The boundary may thus fluctuate in response to events in other than peripheral populations. Abundant data show that many range expansions first involve disproportionately numerous young males, and thus the reproductive output of the population at the expanding fringe may be very low.

Species boundaries of insular endemics are well-defined. Equally obvious are many species boundaries determined by the configuration of continental land-masses, for the world oceans are major dispersal barriers for most birds. Even moderate expanses of open sea seem to act as psychological barriers to many species. For example, more than 100 of the bird species breeding on New Guinea have never been recorded on any of the islands surrounding it. European examples of species whose range boundary is partially set by avoidance of moderate sea-crossings include the Green Woodpecker *Picus viridis*, the Marsh Tit *Parus palustris*, and the Nuthatch *Sitta europaea*. Effective dispersal barriers divide continental land-masses and create species boundaries. The Saharan desert, lowland rain-forest or lowland savanna between mountainous areas in the Andes or in Africa, or the Himalayas, provide good examples.

The HABITAT requirements of species may be inflexible and give rise to clear range boundaries. For example, species of rain-forests, deserts, coniferous taiga forests, or oceans, often have their boundaries at least partially set by the availability of their habitats. But many species boundaries run through apparently suitable habitats where there are no obvious dispersal barriers. Birds of the Eastern Siberian taiga differ considerably from the avifauna of Scandinavian coniferous forests, and the distribution of many species in the seemingly uniform Amazonian rain-forest is quite restricted, to take only two examples.



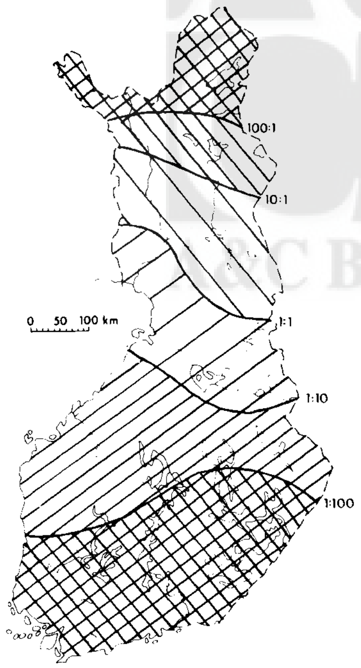


Fig. 1. (*left*) Breeding season densities of the Chaffinch *Fringilla coelebs* (pairs/km^2) in Finland, according to line transect censuses made in 1973–77. True densities are somewhat higher owing to the fact that all birds are not observed in a line transect. Since the proportion of densities at 2 successive lines is 1:2, the northward decline in densities is sharp. (After Järvinen & Väisänen 1981 Studies in Avian Biology).

Fig. 2. (*right*) Ratio of the density of the Brambling *Fringilla montifringilla* to that of the Chaffinch *F. coelebs* in Finland, according to line transect censuses made in 1973–77. The species are ecologically similar and replace each other on a south-to-north gradient. As shown in the figure, there is a 10,000-fold change in the ratio of the densities of the 2 species within about 600 km in Finland. (Redrawn from Järvinen & Väisänen 1979, Oikos).

It is sometimes stated that, in the Northern Hemisphere, northern range boundaries tend to be determined by climate, while southern boundaries are often caused by interspecific competition. But many other factors than climate or competition may be decisive. It is nevertheless true that the climate becomes harsher northwards, in the sense that the percentage of migrants tends to increase northwards, and that the effect of competition may be intensified southwards owing to the general trend that species numbers (often called diversity or preferably, species richness) become progressively higher towards the Equator.

Climatic explanations for enigmatic boundaries are usually supported by a correlation between a particular climatological variable and the range boundary. Such correlations prove nothing, unless independent data are available about the effects of that particular climatological variable on the species. For example, the northern boundary of the Goldcrest *Regulus regulus* has been correlated with a particular isotherm in the breeding season, and this is likely to be biologically meaningful, since the corresponding ambient temperature has been shown to be critical for the survival of the nestlings. Similarly, the ranges of several European species of ducks correlate well with the cold-hardiness of one-day-old ducklings. Annual fluctuations in the weather during the spring migration have a clear effect on the fluctuating species boundaries, as shown by many studies in northern Europe. Warm weather often results in an extension ('prolongation') of migration, while cold spells during migration periods result in 'abbreviation'; and the species boundary may consequently fluctuate several hundreds of kilometres from year to year. It has been suggested that climatic amelioration has, by the same mechanism, caused the northward range expansion of a number of southern species, but the expansions have often been more dramatic than expected from climatic changes. Many authors now believe that habitat changes due to man and his livestock are the major cause behind these shifts in species boundaries.

Interspecific competition is inferred to be the cause of a species boundary when two ecologically and morphologically similar species replace each other geographically. For example, the Carolina Chickadee *Parus carolinensis* and the Black-capped Chickadee *P. atricapillus* show almost completely mutually exclusive ranges in North America. A broader overlap zone is observed in other species pairs, such as the Chaffinch *Fringilla coelebs* and the Brambling *F. montifringilla* in Europe. Direct evidence on the effect of competition on such species boundaries is nevertheless meagre. Mutually exclusive ranges are not always due to competition. For example, the Corsican Nuthatch *Sitta whiteheadi* is restricted to Corsica, while the Nuthatch *S. europaea* is common on the adjacent mainland. However, the Corsican Nuthatch is confined to pine forests on mountains, and thus there are no species of *Sitta* in deciduous forest, the favoured habitat of the Nuthatch, on Corsica. Even though very little supportive evidence is available, other interspecific interactions, such as predator–prey relations or host–parasite relations, may be important in determining range boundaries.

As regards migrant birds, remarkably few studies have been devoted to the role of the non-breeding range in the determination of the range boundaries. For example, Kirtland's Warbler *Dendroica kirtlandii* only breeds in north–central Michigan, USA. This may be a consequence of the low carrying capacity of the wintering range in the Bahamas.

Historical causes have also been offered for certain distributions. Many restricted ranges in the Amazonian rainforest avifauna correspond well to Pleistocene refugia, and the present species boundaries may thus reflect events that took place thousands of years ago. Since *ad hoc* explanations based on past geological history can be used to explain practically everything, historical explanations should not be invoked lightly. This is particularly pertinent as many birds have demonstrably expanded or contracted their ranges very rapidly in response to changing geological conditions.

Major zoogeographical regions. Beginning from P.L. Sclater (1858) and A.R. Wallace (1876), bird distributions have been studied in order to divide the continental land-masses into broadly homogeneous regions.

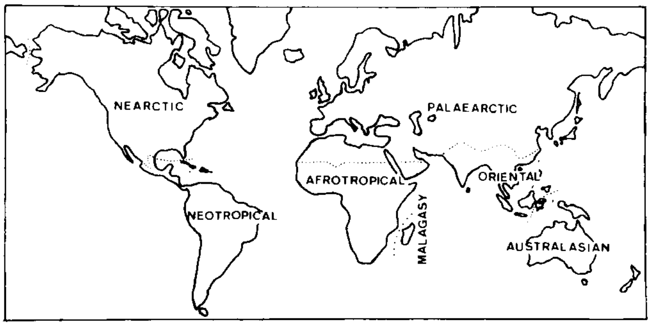


Fig. 3. The six major and one minor zoogeographical regions. Antarctica and the oceanic islands are not included in any region. Boundaries are only approximate, and in reality tend to be represented by transitional zones. Therefore, other classifications often differ in details, and some large islands (such as New Zealand and Madagascar) are classified differently. A distribution in both Nearctic and Palearctic regions is often called Holarctic, and species distributed in several tropical regions are often characterized as pantropical.

Many species have a wide range and inhabit several faunal regions, but the major zoogeographical regions remain a useful descriptive aid. It is an open question whether the avifaunas of each biogeographical region represent coadapted, ecologically more or less compactly 'packed' wholes or not. The success of many introductions and spontaneous invasions in historical time suggests that each avifauna is not a fully packed entity, though this conclusion is debatable—most species from other zoogeographical regions seem to be best established in habitats disturbed by the activities of man. The idea of the coherence of regional avifaunas can be supported by the similarity of the trophic composition of, say, various tropical avifaunas, despite great differences in their taxonomic affinities.

The continents of conventional geography do not provide a satisfactory framework in zoogeography. The avifaunas of the Old World and the New World are fundamentally different. In the Old World, Europe, North Africa north of the Sahara, and northern Asia north of the Himalayas are a fairly coherent region, called the Palearctic. Most of Africa belongs to the Afrotropical region. Tropical Asia and western Indonesia belong to the Oriental region, while the Australasian region comprises eastern Indonesia, New Guinea, Australia, Polynesia, and New Zealand. The Oriental and Australasian faunas are in balance along Weber's Line running through the Indonesian archipelago. Two large islands, Madagascar and New Zealand, are sometimes distinguished as minor regions separate from the Afrotropical and Australasian regions, respectively. As Madagascar supports a reasonably distinct avifauna, it is treated here as a minor region (see MALAGASY REGION). In the New World, North America above the tropics comprises the Nearctic region, and the rest belongs to the species-rich Neotropical region. Despite considerable differences between the avifaunas of the Nearctic and Palearctic regions, it is sometimes convenient to lump them together into the Holarctic region. This classification of the world avifaunas is useful from a pragmatic standpoint, but there are transitional areas, e.g. in Arabia, China, Indonesia, and Mexico, where the boundaries must be drawn arbitrarily. It is also necessary to take some separate account of the Antarctic continent and its neighbouring islands (see ANTARCTIC) as well as of pelagic birds (see OCEANIC BIRDS). See separate articles on the AFROTROPICAL, AUSTRALASIAN, NEARCTIC, NEOTROPICAL, ORIENTAL, and PALEARCTIC REGIONS.

The zoogeographical regions are often grouped into three realms. They are Megagea (previously Arctogea), consisting of the 'paleotropical regions' (Afrotropical, Oriental) and the 'holarctic regions' (Palearctic, Nearctic), Neogea (comprises the Neotropical region), and Notogea (comprises the Australasian region). In early literature, Notogea included both Neogea and Notogea. Other authors combine the Nearctic and Neotropical as Neogaea.

Most of the recent orders of birds are cosmopolitan, i.e. represented in all the main continental regions. Exceptions include the small orders of ratites, the Neotropical Tinamiformes, the Sphenisciformes of the southern hemisphere, the Holarctic Gaviiformes, and certain 'pantropical' orders that are absent from higher latitudes (Trogoniformes, Psittaciformes). Cosmopolitanism is less true of families, for many families are restricted either to the Old World or the New World, or in extreme cases to the minor Malagasy region or to small island groups. The insular families are the Rhynochetidae (New Caledonia), Todidae (West Indies), Drepanididae (Hawaii), and the New Zealand endemics: Apterygidae, Acanthisittidae, Callaeidae and Turnagridae.

The Oriental region shares nearly all its characteristic families with other southern parts of the Old World, but other regions have major families not found elsewhere, though the Palearctic example (Prunellidae) has a slight extension to the Oriental region. The Australasian and, in particular, Neotropical avifaunas are characterized by a great number of unique families.

At the level of genera and species, cosmopolitan distribution is rare. Cosmopolitan, or nearly so, are *Podiceps*, *Phalacrocorax*, *Ardea*, *Circus*, *Falco*, *Rallus*, *Columba*, *Caprimulgus*, *Anthus*, *Turdus*, *Corvus* and several seabird or shorebird genera. A few nonpasserine species are (nearly) cosmopolitan, such as the Osprey *Pandion haliaetus*, the Peregrine *Falco peregrinus*, the Kentish (or Snowy) Plover *Charadrius alexandrinus*, and the Barn Owl *Tyto alba*. The most widespread passerine, in terms of zoogeographical regions, is the Swallow *Hirundo rustica*.

Historical zoogeography. Present geographical distribution is the result of a most complicated process involving the evolution of a taxon and its subsequent dispersal to different regions, where further evolution may have taken place. Two different approaches may lead to quite different conclusions. First, interpretations can be based on a careful examination of the fossil record, though this is incomplete (see FOSSIL BIRDS). Second, the evidence available on continental drift may be examined in order to construct hypotheses on the origin of various taxa.

The evolution and recent distribution of the ratites may serve as an example. The ratites include the Struthioniformes of Africa, the Rheiformes of South America, the Apterygiformes of New Zealand, the Casuariiformes of New Guinea and Australia, and, in addition, the presumably related extinct orders of elephant-birds (Aepyornithiformes, Madagascar) and moas (Dinornithiformes, New Zealand). Before the continental drift separated the present southern continents, there was a huge southern supercontinent called Gondwanaland. It has been suggested that flightlessness evolved once in the ancestors of recent ratites, and the various ratite orders were derivatives from a common stock. This hypothesis, supported by, e.g., ethological data, predicts that late Cretaceous fossils of ratites exist, for South America and Africa separated from each other in that geological period. Such fossils have not been found, however. We are thus confronted with a hypothesis which is parsimonious but not supported by 'critical' fossil finds, and a hypothesis that ratites are in fact polyphyletic, the different orders having evolved long after the splitting of Gondwanaland into several continents. Flightlessness would then have evolved several times. Studies of molecular and chromosomal similarity, however, now seem to rule out the polyphyletic hypothesis. Other taxa suggested to have evolved in Gondwanaland (in predrift configurations of the continents) include the Sphenisciformes, the Galliformes, and the suboscine Passerines.

The differing dispersal abilities of various taxa give rise to special difficulties. The extremely rapid expansion of the Cattle Egret *Bubulcus ibis* (see RANGE CHANGES) shows that a nearly world-wide distribution may be attained within the ecological, in contrast to evolutionary, time scale. On the other hand, many genera or families or even orders may be confined to a particular region.

Faunal analysis has been a major approach in historical zoogeography. The fauna of a geographical region has been studied to examine its probable geographical origins; usually different faunal elements are represented. For example, the avifauna of North America can be divided into three groups: primarily South American families (such as Furnariidae or Formicariidae), Old World and primarily North American families (such as Troglodytidae, Mimidae, or Parulidae), and families with readily colonizing genera (such as Trochilidae, Tyrannidae, or Icteridae). Since most families of suboscine passerines have their distribution centres in South America, this evidence has been given as support for the Gondwanaland origin of the Suboscines. The prevalence of Suboscines in South America has been explained, on one hand, by the relative isolation of the continent, which has sheltered Suboscines from extensive Oscine competition, or, on the other hand, by arguing that Suboscines are competitively adept in their Neotropical environment, which is supported by their extreme taxonomic and morphological diversity there. Smaller regions than continents have also been analyzed to elucidate the probable origins of the fauna. Different habitats usually contain differing proportions of faunal elements, e.g. birds on European mountains frequently belong to northern elements in the fauna.

Faunal analysis may also be based on a certain ecologically defined zone or area, rather than a geographically defined one. Eurasian steppe birds, and the avifaunas of the lowland forests of Africa or of the non-forest habitats of the Andes, have been subjected to such analysis. For example, the high Andean bird fauna, rather than being closely related to forest avifaunas of South America, shows great faunistic similarity to the steppe (and other non-forest) fauna of Patagonia. In several cases, there has probably been extensive radiation after the colonization of the Andean non-forest habitats, while there has been little Andean radiation in other taxa.

Island biogeography. Since the publication of *The Theory of Island Biogeography* by MacArthur and Wilson in 1967, zoogeography has been transformed considerably. They pointed out that species numbers on many islands follow a well-defined relationship with area. In many cases, but not always, there is an approximately linear relation between the logarithms of area and numbers of species (A and S, respectively). This leads to a power-function description $S = CA^z$, where C and z are fitted constants. Of these constants, z often assumes a value between 0.2 and 0.35, implying that species numbers increase much less rapidly than area—a 10-fold increase in area gives rise to a 2-fold increase in the number of species, according to a useful rule of thumb. In many instances the power function is not the best-fitting relationship between species numbers and area.

The species–area relation has three explanations, which are not mutually exclusive. First, large samples are expected to include more species than small samples, for purely statistical reasons. This is a reasonable explanation to the extent that island bird communities can be expected to be random samples from communities on the adjacent mainland—this may be partially realistic as regards, for example, coastal islands or 'habitat islands' in regions where most birds are migrants and thus probably have little difficulty in overwater dispersal. Second, habitat diversity probably increases with island area: certain rare habitats are missing from small islands. This ought to lead to higher numbers of species on larger islands. Third, communities on islands may represent immigration–extinction equilibria.

The immigration–extinction model by MacArthur and Wilson predicts that species numbers on an island tend to be fairly constant, although species composition changes with time owing to immigrations and local extinctions. It is argued that species new to the island colonize at a rate that decreases with increasing numbers of species, because fewer potentially colonizing species are available after many species have already colonized, and the best colonists tend to arrive first. On the other hand, the rate of local extinctions, in terms of the number of species per year that disappear from the island, would increase with increasing species numbers. When there are few species on an island, they may not be competitively so harassed as species on a similar island with more species would be. Also, even if the probability of extinction were independent of species numbers, the number of actual extinctions taking place is expected to increase with the number of species. With a certain number of species on the island, the increasing extinction curve and the decreasing immigration curve intersect, and immigrations and extinctions thus balance each other.

Applying the immigration–extinction model to problems of insular bird distribution has given rise to many new insights. The major contribution has been to focus attention on ecologically meaningful and measurable problems of dispersal and extinction; the theory of island biogeography thus gives rise to predictions that are testable, and there is a major emphasis in this theory on processes leading to various distributions. Further, the view emerging on natural populations stresses dynamic patterns where chance plays a role—immigration (colonization) is certainly partially a random process, and it has also been shown conclusively that small populations have an appreciable probability of chance extinction, i.e. extinction just because deaths happen to occur before births. Accordingly, there is no reason to expect that a species will occur on all islands having suitable habitats, but some islands, depending on the colonization and extinction probabilities of the populations, can be expected to lack the species in question. It can also be expected that small islands have fewer species than large ones (the species–area relation), because the extinction rate on small islands is probably higher than on large islands, owing to the smaller average population size. Also, distant islands are expected to have an impoverished fauna because of lower immigration rates to isolated islands.

Despite its logical simplicity, the theory of island biogeography has been criticized for its lack of realism. The species–area relation has often been interpreted in terms of immigration–extinction equilibria, even if other alternatives have not been excluded. Estimates of immigration and extinction on islands have also been questioned. In our modern world, many estimates are affected by the activities of man on islands, and there are also problems in defining what constitutes an immigration or an extinction—despite their diurnal habits, many birds are elusive, and it is quite difficult to establish definitively whether a breeding population exists on an island or not. Immigration and extinction rates also fluctuate with time—e.g., climatically exceptional 'key years' may account for most of the immigrations to and/or extinctions on an island.

The role of competition in shaping insular communities is controversial. According to one view, low species numbers on islands result in 'competitive release', i.e. the absence of close competitors makes it possible for a species to have higher densities and utilize a broader range of habitats. There are many examples of this phenomenon: insular populations do tend to have higher average densities than on the adjacent mainland, and habitat use is often but by no means always broader than on the mainland. Another view emphasizes alternative explanations, such as habitat differences between islands and the mainland. Further, competitive release is not an easily understood phenomenon anyway, as theoretical models show that, under various conditions, the absence of competitors may give rise to lower, equal, or higher average densities on islands. Therefore, more direct evidence of competition is necessary.

Two other problems of insular distribution are also controversial. First, the absence of a species from a small island may or may not be a result of certain minimum-area requirements. A species may indeed need large tracts of uniform habitat, but, according to another view, a small mainland area would also lack many species merely by chance. Second, it is debatable whether interspecific competition 'forbids' certain species combinations or not. It would be expected by chance that certain species combinations do not occur on real islands in a certain archipelago just because one or several of the species are rare. On the other hand, if a combination of two or three ecologically closely related species never coexist, it is attractive to attribute this to interspecific competition. This is especially so because of the difficulty of conducting experiments with natural populations of birds. But difficulties in making experiments ought not to imply lack of understanding.

Minimum area requirements of a species have been analyzed with so-called 'incidence functions'. They show the percentage of islands in a certain size class that are inhabited by the species; incidence on small islands is frequently low compared with large islands. This approach omits reference to species densities, partially because densities of tropical species are difficult to census. If censuses are possible, an alternative is to construct 'prevalence functions'. They show the average density of the species on islands in a certain size class, as compared with average density on the mainland. Prevalence functions thus include more information than incidence functions, but both are directed towards understanding the colonization 'strategies' of birds. This problem has deep implications for nature conservation, for human activities tend to make natural habitats more patchy and therefore less suitable for species requiring wide expanses of homogeneous habitat.

Various processes operating in insular communities cause profound differences between islands and the adjacent mainland as regards their avifaunas. Coastal islands tend to be similar to mainland communities, though there may be habitat differences that give rise to differences in the species lists. More isolated islands often support endemic taxa not found elsewhere (e.g. Geospizinae on Galápagos), and oceanic islands are therefore not typical representatives of their geographical regions. Particularly good examples of islands supporting fairly unique avifaunas are Sulawesi, New Caledonia, the Hawaiian Islands, the Galápagos Islands, and some Atlantic islands, such as Tristan da Cunha, where there are five independently descended species of land birds. O.J.J.

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DISTRIBUTORS: see SEED DISPERSAL.

DIUCON: substantive name of *Pyrope pyrope*, a tyrant-flycatcher of southern South America (see FLYCATCHER (2)).

DIVER: substantive name of all species of the Gaviidae (Gaviiformes); alternatively 'loon' (generally used in North America), and in the plural general term for the family. (For the question of scientific nomenclature see under COLYMBIDAE.) The family consists of a single genus, *Gavia*. The relation to other genera is uncertain, the relation to the Podicipediformes being more distant than formerly suggested, and the assumed relation to the Laridae and Alcidae still being tentative.

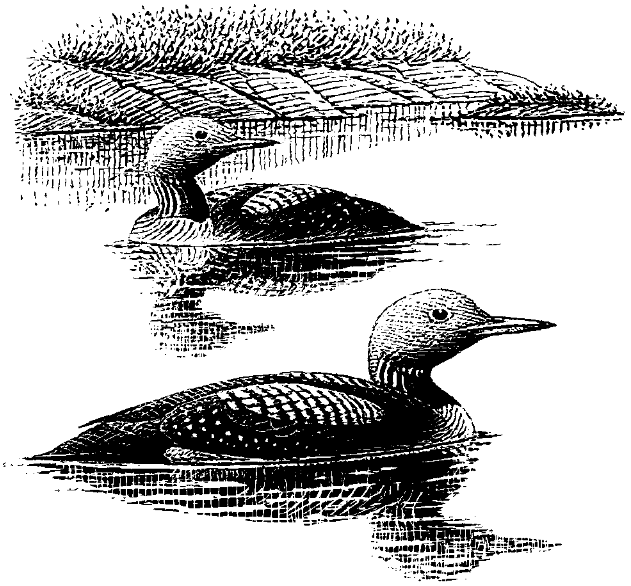
Characteristics. The divers form a well-marked Holarctic group of large (53–100 cm long) aquatic birds, with straight, sharply pointed bills and front toes fully webbed; they are long-bodied and thick-necked, with relatively small, pointed wings and a well-developed but short tail. The tarsi are laterally compressed and the legs are set so far back on the body that progress on land is extremely difficult and awkward. Adult divers are coloured in strikingly contrasting patterns, mostly black and white, and at all times the sexes present the same general appearance. The body plumage is hard and compact, while feathers of head and neck are soft and velvety. Divers moult their flight feathers simultaneously and thus become flightless for a time. The young have two coats of nestling down, the first coat in which they hatch, and a second set of down that pushes out the first and carries it on its tips, later to be pushed out by the feathers of the first winter plumage. The downy young of all divers are somewhat alike; they are uniform blackish brown or greyish brown above, changing to white or dull grey on the under parts.

The Red-throated Diver *G. stellata* is clearly differentiated from the other divers, lacking the chequered pattern, habitually feeding outside the nesting lake, and showing colonial nesting and a more complex social behaviour. The 2 largest species, the Great Northern Diver (or Common Loon) *G. immer* and the White-billed Diver (or Yellow-billed Loon) *G. adamsii* are similar, differing only in bill shape and colour, in the coarseness of the patterning and in size, and may be regarded as allopatric members of a superspecies. Two species, *G. adamsii* and *G. stellata*, have upturned lower mandibles and a field of binary vision below the bill, suggesting different feeding habits.

The divers spend their whole life on the water, only coming ashore for breeding. The normal diving time of 30–60 s can be extended to several minutes, and the body's buoyancy can be changed so that the bird may float with only the bill and eyes above water. The larger species in particular need a long run to become airborne, but once in the air the flight is rapid and powerful, often at higher altitudes than other waterfowl. *G. stellata* has a larger wing beat amplitude than the other divers, and often gives a flight cackle.

Habitat. For the 3 larger species, *G. immer*, *G. adamsii* and *G. arctica*, the normal habitat is large, clear-water lakes in the forest or tundra region. *G. stellata*, in contrast, habitually nests by a small pond or tarn, flying to the sea or to larger lakes to feed, a type of nesting occasionally seen also in *G. arctica*, especially in the high Arctic. Small islands or even tussocks are preferred for nesting.

Distribution. *G. immer* is essentially Nearctic, with a range from south Alaska and northern USA, to Greenland and Iceland. It is replaced by *G. adamsii* in north Alaska and north-west Canada, across the Palearctic region to Murmansk. This species is more confined to the arctic coast, however, and is replaced in the forested region by the large *G.a. arctica*. Both *G. arctica* and *G. stellata* are birds of the arctic coasts, *G. stellata* being circumpolar whereas *G. arctica* is absent from Iceland, Greenland and adjacent parts of Canada. Both these species extend more to the south in the western Palearctic than elsewhere. This extension of *G.a. arctica* into the habitats typical of *G. immer* in North America may be due to the lack of competition with this species, and also explains why *G.a. arctica* is considerably bigger in this range. *G.a. arctica* is replaced by the smaller *G.a. viridigularis* in the eastern parts of the Palearctic, and by the considerably smaller *G.a. pacifica* in the Nearctic range of the species. A similar difference in size is also seen in *G. immer*, the west Nearctic population being smaller. In all species, the choice of winter quarters may be expected to act as a population separation factor, since in the middle of both the Palearctic and the Nearctic the populations switch from wintering in the Atlantic to wintering in the Pacific Ocean.



Black-throated Diver *Gavia arctica*. (*D.W.*).

Movements. All species winter at sea, in inshore waters in the north Pacific and the North Atlantic–Mediterranean–Black Sea regions.

Food. The chief food is fish, with the addition of water insects and larvae (especially to feed the young), crayfish, frogs and also plant matter. In marine waters, molluscs and other invertebrates are included.

Behaviour. All species are extremely territorial and form pairs for life, generally returning to the same lake and even nest from year to year. The 3 larger species normally do not tolerate other pairs within sight, but *G. stellata* may nest colonially where only a few tarns are available close to the fishing grounds. Even so, territories around the nest are vigorously defended, by both parents. In all species, defence consists of threatening intruders with raised neck, alarm or territorial calls, splash-dives and long chases on the water. Vicious fights, even with fatal results, are not uncommon. *G. stellata*, probably as an adaptation to colonial breeding, has some added territorial behaviour (previously interpreted as courtship) involving ritualized zigzag runs and slow races in upright position, often performed simultaneously by the pair.

All species will congregate for cooperative fishing in small flocks, especially in winter and during migration, but also on a neutral area during the breeding period.

Voice. The vocalizations are among the loudest of any birds, especially the yodelling calls used to declare the territory. In the 3 larger species, the male calls with clear notes, sounding like low-pitched whistles, whereas in *G. stellata* the call is performed by the pair as a duet. All species have low-intensity wailing territorial calls. The alarm call is a tremulous laugh in *G. immer* and *G. adamsii*, a ravenlike croaking in *G. arctica* and *G. stellata*. A goose-like cackle is often heard from *G. stellata* in flight.

Breeding. Courtship is scanty, a mutual bill-dipping and dive, and copulation takes place on the shore. The nest, chosen by the male, lies directly by the water and may be quite void of any nest material. The 2 (rarely 3) olive-brown/green eggs are elliptical, with dark spots. Both sexes incubate, for 27–29 days. The young immediately take to the water. They are brooded ashore at night for the first few days but otherwise taken on the back or warmed under the wing. Both parents feed the young, at least for some time after fledging, which is 50 days for *G. stellata* and 60–65 days for the other species. Food is mostly or wholly collected in the breeding territory, except in *G. stellata* where it is flown in (one fish at a time, crosswise in the bill). The young can move well on land, and compete aggressively for food. The death of one young through such competition is a common occurrence. Renesting after the loss of the eggs only occurs early in the cycle, in the same territory but at a new nest site. (F.G.) S.S.

See photos AGGRESSION; SWIMMING AND DIVING.

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DIVERSIONARY BEHAVIOUR: agitated movements or sounds that may, for example, serve to divert a predator's attention from nest or young; in its more elaborate and ritualized form this becomes DISTRACTION BEHAVIOUR; MOBBING.

DIVERTICULUM: see EXCRETORY SYSTEM.

DIVING: see SWIMMING AND DIVING.

DIVING PETREL: see PETREL.

DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA: because the genetic material (DNA) of different species can be compared, and because the structure of protein molecules is genetically determined, these 'informational macromolecules' are valuable sources of taxonomic data.

DNA hybridization. The genetic material is composed of deoxyribonucleic acid (DNA), a linear double-stranded molecule composed of four subunits called nucleotides which differ in the structure of their 'bases'. The four bases, Adenine (A), Thymine (T), Guanine (G), and Cytosine (C), occur in the two strands as complementary pairs; A pairs only with T, G only with C. Chemical bonds between base pairs hold the two strands together. Genetic information is encoded in the sequence of the bases. The two strands of conspecific DNA will separate if heated to *c.* 100°C which ruptures ('melts') the bonds between base pairs. Upon cooling, the double-stranded configuration reforms as the A-T and G-C base pairs reassociate. In the DNA–DNA hybridization technique, the DNAs of two species are mixed, melted into single strands, and allowed to form 'hybrid' double-stranded molecules between homologous sequences. The hybrid molecules are then heated again, under controlled conditions, and their melting temperature is measured. The melting temperature depends upon the complementary matching of A-T and G-C pairs, thus the hybrids melt at a temperature lower than that required to melt conspecific DNA strands. The difference in melting temperature is an index to the degree of base sequence similarity between the two species, thus it is a measurement of the amount of genetic difference that has evolved since the two species diverged from their most recent common ancestor. Details of the technique are described by Sibley and Ahlquist (1981a; 1983).

A DNA hybridization study of the 5 genera of living RATITE birds indicated that the ancestral ratite species was separated into 3 populations when the fragments of the southern protocontinent of Gondwanaland drifted apart in the Cretaceous. One gave rise to the modern ostriches of Africa, a second to the rheas of South America, and the third to the Australasian ratites. The latter subdivided in the Eocene when the ancestors of the moas and kiwis of New Zealand, and the emu–cassowary group of Australia and New Guinea, branched from one another (Sibley and Ahlquist 1981a).

In other studies Sibley and Ahlquist have demonstrated the relationship between the Hawaiian honeycreepers (see HAWAIIAN HONEYCREEPER) and the cardueline finches (1982a); the close relationship between the genus *Sylvia* and the timaliine babblers (1982b); the relationships of the accentors (*Prunella*) (1981b) and the wagtails and pipits (1981c) to the weaver finches (Ploceidae), and the relationship of the Australian sittellas (*Daphoenositta*) to the Australian thickheads or whistlers (*Pachycephala*), not to the nuthatches (*Sitta*) (1982c). The New Zealand wrens (Acanthisittidae) were found to be the descendants of the oldest branch in the suboscine suborder Oligomyodi, a divergence that occurred in the Cretaceous (Sibley *et al* 1982). DNA–DNA comparisons were the basis for the new classification of the Passeriformes (Sibley and Ahlquist in press a, b) which follows this article.

Proteins. Protein molecules are composed of specific sequences of 20 kinds of amino acids and are synthesized on a nucleic acid template, thus they reflect genetic information. A foreign protein injected into an animal will induce the formation of antibodies in the blood serum. This 'immune reaction' may be used to compare the degrees of similarity between species by using various serological methods. Studies using 'microcomplement fixation' have dealt with several avian taxonomic problems (Wilson *et al* 1977). The technique of radio-immuno-assay also promises to be informative in comparing the proteins of living taxa with fossil proteins, up to several million years old (Lowenstein 1981).

Proteins may also be compared by using electrophoresis which characterizes the different proteins in a mixture by their net charge, size, shape, or isoelectric properties. The higher avian categories have been studied using several different protein systems (e.g., Sibley 1970; Sibley and Ahlquist 1972) but the limitations of the technique prevented definitive answers in most cases. Electrophoresis has been more successful in solving problems at the level of genera and species (e.g., Gutiérrez *et al* 1983) and populations (e.g., Corbin *et al* 1979). Sibley *et al* (1974) reviewed the immunological and biochemical taxonomy of birds up to 1972. C.G.S.

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PROPOSED CLASSIFICATION OF THE AVIAN ORDER PASSERIFORMES

- Order Passeriformes
  - Suborder Oligomyodi
    - Infraorder Acanthisittides
      - Family Acanthisittidae, New Zealand Wrens
    - Infraorder Eurylaimides
      - Superfamily Pittoidea
        - Family Pittidae, Pittas
        - Family Eurylaimidae, Broadbills
        - (Family *inc. sedis* Philepittidae, Asities)
    - Infraorder Tyrannides
      - Parvorder Tyranni
        - Superfamily Tyrannoidea
          - Family Tyrannidae
            - Subfamily Tyranninae, Tyrant Flycatchers
            - Subfamily Tityrinae
              - Tribe Schiffornithini, *Schiffornis*
              - Tribe Tityrini, Tityras, Becards
            - Subfamily Cotinginae, Cotingas, Plantcutters, Sharpbills
            - Subfamily Piprinae, Manakins
          - Family Mionectidae, Mionectid Flycatchers
      - Parvorder Furnarii
        - Superfamily Furnarioidea
          - Family Furnariidae
            - Subfamily Furnariinae, Ovenbirds
            - Subfamily Dendrocolaptinae, Woodcreepers
        - Superfamily Formicarioidea
          - Family Formicariidae, Ground Antbirds
          - Family Rhinocryptidae, Tapaculos
          - Family Conopophagidae, Gnateaters
      - Parvorder Thamnophili
          - Family Thamnophilidae, Typical Antbirds
  - Suborder Passeres
      - Parvorder Corvi
        - Superfamily Menuroidea
          - Family Climacteridae, Treecreepers
          - Family Menuridae
            - Subfamily Menurinae, Lyrebirds
            - Subfamily Atrichornithinae, Scrub-birds
          - Family Ptilonorhynchidae, Bowerbirds
        - Superfamily Meliphagoidea
          - Family Maluridae
            - Subfamily Malurinae
              - Tribe Malurini, Fairy-wrens
              - Tribe Stipiturini, Emu-wrens
            - Subfamily Amytornithinae, Grass-wrens
          - Family Meliphagidae, Honeyeaters, incl. *Ephthianura*
          - Family Acanthizidae
            - Subfamily Pardalotinae, Pardalotes
            - Subfamily Dasyornithinae, Bristlebirds
            - Subfamily Acanthizinae
              - Tribe Sericornithini, Scrub-wrens
              - Tribe Acanthizini, Thornbills, Whitefaces, etc.
        - Superfamily Corvoidea
          - Family Eopsaltriidae, Australo–Papuan Robins, incl. *Drymodes*
          - Family Orthonychidae, Log-runners or Chowchillas
          - Family Pomatostomidae, Australo–Papuan Pseudo-babblers
          - Family Corvidae
            - Subfamily Cinclosomatinae, Quail-thrushes, Whipbirds, etc.
            - Subfamily Corcoracinae, Australian Chough, Apostlebird
            - Subfamily Pachycephalinae
              - Tribe Neosittini, Sittellas
              - Tribe Falcunculini, Shrike-tits
              - Tribe Oreoicini, Crested Bellbird
              - Tribe Pachycephalini, Whistlers, Shrike-thrushes, etc.
            - Subfamily Corvinae
              - Tribe Corvini, Crows, Magpies, Jays, Nutcrackers, etc.
              - Tribe Paradisaeini, Birds of Paradise
              - Tribe Cracticini, Currawongs, Wood-swallows, *Pityriasis*, *Peltops*
              - Tribe Oriolini, Orioles, Cuckoo-shrikes
            - Subfamily Monarchinae
              - Tribe Rhipidurini, Fantails
              - Tribe Dicrurini, Drongos
              - Tribe Monarchini, Monarchs, Magpie-larks
            - Subfamily Malaconotinae
              - Tribe Malaconotini, Bush-shrikes
              - Tribe Prionopini, Helmet-shrikes, Vangas
          - Family Laniidae, True Shrikes = *Lanius*, *Corvinella*, *Eurocephalus*
          - (Corvoidea *incertae sedis*)
            - (?Subfamily Vireoninae, Vireos, Pepper-shrikes)
          - Family Callaeidae
            - (?Category *Irena*, *Aegithina*, *Chloropsis*)
      - Parvorder Muscicapae
        - Superfamily Turdoidea
          - Family Bombycillidae
              - Tribe Dulini, Palm Chat
              - Tribe Ptilogonatini, Silky Flycatchers
              - Tribe Bombycillini, Waxwings
          - Family Cinclidae, Dippers
          - Family Turdidae
            - Subfamily Turdinae, Typical thrushes, incl. *Chlamydochaera*
            - Subfamily Muscicapinae
              - Tribe Muscicapini, Old World Flycatchers
              - Tribe Erithacini, Chats
          - Family Sturnidae
              - Tribe Sturnini, Starlings
              - Tribe Mimini, Mockingbirds, Thrashers, Catbirds
        - Superfamily Sylvioidea
          - Family Sittidae
            - Subfamily Sittinae, Nuthatches
            - Subfamily Tichodrominae, Wallcreepers
          - Family Troglodytidae
            - Subfamily Certhiinae, Northern Creepers
            - Subfamily Troglodytinae, Wrens
            - Subfamily Polioptilinae, Verdin, Gnatwrens, Gnatcatchers
          - Family Paridae
            - Subfamily Remizinae, Penduline Tits
            - Subfamily Parinae, Titmice, Chickadees
          - Family Aegithalidae, Long-tailed Tits, Bushtits
          - Family Hirundinidae, Swallows
          - Family Regulidae, Kinglets
          - Family Pycnonotidae, Bulbuls
          - Family Cisticolidae, African Warblers
          - Family Zosteropidae, White-eyes
          - Family Sylviidae
            - Subfamily Phylloscopinae, Leaf Warblers
            - Subfamily Megalurinae, Grass Warblers
            - Subfamily Sylviinae
              - Tribe Sylviini, Old World Warblers
              - Tribe Timaliini, Babblers and Wrentits
        - Superfamily Fringilloidea
          - Family Alaudidae, Larks
          - Family Nectariniidae
            - Subfamily Melanocharinae, Papuan Berrypeckers, etc.
            - Subfamily Promeropinae, Sugarbirds
            - Subfamily Nectariniinae
              - Tribe Dicaeini, Flowerpeckers
              - Tribe Nectariniini, Sunbirds, Spider-hunters
          - Family Ploceidae
            - Subfamily Passerinae, Sparrows, Rock Sparrows, etc.
            - Subfamily Estrildinae, Waxbills
            - Subfamily Motacillinae, Wagtails and Pipits
            - Subfamily Prunellinae, Accentors
            - Subfamily Ploceinae, Weaverbirds
          - Family Fringillidae
            - Subfamily Fringillinae
              - Tribe Fringillini, Chaffinches, Bramblings
              - Tribe Carduelini, Goldfinches, Crossbills, etc.
              - Tribe Drepanidini, Hawaiian Honeycreepers
            - Subfamily Emberizinae
              - Tribe Emberizini, Buntings, Longspurs, etc.
              - Tribe Parulini, Wood Warblers, incl. *Zeledonia*
              - Tribe Cardinalini, Cardinals
              - Tribe Icterini, Troupials, Meadowlarks, Oropendolas, etc.
              - Tribe Thraupini, Tanagers, Neotropical Honeycreepers, Swallow-Tanager, Plush-capped Finch, Tanager-finches.

DNA–DNA HYBRIDIZATION: a technique for determining degrees of genetic similarity, by splitting the double helix of the genetic material into single strands, and mixing preparations from different species. Single strands of DNA pair to re-form double helices, but only where they possess complementary sequences of the nucleotides which carry the genetic code. This means that the percentage of 'hybridization' is a measure of the similarity in nucleotide sequences between the species being compared.

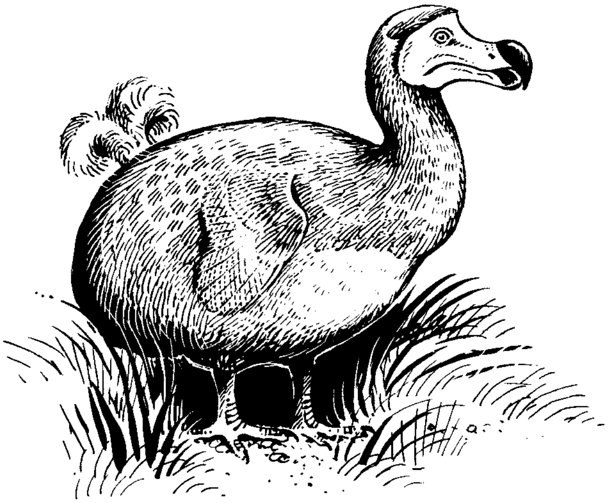
Sibley, C.G. & Ahlquist, J.E. 1981. The phylogeny and relationships of the ratite birds as indicated by DNA–DNA hybridization. Evolution Today, Pittsburgh. Proc. II Int. Congr. Systematic & Evolutionary Biology: 301–335.

DODO: *Raphus cucullatus* (=*Didus ineptus*); type species and best known member of the family Raphidae, usually considered to have been derived from pigeons and placed in the order Columbiformes. This family was only found on the Mascarene Islands, in the Indian Ocean east of Madagascar; all its members have become extinct in historical times (see EXTINCT BIRDS). Remains are only known for 2 of the species, and Storer (1970) has proposed that the second of these, the Rodriguez Solitaire (genus *Pezophaps*), be raised to familial status ('Pezophapidae') on the grounds that it must have evolved flightlessness independently from the Dodo. This approach seems to over-stress the differences rather than the affinities of the forms and has not found wide acceptance; neither has Lüttschwager's (1959) suggestion that an affinity with rails (Rallidae) rather than columbids is to be considered.

The flightless Dodo from Mauritius and the Rodriguez Solitaire *P. solitaria* are well known both from 17th century eye-witness accounts and a mass of skeletal material excavated from swamps and caves on the islands in the 19th century. Réunion also harboured a 'Solitaire', but travellers' accounts are somewhat contradictory, leading Hachisuka (1953) to postulate the presence on the island of 2 large white-plumaged flightless 'didine' birds, '*Ornithaptera solitaria*' and '*Victoriornis imperialis*'. Cheke has recently argued that paintings of 'White Dodos' usually considered to come from Réunion are in fact of albino Mauritian birds, and that no illustrations exist of the species on Réunion. He further considers, using previously unknown accounts, that only one 'Solitaire' occurred there; as Storer points out, it cannot, without evidence of remains, be legitimately assigned to either of the other 2 genera, so must be known by Selys's name *Ornithaptera solitaria*.

The turkey-sized Dodo was regarded as a curiosity by early 17th century visitors to Mauritius, and a number were shipped alive to Europe, India, Java and even Japan. Numerous paintings and sketches by Roelandt Savery survive of birds drawn from life in Holland, an excellent Moghul miniature depicts a bird in India, and rough sketches done by a Dutch sailor in Mauritius also survive. Despite the attention the birds received, virtually nothing was recorded of their habits. The only description of the egg is from a rather dubious source, and nothing is known about their feeding, although they always had, as did the Rodriguez Solitaire, a large stone in the gizzard. A marked annual fat cycle has been postulated (see Hachisuka) on the basis of 'fat' and 'gaunt' individuals in old pictures; this cycle was common to many Mascarene species (Cheke). Temple has suggested that the seeds of a Mauritian tree needed to pass through a Dodo's gut to germinate, and that the present near-extinction of the tree is due to a 300-year absence of Dodos. The evidence for this intriguing theory is, however, very tenuous (Owadally 1979); introduced seed predators account for most of the seeds on the remaining trees, and seeds planted in the forest nursery germinate adequately by themselves. Dodos were reported to be clumsy and stupid, and were slaughtered in large numbers by sailors visiting Mauritius. They became very rare on the mainland by 1640, though some survived to 1662 at least on offshore islets (Cheke). There is an unconfirmed report *c.* 1665–70, but that is the last. The 'dodos' reported in 1681, the generally accepted date of the last record, were Red Rails *Aphanapteryx bonasia* (Cheke). The cause of extinction is likely to have been egg predation from introduced pigs, monkeys and cats.

By contrast the habits of the Rodriguez Solitaire are quite well documented, as the Huguenot castaway Leguat has left us a detailed description of their behaviour, recorded in 1692, supported in 1726 by another good, if brief, account. These large birds were strongly sexually-dimorphic in size (males larger), lived in pairs, were territorial, and laid a single egg. The hatched young apparently joined crèches after a period with their parents. The birds fed on seeds, *Latania* palm fruit, and foliage. They, like the Dodo, appear to have had a marked annual fat cycle. A few were reported in 1755 and 1761, but these seem to have been the last. The last witness blamed feral cats for their demise, but later authors have argued that dry season fires sweeping the island may have been a very significant factor.



Dodo *Raphus cucullatus*. (*D.A.T.*).

The Réunion bird, also known to early French settlers as the 'Solitaire', is described in 17th and 18th century accounts. It was a solitary bird living, latterly at least, in remote mountain forests and rarely seen. It fed on worms and soil insects. Nothing is known of its breeding. It was considered quite frequent around 1705, but seems to have disappeared rather suddenly thereafter. It was last reported in 1708, but perhaps survived in remote places to about 1715–20 (Cheke). The bird commonly reported as having been shipped to France around 1735 was a Rodrigues Solitaire (Cheke).

These birds were all about the size of a turkey *Meleagris gallopavo*, heavily built, with strong feet and bills. The wings were rudimentary, though used in fighting by the Rodriguez birds. As the islands never had any land connections, the birds must have arisen from flying ancestors; flightlessness and gigantism were able to evolve in the absence of native ground predators. The Dodo was remarkable for its clumsy shape, very large head, heavy hooked bill and little tail of curly feathers. The plumage was bluish or brownish grey. The Rodriguez Solitaire was taller and slenderer, with a smaller head and slighter bill, largely brown in plumage. The Réunion bird was whitish with black wing-tips, and was described as turkey-like in size and in its feet.

The only complete stuffed Dodo, in Oxford, was destroyed by burning in 1755, but the head and a foot were saved and are still displayed in the University Museum. One or two other skulls and feet from live birds brought to Europe exist, but most of our knowledge of the bird's anatomy comes from bones dug up in Mauritius in the 19th century—complete skeletons reconstructed from these can be seen in many museums. The Rodriguez Solitaire is known anatomically from huge numbers of bones found in limestone caves on the island in the 19th century, and reconstructed skeletons are numerous. Remains of Réunion Solitaires have yet to be found. A.S.C.

Cheke, A.S. 1985. An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates. *In* Diamond, A.W. (ed.). Studies of Mascarene Island Birds. Cambridge.

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Storer, R.W. 1970. Independent evolution of the Dodo and the Solitaire. Auk 87: 369–370.

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DOLLARBIRD: *Eurystomus orientalis* (see ROLLER).

DOMESTICATION: a term that may be defined as the state of animals the breeding and maintenance of which are continuously controlled by man. Further criteria of domestication which stress the economic value of the animal, the morphological and behavioural differences between the domestic animal and its wild type progenitor, or its degree of tameness, cannot be applied *in toto* to all domestic species. Some of our domestic species were first domesticated for religious rather than economic reasons; others are little altered morphologically from the original wild type, while others can scarcely be called tame and indeed are less tame than some wild birds in rarely frequented places. While most domesticated species usually fulfil one or more of these secondary criteria, the important implication in the definition is that, with control over the breeding and maintenance, man can change the animal as far as its genetic potentialities will allow. The number of species that have been domesticated at some time or other is probably very large; in many cases domestication has been on only a very small scale and of very short duration. Most of the avian examples considered here fulfil one or more of the secondary criteria of domestication listed above and have been domesticated in relatively large numbers and for considerable periods of time. Cage and aviary birds, together with ornamental waterfowl, have been excluded (see AVICULTURE; CAGE BIRD). The differences seen in our domestic birds, including the degree of change from the wild progenitor and the amount of intra-specific variation, have developed from the interaction between man's breeding and selection practices and the genetic variability available within a species. Assuming that mutation rates are approximately equal in our domestic birds, any differences between species in the initial amount of genetic variability available for selection would have depended on the population structure of the ancestral species, on the number of the breeding birds first brought into captivity, and on the introduction of further wild birds from other places and at other times. In general, however, the breeding practices and the amount of conscious or unconscious selection exercised by man have been responsible for the state of our domestic birds today.

Domestication could be facilitated in birds by their possession of a catholic diet, plasticity in reproductive behaviour, and ability to become accustomed to man and the environment supplied by him. Although all these traits are not found in every ancestral species of our domestic birds, domestication of one species might have aided the process with another species; e.g. the hatching of wild ducks' eggs by domestic hens. It appears that food production was not always the primary object of domesticating what are now important agricultural species; as will be seen from the histories of many individual species, a species may have had varying functions in societies in different times and places.

Domestic fowl. This species, usually regarded as a domesticated form of *Gallus gallus gallus*, may in fact be descended from any one or more of all 4 species of jungle fowl *Gallus* spp. inhabiting south-eastern Asia. The exact date of its domestication is unknown; it was recorded in India as early as 3200 BC and in China it was known as a domesticated bird by 1400 BC. It reached Persia at a very early date, and appeared in Egypt and Crete in 1500 BC. However, it may not have become a common domestic animal in Egypt until after the Persian conquest of the country in 525–524 BC.

The different attitudes of early European societies to the domestic fowl suggest that it entered Europe by two routes: one through Scythia to the Teutons and Celts and from Gaul to Italy; the other through the Dardanelles to the Aegean. In Greece the cock is first found on coins from the Temple of Artemis at Ephesus of at least 700 BC. Its arrival in the New World was formerly considered to have been shortly after the voyage of Columbus, but now it seems more likely that it was brought from Asia to the coasts of Peru and Ecuador.

The fowl was popular in many societies as a sacrificial or religious animal, so that this usage and cock-fighting were probably more responsible for its distribution than were its food-producing potentialities. In Persia, for example, it had an exalted position in the Zoroastrian religion. In Greece and Rome it also had religious significance, but whereas the Greeks valued it primarily as a fighter, the Romans also developed its agricultural potentialities; a complex poultry industry was formed, together with specialized breeds, but with the decline of the Roman Empire the industry collapsed and it was not until the 19th century that poultry keeping on a large scale was resumed.

The modern breeds are divided into Mediterranean and Asian; within these two groups numerous breeds and varieties have been developed. In Western countries today 37 breeds (including 5 Asian breeds) are kept for food production, while there are at least 24 ornamental breeds. The variation produced during domestication includes differences in plumage, body size, shape and size of comb, number of toes, egg-shell colour, skin colour and osteology. Physiological differences are found in many traits including egg production, fertility, hatching quality, broodiness, efficiency in food conversion, resistance to certain diseases, and responsiveness to certain hormones. Behavioural dissimilarities are also present. The large-scale breeding methods employed today entail the use of inbred lines derived from one or more breeds, and many of these lines may differ from one another to an extent comparable to that found between breeds.

Domestic duck. All breeds of this species are descended from the Mallard *Anas platyrhynchos*, which is thought to have first been domesticated in China or south-eastern Asia at a very early date. Birds were doubtless domesticated elsewhere at later dates, as there are records from Roman times of eggs being collected from the wild and being hatched by domestic hens. Although the wild Mallard does not breed in captivity, its young if hatched artificially will do so.

The amount of variability in the domestic duck is very small compared with that found in the domestic fowl. There are approximately 12 breeds in the United Kingdom used for meat or egg production or as dual purpose breeds. Morphologically the most striking ones are the Indian Runner, with its upright carriage and cylindrical conformation, and the Crested Duck, which possesses a large globular crest of feathers on the head. Modern breeding methods are similar to those used with chickens.

Domestic goose. The European goose was domesticated probably in south-east Europe and the Chinese goose in Asia, either in China or south-eastern Asia. It is generally agreed that the European goose is descended from the Greylag Goose *Anser anser* and the Chinese goose from the Swan Goose *Anser cygnoides*. They cross easily and the progeny are fully fertile. (For the Egyptian Goose *Alopochen aegyptiacus*, a not closely related bird, see below.) The domestic goose was already known in Europe by the time of Homer. There are about 9 breeds, some of which are very distinctive. The Chinese and African geese both possess large tubercles at the base of the bill; the Toulouse and the African have 'dewlaps'. The Crested Roman goose, which is of great antiquity and has a large globular crest, reputedly saved the Capitol in Rome from the Gauls in 390 BC by cackling and giving the alarm; geese are used as 'watch dogs' today. The Sebastopol has curled breast feathers and long-plumed feathers on the back. Little known in the West is the Russian fighting goose, which is a very old breed (with several sub-breeds) that was used for gaming in Russia for a long time.

Turkey. The Mexican subspecies of the wild Turkey *Meleagris gallopavo gallopavo* is considered to be the ancestor of this bird, and domestication probably took place near Oaxaco in Mexico. The date, however, is uncertain although it may have occurred at a time equivalent to the Neolithic age in Europe. Its importation into Britain between 1525–1532 may have been effected by William Strickland of Boynton-on-the-Wold, Yorkshire, for he was allowed to incorporate a turkey cock in his family crest. 'A Dietarie' published in 1541 by Archbishop Cranmer mentions the turkey, but during the 16th and 17th centuries much confusion existed between the Turkey and the Guineafowl, which had been called *Meleagris* by the Romans.

Several studies have sought to compare the wild Turkey with domestic birds in the United States of America. In a comparison of the Missouri sub-species *M.g. silvestris* and the domestic Bronze turkey, differences in body conformation, thickness and colour of tarsus, head appendages, plumage colour and tranquillity were apparent. Also the weights of brain, adrenal and pituitary glands expressed as a percentage of body weight were greater in wild birds. Three varieties have been widely bred in Britain today, *viz.* the Brown, the White and the Black, and now large-scale methods as in the fowl are used. Turkey first appeared on the Christmas menus in England in 1585.

Muscovy Duck. This bird was also domesticated in pre-Columbian times in the New World, where the wild Muscovy Duck *Cairina moschata* is a tropical tree-nesting bird that apparently avoids human habitation. Its name may have come from the Muisca Indians of central Colombia. Apart from the establishment of 3 varieties differing in colour, there has been no selection for more divergent breeds. The domesticated Mucovy Duck has been introduced into other parts of the world; it is familiar, for instance, in West African villages. It is sometimes crossed with domestic ducks of Mallard stock, but the progeny are infertile.

Guineafowl. Subspecies of the wild Guineafowl *Numida meleagris* are widespread in Africa. The isolated north-west African subspecies *N.m. sabyi* was present as a sacred bird on an Aegean island in the 4th century BC. The Romans called this subspecies the Numidian fowl, and they kept it as well as the north-east African subspecies which they called *Meleagris*; both were used for food, but the latter was the more popular. With the decline of the Roman Empire both forms appear to have been lost to Europe. One reference, however, shows that birds were kept in Athens in the 10th century AD. After the voyages of the Portuguese navigators in the 15th and 16th centuries, the West African subspecies *N.*

m. galeata was brought to Europe. No breeds have been developed.

Domestic pigeon. Descended from the Rock Dove *Columbia livia*, this may well be one of our oldest domestic animals, for it was a sacred bird in the early cultures of the Near East. It was associated with Astarte, the Goddess of Love and Fertility, and images of pigeons dating from 3100 BC have been found. In Egypt it was used not only as a source of food but also as a carrier and was domesticated before 2600 BC. There are records of it in Crete in the 2nd millennium BC. In classical Greece it became sacred to Aphrodite, and later in Rome it was associated with Venus but was also used for food and as a messenger. After the rise of Islam it was protected on religious grounds in most Mohammedan countries. It arrived in India and China at a very early date, but its role differed from place to place.

Nearly a century ago Darwin estimated that there were 150 breeds of pigeons, many of which he noted 'differ fully as much from each other in external characters as do the most distinct genera'. He divided the breeds or races into 4 groups. Group I contains the Pouter pigeons in which the oesophagus is of great size, barely separated from the crop and often inflated; the body and legs are elongated and the bill is of moderate dimensions. In Group II the breeds are characterized by bills with the cere swollen and often carunculated or wattled, and by large feet. Group III contains very divergent breeds, but the type of the group is characterized by the bill being shorter than that of the Rock Dove and the bare patch of skin round the eyes not being much developed. The breeds of Group IV resemble the Rock Dove in all important points of structure.

Peafowl. Our domesticated birds are descended from the Peafowl *Pavo cristatus* inhabiting parts of India, Assam and Ceylon. Although the bird was known in ancient Egypt, it was probably not widely known in Europe until the time of Alexander the Great. It is thought to have been introduced into Britain by the Romans and in mediaeval times was a popular bird for banquets. No varieties have been developed under domestication. Another species, the Green Peafowl *P. muticus*, has also been domesticated.

Ostrich. The subspecies of the Ostrich *Struthio camelus camelus*, *S.c. molybdophanes*, *S.c. massaicus* and *S.c. australis* appear to have been at least partially domesticated at some time during the recorded history of man. The greatest incidence of domestication occurred in the latter half of the 19th century, when the feathers became fashionable. The main area of ostrich farming was in the Cape Province of South Africa, which is within rage of *S.c. australis*. The first records of birds hatching eggs in captivity at the Cape date from the 1860s. In 1865 there were 80 birds in captivity there and by 1913 there were 776,313 domesticated birds, the vast majority of which had been hatched by artificial incubation. Ostrich farming was also carried out in North Africa, the United States of America, France, Spain, Italy and Australia. In 1914–18 the industry collapsed, but in 1960 about 30,000 birds were farmed in South Africa for the production of high-quality leather as well as the feathers.

Little Egret. When the ostrich feather trade was at a maximum the Little Egret *Egretta garzetta* was domesticated and farmed on a small scale for its plumes in what is now Pakistan and in Tunisia.

Cormorant. The custom of using Cormorants *Phalacrocorax carbo sinensis* for fishing dates back to the Sung dynasty (960–1298 AD) in China and to the 6th century AD in Japan. In China the birds are bred by special breeders while in Japan birds are obtained from the wild. The truly domesticated birds are sometimes variable in colour (see COUNTING).

Egyptian Goose. In ancient Egypt the Egyptian (or Nile) Goose *Alopochen aegyptiacus* was the main domestic bird. Its domestication took place very early and in the Old Kingdom, which ended in 2300 BC, it was very common. Its flesh was widely eaten, although the bird was the sacred bird of the God Geb, but its eggs also had symbolic value and were not eaten. There are very few records of the domesticated bird outside Egypt; and after the Persian conquest of Egypt in 525–524 BC the species ceased to be a domestic animal.

Game birds. Between the 13th and 16th centuries pheasants are reported to have been bred domestically for the London markets. Today many enterprises breed game birds on a very large scale for restocking wild populations and marketing. The most usual birds include the Pheasant *Phasianus colchicus*, the Partridge *Perdix perdix*, the rock partridges *Alectoris*, the Bobwhite Quail *Colinus virginianus* and several species of true quails *Coturnix* spp. In China and Japan the Quail *Coturnix coturnix japonica* is also kept for egg production. A number of aquatic species have also been bred on a large scale for re-stocking. Although no conscious selection has been practised on these birds, and they may not be considered domesticated in the generally used sense of the word, difficulty is often encountered in maintaining wildness in these stocks; this point again emphasizes the difficulty in defining domestication.

(For the wild birds concerned see chiefly under DUCK (goose and swan); GUINEAFOWL; OSTRICH; PHEASANT; PIGEON; TURKEY.)

See also CAGE BIRD. D.G.M.W-G.

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DOMINANCE (1): see GENETICS.

DOMINANCE (2): term used to describe relationships between birds in aggressive encounters which have predictable outcomes. The dominant individual regularly defeats or displaces its rival, which is described as being subordinate or 'subdominant' (an incorrect usage best avoided).

Males tend to dominate their partners during the early stages of pair-formation in many species, although a subsequent reversal of roles, with the female assuming dominance, has been described in various gulls, buntings and finches. The context in which aggression occurs between members of a pair may, nevertheless, affect its outcome; male Chaffinches *Fringilla coelebs* dominate their partners in most social situations early in the breeding season but are often attacked by them during courtship. Dominance relationships are also important in non-breeding groups of birds. So-called 'peck orders' or 'dominance hierarchies' have been described in, among others, groups of domestic fowl, cage birds, such as Canaries *Serinus canaria*, Bengalese Finches *Lonchura striata* and Zebra Finches *Poephila guttata*, and broods of young Magpie Geese *Anseranas semipalmata* and Oystercatchers *Haematopus ostralegus*. Classically such orders are linear; the birds can be ranked so that each of them is dominant to all of those below it in the order but subordinate to those above it. Stable orders of this kind have been described in small groups of domestic fowl, but the order is frequently more complex. Those in large groups of fowl, for example, tend to be unstable, presumably because individuals cannot learn to recognize all members of the group. Hierarchies may also be complicated by cases of incomplete dominance between individuals, and by triangular relationships, i.e. Bird A is dominant to B, and B is dominant to C, but C dominates A.

Assessment of dominance is important to individual members of social groups because it enables subordinates to recognize birds of higher rank and to avoid them without fighting. Dominants also benefit because they may suffer injury in fights, even against birds which they are capable of defeating. It is not surprising therefore that social status is signalled in a variety of different ways. Behavioural postures are important in domestic fowl but plumage characteristics are used in some other birds. It is possible to increase the ranking of female Chaffinches by dyeing their breasts red so that they are more like those of males. Similarly, Rohwer (1977) has shown that the amount of black plumage on the throat, crown and breast is an indication of dominance in Harris Sparrows *Zonotrichia querula*. Subordinate individuals which are made to 'cheat' by dyeing their feathers black are persecuted by other birds, whereas dominants with bleached feathers have to fight more often than usual in order to maintain their rank. Dominance relationships can also be manipulated experimentally by injections of hormones. Doses of testosterone propionate increase the social status of recipients in groups of canaries and domestic fowl, as do doses of testosterone and the luteinizing hormone in male Red-billed Queleas *Quelea quelea*.

There is surprisingly little information on the advantages that are gained by high status in social groups, although there is some evidence that dominant Slate-coloured Juncos *Junco hyemalis* and Harris Sparrows survive better than birds of low rank. One probable advantage is that dominant birds forage more efficiently than subordinates because they can occupy the more rewarding feeding patches. Caraco (1979) has shown that dominants in groups of Volcano Juncos *Junco vulcani* maintain access to sites of high seed density and use foraging time more efficiently than subordinates. Furthermore, individuals in captive groups of crossbills *Loxia* are said to feed in order of dominance when there is competition for food. Another advantage may be over competition for mates. Dominant males in groups of domestic fowl achieve more matings, and father more offspring, than subordinates. S.M.E.

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DONACOBIUS, BLACK-CAPPED: *Donacobius atricapillus.* Formerly in Mimidae (see MOCKING-THRUSH). For family now see WREN (1).

DORADITO: substantive name of the 4 species of *Pseudocolopteryx*, small tyrant-flycatchers inhabiting open country, so named because of their yellow underparts (see FLYCATCHER (2)).

DORSAL: pertaining to the back, or generally to the upper surface of the body (in a more or less horizontal position); opposite of VENTRAL.

DOTTEREL: properly *Eudromias morinellus* (see PLOVER (1)); also used, particularly in Australia and New Zealand, as substantive name of various *Charadrius* spp., and even of *Peltohyas australis* (Glareolidae—see COURSER).

DOUBLE BROODED: species which normally lay a second clutch after fledging of the first brood (see CLUTCH-SIZE).

DOVE: substantive name of some species of Columbidae (see PIGEON). The names 'dove' and 'pigeon' are to some extent interchangeable (see also AVICULTURE).

DOVEKIE: alternative name of the Little Auk *Plautus alle* (see AUK).

DOWITCHER: substantive name of *Limnodromus* spp. (see SANDPIPER).

DOWN: feathers characterized by their fluffy vanes (see FEATHER; PLUMAGE). The use of down, plucked by the female from her own body, is characteristic of ducks and lyrebirds (see EIDER; UTILIZATION BY MAN).

DRAKE: special term for a male DUCK.

DREAD: see PANIC.

DREPANIDIDAE: a family of the PASSERIFORMES suborder Oscines; HAWAIIAN HONEYCREEPER.

DRIFT: (a) lateral displacement of a migrant from its heading by the wind, resulting in an achieved flight TRACK. Many migrants probably attempt to maintain a chosen track by altering their heading to allow for drift. (b) displacement of a migrant downwind at the speed of the wind, resulting from disorientation of the bird and consequent flight in random directions. (c) actively flying downwind under certain circumstances which do not permit a migrant to maintain its chosen course (see also MIGRATION).

DRINKING: birds drink so as to balance the loss of water by excretion and pulmocutaneous evaporation (loss of water through the lungs and skin). Even though birds do not sweat, a small amount of water may be lost through the skin quite incidentally. Birds need to drink only if their food does not provide enough water to effect a balance. It is therefore not surprising that birds with dry diets (especially seeds) need to drink more often than those with succulent diets (insects, meat, fruit, nectar, etc.).

Sources of water. Drinking water may be obtained from free open water such as rivers, streams, lakes and the sea, as well as from rainwater puddles on the ground or in the bases of leaves of large plants, falling rain, condensed fog, and dew.

Drinking methods. The methods by which birds actually take up water vary somewhat, but fall into five basic types which may intergrade.

Black-headed Gull *Larus ridibundus*, in winter plumage, drinking. (*Photo: H.E. Grenfell*).

(a) Sipping—this is the 'dip-and-tilt' method of drinking, in which the bill is dipped into the water and the head then raised with the bill tilted slightly upward to allow the water to run down the throat and be swallowed with the aid of rapid tongue movements. This is probably the commonest method in birds and is exemplified by the domestic fowl and most passerines.

(b) Suck-and-tilt—instead of merely dipping the bill and allowing water to be taken up between the jaws by capillary or surface tension, some birds (notably sandgrouse (Pteroclididae)) actively suck up water into the buccal cavity before raising the head to swallow the mouthful in a single gulp; this movement is repeated until the crop is full. The appearance of suck-and-tilt drinking is similar to that of sipping but is quicker and more vigorous.

(c) Sucking—the bill is immersed in the water which is taken in by a series of sucking movements of the gular region, without raising the head until the bird has drunk its fill. This is the common method of drinking seen in doves, but is found also among some waxbills (Estrildidae), the mousebirds and some other groups, including the waders (Charadrii). The waxbills appear to use a tongue-pumping mechanism rather than a gular mechanism, although it is often difficult to decide if the two mechanisms are mutually exclusive. A few birds may change their drinking pattern with age; thus, young sandgrouse are said to drink by sucking, but the adults use the suck-and-tilt method.

(d) Tongue drinking—two types of specialized tongue structures are involved here. One is a grooved or tubular tongue adapted for sucking up nectar or fruit juice as found in sunbirds and hummingbirds and which can be used for sucking up water in the same way. The second is a brush-like tongue found in some honey-eaters and parrots, also adapted for feeding on nectar, but which can be used for lapping up water.

(e) Drinking in flight—good flyers like swifts and swallows drink on the wing by swooping over the surface of a body of water with the bill open; water is scooped up in the lower jaw as it touches the water. Presumably the mouthful thus obtained is swallowed as the bird circles for the next swoop and scoop. A great advantage of this drinking method is that the birds avoid landing on the ground where they are vulnerable to predators.

Frequency of drinking. The frequency with which birds drink depends largely on their ecology and body size. In most environments birds have water available all the time and may drink several times a day, although one or two drinking times seem to be the rule for most birds—either morning or evening, or both. Birds of arid zones have to time their drinking more critically to avoid flying to and from water in the heat of the day and to avoid the main pressure by predators. For example Gambel's Quail *Callipepla gambelii*, a gamebird of the Sonoran Desert in Arizona, drinks between 0700 h and 0900 h and again between 1700 h and 1800 h; avian predators around the waterholes are active mainly between 0900 h and 1500 h.

Birds with a crop need to drink only once a day as a rule (parrots, doves, sandgrouse) unless, like finches, they are very small, in which case they may need to drink several times a day, especially in hot weather. Indeed, most small granivorous passerines drink frequently throughout the day, including the midday hours.

Birds that are fully water-dependent, even if they limit their drinking to certain times of the day, will be restricted in their distribution to the vicinity of water. The degree of restriction will depend in part on their powers of flight; larger birds with good flying ability (like doves and sandgrouse) can exploit food sources further from water than can small birds like buntings (Emberizinae), waxbills, finches and sparrows (Ploceidae).

Water requirements. The minimum drinking-water requirement for small granivorous birds in arid environments is about 10% of the body weight per day, but this amount will increase in hot weather. Most birds can reduce evaporative water loss when deprived of water, while at the same time increasing the rate of water resorption in the cloaca so that their excreta may contain as little as 50% of water by weight. At moderate ambient temperatures (20–30°C) many small birds such as larks, waxbills and the Budgerigar *Melopsittacus undulatus* can survive on dry seed without drinking and without losing body weight, but in hot dry weather they do need to drink to offset water lost by evaporative cooling. Presumably these birds augment the small amount of water in their food (as little as 12–15% in air-dried seeds) with metabolic water produced during cellular respiration.

Most birds prefer fresh water for drinking, but saline or brackish waters can be drunk by birds possessing a salt gland (see EXCRETION, EXTRARENAL) which removes excess salts from the body fluids. Seabirds can drink seawater for this reason and the salt gland, kept as a legacy from a marine ancestor, has enabled several desert-dwelling waders (coursers, pratincoles and plovers in particular) to process the body fluids of their insect food and to become quite independent of drinking water. Few land birds, however, can drink water with a salt content higher than about a third to a half that of seawater.

Opportunistic drinking has been seen in the Australian Pelican *Pelecanus conspicillatus* in which the birds open their bills and expand the pouch of the lower jaw to catch falling rain. The pouch forms a catchment area of about $0.039\,m^2$. This further illustrates birds' preferences for fresh water, since lake water was available nearby. G.L.M.

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DRIVE: see BEHAVIOUR, HISTORY OF.

DROMADIDAE: see under CHARADRIIFORMES; CRAB-PLOVER.

DROMAEOGNATHOUS: see PALATE.

DROMAIIDAE: see under STRUTHIONIFORMES; EMU.

DRONGO substantive name of most of the species of Dicruridae (Passeriformes, suborder Oscines), and in the plural (drongos) as a general term for the family. 'Drongo' is the indigenous vernacular name for *Dicrurus forficatus* used by the Betsimasaraka and Sakalava tribes of northern Madagascar, and has passed into universal use for the family.

Characteristics. The drongos are a natural and well-defined family of 20 species of the Old World tropics, characterized by their long forked tails, a variety of modifications of the head and tail feathers and, in all but 2 species, glossy black plumage. Their relationships have been the subject of much speculation, and they have certain features in common with such groups as bulbuls, shrikes, crows, orioles (Oriolidae), flycatchers (Muscicapidae), and birds-of-paradise. In behaviour, drongos seem most similar to, and are to some extent the ecological counterpart of, the tyrant-flycatchers of the New World, although no relationship is implied in this observation.

African Drongo *Dicrurus adsimilis*. (*C.E.T.K.*).

Drongos are birds of medium size, varying from about 18 cm to 38 cm, though the elongated tail feathers of some species can extend total length to around 72 cm. The shape and structure of the tail varies enormously, but typically it is long and deeply forked, with the tips of the outer feathers curving outwards or sometimes upwards, or with the outer feathers extremely long or curled. In some species there is a marked prolongation of the shaft of the outer feathers, which ends in a second barbed section of the feather known as a racket (or racquet) or spatula. In all but one species, the tail is composed of 10 feathers. There are 10 primaries in the wings, which are long and pointed, and together with the tail confer great aerial manoeuvreability, seen to advantage as the bird twists and turns in pursuit of an insect or when harrying a foe. The Papuan Mountain Drongo *Chaetorhynchus papuensis* of New Guinea is the only member of the family to have 12 tail feathers, and also differs in some details of structure and colour pattern.

The bill is stout, arched and slightly hooked, with a small notch in the upper mandible, the nostrils often being partly concealed by dense feathering over the base of the bill. The rictal bristles are well developed, being long and stiff. The legs are short, with strong toes and sharp claws. The iris is red in most species.

The sexes are alike in plumage, which is black in all except 2 species which are grey to whitish. Juveniles are less glossy than adults, with shorter wings and tails, and in most species apparently acquire adult plumage in their first complete, post-juvenile, moult in their second year. Full development of crests and tails in the Greater Racket-tailed Drongo *Dicrurus paradiseus* and the Lesser Racket-tailed Drongo *D. remifer* is attained in succeeding moults. In adults, all but the 2 greyish species have the black velvety, or glossed with greenish, bluish or purplish. The intensity of the gloss, which can be brilliant and metallic, and its distribution to certain areas of the plumage or to certain parts of individual feathers, vary from species to species but are constant in each, and provide the best systematic character. In some species the gloss forms brilliant spangles on the throat and chest, and some have glossy hackles at the side of the neck. Many species are crested, and the structure and shape of the crest varies as much as the tail feathers. It may consist of only a little brush at the base of the bill, or may extend over the culmen, or may be very full, consisting of webbed feathers which curl over the crown and nape. In some species the crest feathers are partly or completely denuded of barbs and vary from a little erect tuft about 2 cm long, to filaments which may reach a length of 12 cm. The ornamental modification of some body feathers, the crest and the tail vary geographically in the same species and are of much interest. A few forms (species or subspecies) are white on the abdomen, upper wing coverts or face, or have a white spot at the corner of the mouth. In one found in the Comoro Islands the wings and tail are reddish brown.

Habitat. Drongos are largely arboreal birds, and are found in a wide range of woodland habitat from open country with scattered trees to dense secondary jungle or primary forest, at altitudes ranging from sea-level to around 3,300 m in the Himalayas. The most widely distributed species, the African Drongo *D. adsimilis* of Africa and the King-crow *D. macrocercus* of Asia (often regarded as conspecific), are characteristically more tolerant of open country, and perch readily on large mammals, vantage points such as ant-heaps or posts, or even on level ground.

Distribution, populations and movements. With a total of 10 species, the drongos are most numerous (and also have more highly evolved ornamental characters) in southern Asia, from Iran to China. The most noteworthy of all is the Spangled Drongo *D. hottentottus*, which occurs almost throughout this area from the west coast of India, and also in Indonesia, the Philippines, New Guinea, the Solomon Islands and north and east Australia. Over 30 subspecies of this bird have been described, and it has freely colonized oceanic islands, some of them by repeated invasions. A further 3 species are endemic in the Australo–Papuan region. In the Afro–tropical region there are 3 endemic species, while a further 4 are endemic to Madagascar, the Comoro Islands and Aldabra. Three of the Oriental species have penetrated deeply into the Palearctic region, to south-east Iran in the west and to Manchuria and the Amur river valley in the north-east. These northerly populations are migratory, but otherwise drongos are largely resident, though there is some seasonal wandering, often altitudinal in the Himalayas, or in the case of the Spangled Drongo, in search of flower nectar.

Food. Drongos are mainly insectivorous, the prey ranging in size from the smallest Diptera to large moths, termites, beetles and mantids. When opportunity arises they will also take other animal food such as lizards and small birds, and even bats have been reliably recorded. At least some species are piratical, robbing other birds of food in flight. Flower nectar is also an important element in the diet of many species.

Behaviour. Drongos are well known for their pugnacity and fearlessness in attacking and chasing larger birds such as crows and hawks. Other species of birds often nest in the same tree as a pair of drongos and this is assumed to be an association in which they benefit from the drongos' pugnacity. Other behavioural traits worthy of note are that drongos associate with cattle or man, are inquisitive, and follow grass or forest fires to prey on the disturbed animal life. They are also regular members of the mixed parties of birds which hunt through the forest, and which are a characteristic feature of the woodland bird-life in southern Asia. Although often described as solitary, drongos commonly gather in small or large groups either when feeding at forest fires, or in flowering or fruiting trees, or when flying into communal roosts which are used outside the breeding season.

Voice. The normal vocabulary is a mixture of harsh, scolding notes and pleasant musical whistles, but some species are good mimics, and can produce a wide variety of different calls with great skill. The Greater Racket-tailed Drongo is particularly noted in this respect, while the Spangled Drongo is often noisy on its own account, with its fluty rather oriole-like calls interspersed with metallic or grating noises.

Breeding. The nest is normally a rather shallow cradle or saucer, made of rootlets, fibres, fine grass or leaves, often bound together or decorated and camouflaged with lichens and cobwebs. Although inconspicuous, it is often placed in an exposed position on the outside of a bush or tree, from 3 m to 20 m, and is partially suspended from a horizontal or vertical fork in a slender branch. The normal clutch is 3–4 eggs, less in some species. The eggs are sometimes immaculate, but typically are speckled and blotched with dark or reddish brown on a creamy or pinkish background. Nests are sometimes brood-parasitized in India by the Drongo-Cuckoo *Surniculus lugubris* and the Koel *Eudynamys scolopacea*. Both sexes share in nest-building, incubation and care of the young. The incubation period remains unrecorded for many species, but is given as 16 days for the African species *D. adsimilis*, which may raise two or three broods. M.W.

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DROP NET OR **DROP TRAP**: see TRAPPING; MARKING.

DROPPINGS: consist of a combination of materials from the EXCRETORY SYSTEM (urine) and the ALIMENTARY SYSTEM (faeces). The mixture of renal and alimentary products occurs because the ureters empty into the cloaca at the posterior end of the alimentary tract where the faeces collect before defaecation. The faeces, which generally contain indigestible residues, water, microbes and microbial products, are formed in the posterior small intestine and in the large intestine, where some water is absorbed during their formation. The water content varies according to the environment of the bird; the droppings of birds from arid regions usually contain less water than those of birds from humid places. In birds which possess substantial caeca, some of the contents of the posterior part of the tract enter the caeca where changes occur to produce the very distinctive caecal faeces. These are usually discharged separately from the intestinal faeces, but not without urinary contamination. About 7 to 11 times as much material may be discharged from the intestine proper as from the caeca of a healthy domestic fowl during a given period. Caecal faeces are rarely discharged from the bird during darkness. The pattern or rhythm of defaecation is often disturbed during the course of an infection of the alimentary tract. Predatory birds and several other widely differing species eject some of the indigestible parts of their diet in the form of pellets in addition to droppings (see PELLET).

The droppings of the nestlings of many species of passerine bird and of some others are often produced in a form which facilitates easy disposal for nest sanitation (see PARENTAL CARE). The droppings are sometimes fairly characteristic of a species; those of adult geese and grouse are easily recognized. The droppings of sea and cave birds, which breed in enormous colonies, accumulate to form deep deposits (see GUANO; GUANO, CAVE). Examination and analysis of droppings can give much qualitative information about the diet of the species involved. Some indigestible plant and animal remains are relatively easy to identify and sometimes the colour of the droppings provides a clue to the diet of the birds under observation. When experimental methods are used, analysis of the droppings can aid in studies of the digestion, growth and diseases of birds. The dispersal of various seeds, spores and parasites may take place through the defaecatory habits and droppings of birds. D.W.T.C.

DRUMMING: see MECHANICAL SOUNDS.

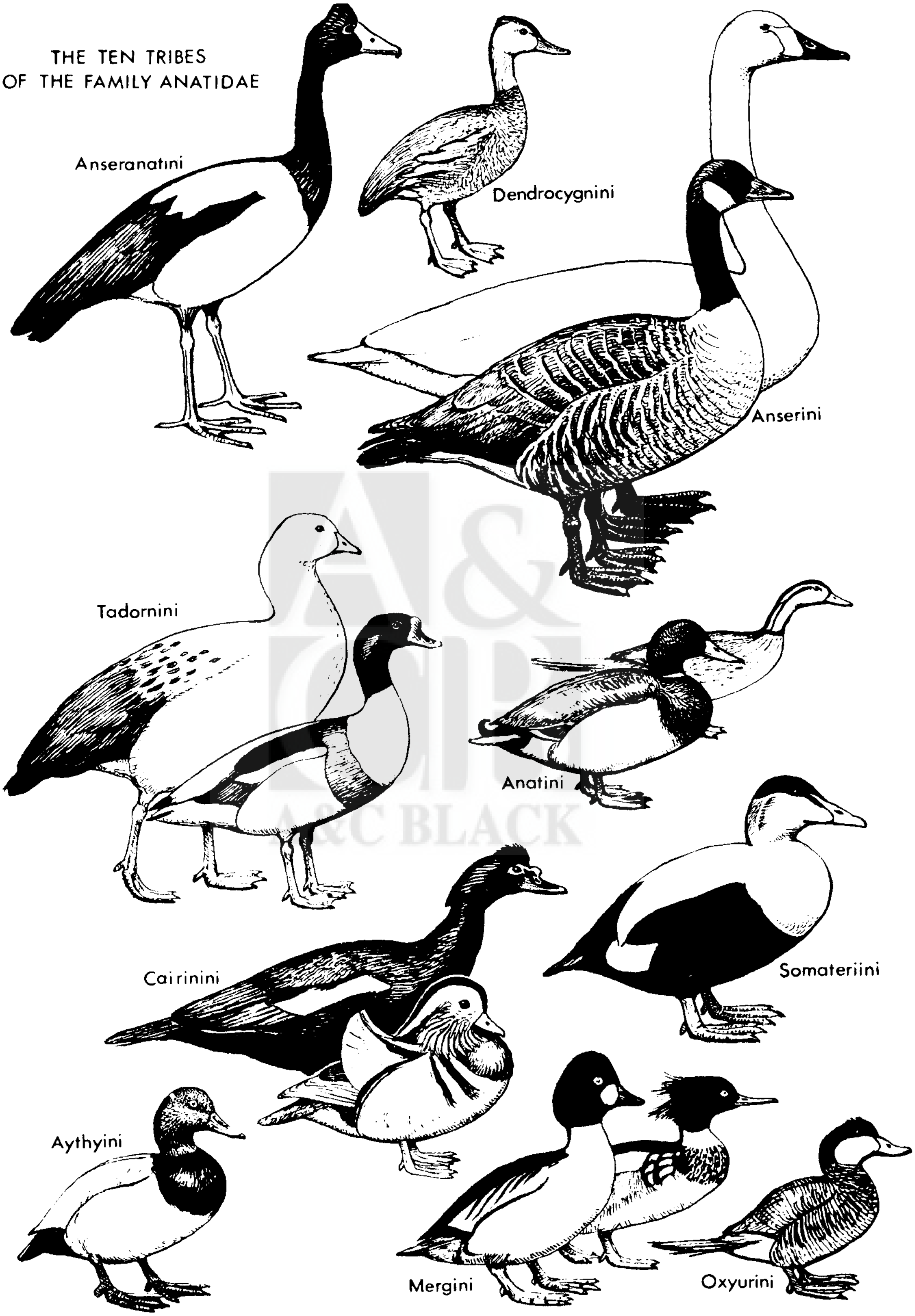
DRYING: see COMFORT BEHAVIOUR and photo.

DUCK: substantive name of most of the smaller species of Anatidae (Anseriformes, suborder Anseres); in the plural, usually in the combination 'ducks, geese, and swans', general term for the family. Apart from a number of ducks that have special names, the other species have the substantive names 'goose' and 'swan'. As the application of 'duck' and 'goose' does not correspond with the taxonomic subdivisions, the whole family is dealt with in this article; but see also GOOSE; SWAN; COUNT; DOMESTICATION; HYBRID.

Ornithologically 'duck' is applied irrespective of sex, but one usage restricts this to the female (even in species with special substantive names, e.g. 'duck Shoveler'), the corresponding term for the male being 'drake'; in North America 'hen' is often used for the female. The diminutive 'duckling' is used for the young. 'Duck' is often used unchanged in the plural as a collective term—for individuals rather than species.

The members of the family are essentially aquatic, many species obtaining their food principally by diving; three of the toes are linked by webs (see SWIMMING AND DIVING). All have relatively long necks and blunt, rather spatulate bills. All lay unspotted eggs, mostly nearly white or pale coloured, in nests on the ground, in thick vegetation, or in holes in trees, rocks, or earth, usually lined with down plucked by the female from her breast; and all have nidifugous down-covered young. All ducks, swans, and most geese moult the flight feathers of the wings simultaneously and pass through a flightless period, lasting from 3 to 4 weeks, after the breeding season; in all the Anatidae the only exceptions to this are the Magpie Goose *Anseranas semipalmata*, and at least some individuals of at least one of the species of sheldgeese of the genus *Chloephaga* (see below).

The classification of the Anatidae now generally accepted is based, with minor modifications, on that proposed by Delacour and Mayr. They used the following special characters in arriving at the new system: the



THE TEN TRIBES
OF THE FAMILY ANATIDAE

pattern of the scales on the tarsus, the plumage pattern in adults and downy young, the presence or absence of a double moult, the posture and general body proportions, the structure of the trachea and syrinx, and the behaviour, particularly courtship display.

In all, 247 forms, belonging to 147 generally accepted species, have been described. These are placed in 43 genera, grouped in 10 tribes and more broadly divided into 3 subfamilies, thus:

Family:	Anatidae	
Subfamily:	Anseranatinae	
Tribe:	Anseranatini	Magpie Goose
Subfamily:	Anserinae	
Tribes:	Dendrocygnini	Whistling ducks or tree ducks
	Anserini	Swans and true geese
Subfamily:	Anatinae	
Tribes:	Tadornini	Shelducks and sheldgeese
	Anatini	Dabbling ducks
	Aythyini	Pochards
	Cairinini	Perching ducks and geese
	Somateriini	Eiders
	Mergini	Scoters, goldeneyes, and mergansers
	Oxyurini	Stifftails

Of the 10 tribes, 8 contain species to which the substantive name 'duck' is applied, and the degree to which some ducks may differ in their relationships from other ducks is illustrated by the fact that the single tribe Anserini includes such apparently different birds as swans and geese, while much greater taxonomic differences exist between, say, pochards and stifftails, in spite of their similarities of appearance and habit. Similarly, 'goose' is the substantive name of some species of 4 of the 10 tribes and all 3 of the subfamilies. 'Swan' is applied only in 1 tribe, but not to all its members.

Magpie Goose. The subfamily Anseranatinae (and sole tribe Anseranatini) consists of a single species, the aberrant and apparently primitive Magpie Goose *Anseranas semipalmata* of Australia, an untidy black-and-white bird in which the elongated toes are only slightly webbed and in which, unlike almost all other Anatidae, the flight feathers are moulted progressively instead of simultaneously, so that there is no flightless period. The Magpie Goose seems to form some kind of link with the family Anhimidae, placed in the same order (see SCREAMER and NEST FUNCTION).

Whistling ducks (tree ducks). The Dendrocygnini are confined to the tropics. They show no sexual dimorphism, and, as in the Magpie Goose and some swans, both sexes incubate the eggs. They dive freely for food, and they indulge in mutual preening. One species, the Fulvous Whistling Duck *Dendrocygna bicolor*, has a remarkably wide range, occurring (apparently without geographical subspeciation) in North America, South America, Africa, and India.

Swans and 'true geese'. The Anserini comprise the swans, in the genera *Coscoroba* and *Cygnus*, and the geese of the genera *Anser* and *Branta*. There are 9 forms of swan—all large, herbivorous, aquatic birds with notably long necks and powerful, spatulate bills. They show no sexual dimorphism in plumage, and all the species lay pale-coloured eggs in a bulky nest on the ground; the nidifugous down-covered young ('cygnets') hatch after an incubation period of from 34–40 days. The immature plumage is brownish or greyish.

Fig. 1. (opposite). Examples of the 10 tribes of the Family Anatidae.
Anseranatini: Magpie Goose *Anseranas semipalmata* (Australo-Papuan area).
Dendrocygnini: Fulvous Whistling Duck *Dendrocygna bicolor* (pantropical).
Anserini: Bewick's Swan *Cygnus columbianus bewickii* (northern Palearctic), and (in front) Canada Goose *Branta canadensis* (northern Nearctic).
Tadornini: Andean Goose *Chloephaga melanoptera* (western Neotropical), and (on right) Shelduck *Tadorna tadorna* ♂ (Palearctic).
Anatini: Mallard *Anas platyrhynchos* ♂ (Northern Hemisphere), and (behind) Peruvian Torrent Duck *Merganetta armata leucogenis* ♂ (Peru and Ecuador).
Cairinini: wild Muscovy Duck *Cairina moschata* ♂ (Neotropical), and (in front) Mandarin Duck *Aix galericulata* ♂ (eastern Asia).
Somateriini: Eider *Somateria mollissima* ♂ (northern Holarctic).
Aythyini: Pochard *Aythya ferina* ♂ (Palearctic).
Mergini: Goldeneye *Bucephala clangula* ♂ (northern Holarctic), and (behind) Red-breasted Merganser *Mergus serrator* ♂ (northern Holarctic).
Oxyurini: North American Ruddy Duck *Oxyura jamaicensis jamaicensis* ♂ (North America and West Indies). (*Peter Scott*)

The Coscoroba Swan *Coscoroba coscoroba*, a South American species, is the smallest of the world's swans, and has been held to show some affinities with the whistling ducks (Dendrocygnini). The remaining swan species are now generally placed in a single genus, *Cygnus*, and include 2 Southern Hemisphere forms, the Black-necked Swan *C. melanocoryphus* of South America and the Black Swan *C. atratus* of Australia, and in the Northern Hemisphere 5 distinct forms in which the adult plumage is white (and a sixth poorly differentiated local race).

The Mute Swan *C. olor*, which has some affinities with *C. atratus*, is an Old World species semi-domesticated in western Europe for about 900 years, originally as a source of food. In England these swans were subject to special legislation and the Crown granted 'royalties' enabling certain noblemen and corporate bodies, such as livery companies of the City of London, to own swans and to mark their bills with registered symbols or 'swan marks'. Any Mute Swans on the River Thames not so marked were the property of the Crown. Annually on the Thames the young swans were, and still are, captured for marking in a traditional colourful ceremony known as 'swan upping'. The only royalties in swans still remaining are those granted to the Dyers and Vintners Companies and to the Earl of Ilchester, owner of a famous 'swannery' or colonial nesting site for Mute Swans at Abbotsbury in Dorset, where in some years more than 50 pairs nest in close company. An albinistic phase of the Mute Swan known as the Polish Swan, in which the legs and feet are pinkish grey instead of black and the first plumage of the cygnets is white instead of the normal brownish grey, is rare in Britain but common in parts of Europe and among introduced Mute Swans in North America.

In the Palearctic Region are 2 rather similar migratory wild swans with yellow patches on their bills—the larger Whooper Swan *C. cygnus cygnus* and the smaller Bewick's Swan *C. columbianus bewickii*, from which an eastern race, Jankowski's Swan *C. columbianus jankowskii*, has been separated. In North America, the largest of the world's swans, the Trumpeter Swan *C. cygnus buccinator* and the smaller Whistling Swan *C. columbianus columbianus* are held to be analogous to the Whooper and Bewick's Swans, although by some not to be respectively conspecific. The Whistling Swan breeds in the Arctic and is migratory, while the much less numerous Trumpeter Swan does not apparently migrate far from its breeding grounds in the Rocky Mountains and Alaska.

There are 14 species of 'true geese'—grey geese *Anser* spp. and 'black geese' *Branta* spp. They are wary birds which graze in flocks or 'gaggles', fly in 'skeins', and are confined to the Northern Hemisphere. Most of them breed in Arctic or subarctic latitudes, and many are divided into numerous and well-marked geographical races in spite of a strongly migratory habit. In such cases, populations from a particular breeding area preserve a high degree of reproductive isolation because of strong social bonds uniting the families (and probably larger groupings) during the winter migrations. They show no sexual dimorphism in plumage; and they lay unspotted, almost white eggs, which require from 24–33 days of incubation before hatching into nidifugous down-covered young. For the most part geese are less aquatic in habit than swans or ducks. Geese have been recorded as living in captivity to an age of at least 42 years.

The typical 'grey goose' is the Greylag Goose *Anser anser*, a widespread Palearctic species from which, by selective breeding, man has evolved various domestic forms of farmyard geese; the domestic Chinese Goose was derived (probably more than 2,000 years ago) from the Swan Goose *A. cygnoides* breeding in Siberia and wintering in China (see DOMESTICATION). The White-fronted Goose *A. albifrons* has the widest range of all the grey geese, 4 races spanning the Palearctic and Nearctic Regions. The Bean Goose *A. fabalis* has a number of distinguishable races, all confined to the Old World. The most westerly form, the Pink-footed Goose *A. fabalis brachyrhynchus*—the commonest wild goose in Britain in winter—is sometimes regarded as a distinct species. In Europe and Asia these grey geese have been extolled in poetry, prose, and painting as the most romantic of wildfowl, the traditional quarry of particular wariness, the mysterious wanderers whose wild musical cries on migration mark the changing seasons. In many parts of Europe their great assemblies are the finest wild-life spectacle that remains to be seen.

The Bar-headed Goose *A. indicus* is probably the species of which a skein of 17 was recorded on a photograph of the sun taken at Dehra Dun, India, at a height variously estimated at between 7,500 and 8,500 m; it has a slightly larger wing area for its weight than the other grey geese, perhaps because of the high altitudes required for its migration from breeding grounds in Tibet to the plains of India.

In North America the Snow Goose *A. caerulescens* is dimorphic. In adult plumage one phase is pure white with black primaries, while in the other—the 'Blue Goose'—there is a variable amount of slate grey on the body, most characteristically only the head and part of the neck being white. This dark plumage, perhaps a recent mutation, appears to be dominant (although the genetics are complex), increasing in its incidence and spreading westwards in the most widespread race of the species, the Lesser Snow Goose *A. c. caerulescens*. No blue phase is known in the larger eastern race, the Greater Snow Goose *A. c. atlanticus* (although some blue Lesser Snow Geese are found in flocks of Greater Snow Geese), or in the much smaller Ross's Goose *A. rossii*, which is specifically distinct and confined to a narrow western range in very much smaller numbers. The handsome Emperor Goose *A. canagicus*, with small heavily loaded wings, has a short migration route from the Alaskan coast along the Aleutian chain; the white head of this species in the wild state is usually stained to a deep orange yellow by iron deposits in the water, a condition also seen in Snow Geese and in swans.

The name *Branta*, like the English 'brent' and the American 'brant', is taken from the rolling call of the bird. Three or possibly 4 distinguishable races of the Brent Goose (or Brant) *Branta bernicla* breed in the high Arctic in a circumpolar distribution and winter in the intertidal zones of temperate coasts. The failure (probably through disease) of its principal food supply, the sea-grass *Zostera*, caused catastrophic reductions in the numbers all over the world between 1930 and 1940. Unlike other species of geese, wild-caught Brent Geese rarely nest in captivity. The Barnacle Goose *B. leucopsis* is also a high Arctic breeding species but has a very restricted winter range in western Europe. In the Middle Ages it was believed that these geese were hatched from ship barnacles (*Cirripedia*) and were therefore 'fish' rather than 'fowl'; they were thus permitted as food on Fridays. This belief also extended to the Brent Goose, which was known—particularly in Roman Catholic Ireland—as the 'Barnacle' (or 'Bernicle'); *B. leucopsis* was called the 'Land Barnacle'.

The most elaborate and striking plumage pattern among the Anserini is that of the Red-breasted Goose *B. ruficollis*, breeding in northern Siberia and wintering now mainly near the Black Sea. It is handsomely marked in black and white and chestnut brown and is the smallest of the true geese (although Ross's Goose is scarcely larger).

The Canada Goose *B. canadensis* has been divided into at least 12 distinguishable geographical races. Some authorities hold that many more discrete populations can be recognized. All have the same black head and neck with white cheek patches, but they vary greatly in size and in the shades of brown of the body plumage. The larger races, known as 'honkers', provide one of the principal quarry species of the American 'duck-hunter'. The Ne-ne or Hawaiian Goose *B. sandvicensis* is an island species, probably of common stock with *B. canadensis*, which now has reduced webs to its feet and shorter wings because of its less aquatic and non-migratory habit. In 1950 the total population was believed to be under 50, but intensive captive breeding projects in Hawaii and England had increased the figure to more than 2,000 by 1979. The Ne-ne is the 'state-bird' of Hawaii.

Shelducks and sheldgeese. Somewhat gooselike are the shelducks in the tribe Tadornini. The Crested Shelduck *Tadorna cristata* is believed to have become extinct; it is known only from 3 specimens, 2 from Korea and 1 from near Vladivostok, although it is illustrated in several ancient Japanese prints. The New Zealand Shelduck *T. variegata*, and to a lesser extent the South African Shelduck *T. cana*, exhibit a bright plumage in the female that is evidently analogous to the bright plumage in the males of other duck species; for example, in *T. variegata* the immature plumage resembles that of the male, in which the head is black, while the adult female assumes a white head and moults annually into a slightly duller post-nuptial 'eclipse' plumage. This sexual inversion is incomplete and, in contrast to the phalaropes (Phalaropodinae) and certain Accipitriformes, the male shelduck is larger than the female and dominates the pair.

In Australia the Cape Barren Goose *Cereopsis novaehollandiae*, a large grey bird mainly confined to islands in the Bass Strait and now apparently increasing in numbers, has been held to link the 'true geese' with the Tadornini although it may more properly belong to the Anserini. The South American genus *Chloephaga* consists of 5 species of goose-like grazing birds all with a sharply defined mirror or 'speculum' of iridescent colours on the secondary coverts (in contrast to the iridescent secondaries in the 'true ducks' of the tribe Anatini). At least some individuals of one species, the Ruddy-headed Goose *C. rubidiceps*, now considered an endangered species, moult their flight feathers progressively and have no flightless period; this may be true of other *Chloephaga* species. Two of the species, the maritime Kelp Goose *C. hybrida* and the Upland (or Magellan) Goose *C. picta*, display very marked sexual dimorphism, the males being white or predominantly white, the female predominantly dark brown or reddish brown. In the other 3 the sexes are scarcely to be distinguished by plumage differences, although in the Andean Goose *C. melanoptera* both are largely white ('male' colour), while in the Ashy-headed goose *C. poliocephala* and the Ruddy-headed Goose both are dark ('female' colour). In the Abyssinian Blue-winged Goose *Cyanochen cyanoptera* (which is closely related to *Chloephaga*), there is no sexual dimorphism, and the same applies to the Egyptian Goose *Alopochen aegyptiacus* and the Orinoco Goose *Neochen jubatus*, which seem to link the sheldgeese with the shelducks of the genus *Tadorna*.

Certain further South American species have been included in this tribe—the Crested Duck *Lophonetta specularioides*, and the 3 steamer ducks *Tachyeres* spp.—but doubt has been cast on this relationship. The latter are marine diving ducks of heavy build and plain plumage, and 2 of them are unable to fly (see FLIGHTLESSNESS).

Dabbling ducks. The great majority of the Anatini or dabbling ducks have been placed in the large and very various genus *Anas*, which includes the mallards, pintails, wigeons, shovelers, and many different species of teal. In some, especially those frequenting the Northern Hemisphere, there is a sharp sexual dimorphism, the males having a bright nuptial plumage (linked with a more or less elaborate courtship display), which is replaced by a cryptic 'eclipse' plumage (resembling the plumage of the female) during the annual flightless period. The males of most Southern Hemisphere species, however, remain similarly coloured throughout the year; the bright plumage of the males of northern species seems to have been lost (rather than never developed) in sedentary and island races, and the brightness is most marked in the most migratory forms.

Of the dabbling ducks only the Mallard *A. platyrhynchos* has been domesticated, giving rise to various familiar forms (see DOMESTICATION). Aberrant species that have been included in the dabbling duck tribe are the Torrent Duck *Merganetta armata* subspp. of the Andes, the now probably extinct Pink-headed Duck *Rhodonessa caryophyllacea* of India (which may have formed a link with the pochards), the Marbled Teal *Marmaronetta angustirostris* of the Mediterranean and Near East (which almost certainly forms such a link), and 2 strange species from Australia—the little Pink-eared Duck *Malacorhynchus membranaceus* specially adapted for feeding on blue-green algae, and the Freckled Duck *Stictonetta naevosa* which shows some affinities with the geese and may finally prove to belong to the subfamily Anserinae, perhaps in a tribe of its own. The taxonomic position of the Blue (or Mountain) Duck *Hymenolaimus malacorhynchos* of New Zealand, of which the bill is adapted as a sucker and the principal food is probably green algae sucked from the stones of fast running streams, is still obscure; but the Ringed Teal *Callonetta leucophrys* is now believed to belong to the tribe Cairinini, perhaps forming a link with the Anatini.

The Pintail *Anas acuta*, which has a wide circumpolar range, is probably the most numerous duck species in the world, and the dabbling ducks of the genus *Anas* provide three-quarters of the quarry for the wildfowler or duck-hunter (see WILDFOWL); most of the other quarter is provided by the next tribe.

Pochards. The Aythyini include the famous North American sporting bird the Canvasback *Aythya valisineria*, which is closely related on the one hand to the Pochard *A. ferina* of Europe and on the other to the sympatric American Redhead *A. americana*. The Tufted Duck *A. fuligula* is the most familiar representative in Britain. The Greater Scaup *A. marila*, called in North America 'Bluebill' or 'Broadbill', has a circumpolar breeding range and is found in huge 'rafts', principally on salt water, in many parts of the world. Several of the species share the substantive name 'white-eye'. With the exception of the genus *Netta*, the pochards are all accomplished divers.

Perching ducks and geese. The tribe Cairinini shows the widest range in size in the Anatidae. Male Spurwinged Geese weigh up to 10 kg, while the smallest of the Pygmy Geese (or Cotton Teal) *Nettapus* spp. weigh only 230 kg. The tribe also includes the most brilliantly coloured and fantastically marked of the Anatidae. The drakes of the Mandarin Duck

Aix galericulata of China, and of the related Wood (or Carolina) Duck *Aix sponsa*, of North America, have patterns of astonishing complexity and beauty. Pairs of caged Mandarin Ducks were formerly given as presents at Chinese weddings as symbols of marital fidelity. The influence of the drake's pattern and colour on Chinese art and culture is demonstrated by the inescapably 'Chinese' appearance of the bird.

The large polygamous Muscovy Duck *Cairina moschata* of Central and South America is one of the 4 species of Anatidae to be domesticated (the others being the Greylag Goose *Anser anser*, the Swan Goose *A. cygnoides*, and the Mallard *Anas platyrhynchos*). The wild form of the Muscovy Duck is black, glossed with green, with extensive white patches on the wings. Domestic birds are of increased size (although relatively less so than in some domesticated varieties of the Mallard) and have white, grey, and speckled plumage patterns; the enlarged caruncle on the bill becomes conspicuously scarlet.

The largest of the Cairinini is the Spurwinged Goose *Plectropterus gambensis* of Africa, an untidy bird of dark glossy green with variable amounts of white. Related is the polygamous Comb Duck *Sarkidiornis melanotus* subspp., often called Knob-billed or Knob-nosed Goose, in which the metallic colours of the mantle are very brilliant; one form is common in Africa and India, while the other is found in South America. The Australian Wood Duck (or Maned Goose) *Chenonetta jubata* is rather closely related to the ducks of the genus *Aix* (above) in spite of its gooselike bill and gait. The 3 species of Pygmy Geese of the tropical genus *Nettapus* (the smallest of the Anatidae) must have been called 'geese' because of the triangular gooselike bill, apparently adapted for eating the seeds of water lilies, but they are in fact tiny perching ducks.

Eiders. The Somateriini are a tribe consisting of 4 species of marine ducks all living in the north. The Eider *Somateria mollissima* is divided into 5 races and commonly nests in colonies, which have been exploited by man for the manufacture of eiderdowns. As in most other species of Anatidae, the female plucks down from her breast in order to line the nest. The best quality down is taken from the Eider's nest, without harmful effect, a few days before hatching, and the second best quality after the eggs are hatched and the young have left the nest. No artificial substitute for this down has been found, and that from a single nest may be worth about £3.00. Some Eider colonies in Iceland have up to 10,000 nests and are intensively encouraged by their owners by methods that include the spreading of coloured ribbons, musical instruments which play in the wind, and rows of 'semi-detached' artificial nesting sites. The species is common in northern parts of Britain.

Scoters, Goldeneyes, and Mergansers. The tribe Mergini includes a number of ducks which, like those in the Cairinini, do not at first sight appear to be closely related. All are good divers. With the exception of the rare Brazilian Merganser *Mergus octosetaceus* and the now extinct Auckland Island Merganser *M. australis*, the tribe is confined to the Northern Hemisphere. The small extinct Labrador Duck *Camptorhynchus labradorius*, of which the last was shot in 1875, was related to the scoters and may have linked them to the eiders (by way of the small Steller's Eider *Polysticta stelleri*). The 3 scoters *Melanitta* spp. are largely marine except in the breeding season; the males are predominantly glossy black.

The affinities of the goldeneyes *Bucephala* spp., Harlequin Duck *Histrionicus histrionicus*, and the Long-tailed Duck (or Oldsquaw) *Clangula hyemalis*, are evident; but the last exhibits an unusual moulting sequence, with contrasting dark summer and light winter plumages in the male, which may or may not be strictly analogous to the 'eclipse' in other species. The Long-tailed Duck is one of the fastest fliers among the Anatidae; a speed of 115 kph has been reliably recorded in level flight. The little Bufflehead *B. albeola* links the goldeneyes with the scoters, and perhaps also (by way of the Smew *M. albellus*) with the sawbills of the genus *Mergus*, which is held to be rather closely related to the goldeneyes in spite of the long narrow serrated bill adapted for catching fish.

Stifftails. The last and rather isolated tribe of the Anatinae is the Oxyurini, a group of extremely aquatic and largely nocturnal freshwater ducks, in most of which the rectrices are long and stiff and evidently have an important underwater control function. The genus *Oxyura* is represented in all 6 continents by small round diving ducks in which the male in breeding plumage is chestnut red with a brilliant blue bill. The display is elaborate and differs widely in the various species. The male of the very large Musk Duck *Biziura lobata* of Australia carries a large fleshy lobe under the bill. The Black-headed Duck *Heteronetta atricapilla* of South America lacks the long tail of the tribe and is interesting specially for its apparently parasitic egg-laying habit; the eggs have been found in nests of coots and rails (Rallidae), herons, and even of a carrion-eating hawk, one of the caracaras *Polyborus* spp. (see BROOD-PARASITISM). The African White-backed Duck *Thalassornis leuconotus* appears to be an aberrant stifftail, although its voice, anatomy, and behaviour, and the pattern of the downy young suggest that the relationship may not be very close.

See photos AGGRESSION; DISPLAY; FEEDING HABITS P.S.

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DUCKLING: special term for a young (not full grown) DUCK.

DUCTLESS GLANDS: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

DUETTING: male and female of a pair singing or calling together, or almost together and responsively (see VOCALIZATION).

DUIKER, REED: name, in South Africa, for the Long-tailed Shag *Phalacrocorax africanus* (see CORMORANT).

DULIDAE: a family of the PASSERIFORMES, suborder Oscines; see PALMCHAT and under BOMBYCILLIDAE.

DUMP NESTING: laying of eggs by more than one female of usually the same species in one nest.

DUNLIN: *Calidris alpina* (see SANDPIPER). See photo COMFORT BEHAVIOUR.

DUNNOCK: alternative and often preferred name of the Hedge-sparrow (misnomer) *Prunella modularis* (see ACCENTOR).

DUODENUM: the anterior part of the small intestine (see ALIMENTARY SYSTEM).

DUSTING: highly specialized, stereotyped behaviour of birds whereby 'dust' (fine earth, sand, etc.) is deliberately introduced into the plumage and later expelled. The synonyms 'dust-bathing' and 'sand-bathing' are also used but it seems preferable to restrict the term 'bathing' to true bathing in water; see COMFORT BEHAVIOUR. The habit is most characteristic of species living in or originating from bare open habitats, particularly desert, steppe, and savanna, where water for bathing—especially of the 'stand-in' type—is scarce or absent, seasonally at least. Among non-passerines, dusting occurs regularly in the Ostrich *Struthio*, rheas, gamebirds, buttonquails, seriemas, bustards, seed-snipes, sandgrouse, nightjars, mousebirds, motmots, bee-eaters, rollers, hoopoes, and hornbills; it has also been reported among some hawks, falcons, doves, and owls. Fewer passerines are known to dust but the habit is well-documented for the larks, wrens, and sparrows of the genera *Passer*, *Petronia*, and *Montifringilla*, and has also been reported in the Wren-tit *Chamaea*, White-winged Chough *Corcorax melanoramphus*, some American sparrows of the genera *Spizella* and *Pooecetes* (Emberizinae), and the Common Grackle *Quiscalus quiscula* (Icteridae). Many birds that dust do not bathe at all and others only in the rain (e.g. larks) or from flight (e.g. bee-eaters); some, however, both dust and stand-in bathe (e.g. Ostrich, Common Rhea *Rhea americana*, falcons, grouse *Lagopus*, seed-snipes, owls, mousebirds, rollers, wrens, and sparrows *Passer*).

Dusting bouts are typically organized in three main phases, often repeated: (1) loosening the substrate if necessary and the formation of dusting hollows or wallows by scraping and digging; (2) tossing the dust up into and on the plumage and rubbing the head in the dust; and (3) ruffling the dust through the plumage and shaking it out. Though the dusting bird may stand initially, it squats or lies down for most of the bout with feathers ruffled and wings drooped, often rotating its body, rising from time to time and at the end to shake. Details vary between groups and the behaviour has evidently evolved independently a number of times, even among birds of the same order in some cases (e.g. passerines). No species, however, really 'bathe' in dust, i.e. confine their activity to the movements and co-ordinations of true stand-in bathing in water, though some use odd water-bathing elements; neither is there any good reason to believe that dusting is the exact functional replacement for bathing. Among passerines, the House Sparrow *Passer domesticus* gets dust into the plumage mainly by wing-flicking (a bathing movement) but loosens the earth and forms its dusting hollow by leg-scraping (scratching) and bill-flicking; the Wren *Troglodytes troglodytes* dusts similarly but uses a wing-flipping action (also a bathing movement); the White-winged Chough dusts in an aberrant manner while standing, applying billfuls of dust to various parts of its plumage and dealing with the wings by movements like those used in oiling (see COMFORT BEHAVIOUR) and active anting behaviour (see ANTING). Among near-passerines, the Hoopoe *Upupa epops* digs up earth round its breast with a hoe-like raking movement of the bill, mandibles opening and closing as it pecks up detritus and flicks it inwards; it then tosses up the dust into the plumage mainly with the feet, moving forward repeatedly into freshly prepared earth. Among galliform birds, dusting has been studied best in the Phasianidae, especially the Bob-white *Colinus virginianus*, Red-legged Partridge *Alectoris rufa*, and Japanese Quail *Coturnix japonica*, their behaviour being closely similar to that of fowls *Gallus* and pheasants *Chrysolophus* and *Phasianus*; all loosen earth by pecking with the bill, scratch up dust into the plumage with the feet, and throw it up on the back with the wings.

Recent evidence strongly suggests that dusting helps in feather maintenance (see COMFORT BEHAVIOUR), either on its own or in combination with the head-scratching and preening that intersperse or follow bouts (but see ANTING and SUNNING). Experiments on quails (both *Colinus* and *Coturnix*) indicate that regular dusting maintains the optimum amount of oil on the plumage by removing excess preen-oil and other feather lipids, these being absorbed by the dust and then removed with it plus any dry skin, feather débris, etc.; the plumage of birds deprived of the opportunity to dust becomes oily and matted within a few days. (Similar results have been obtained in studies of small mammals, including gerbils *Meriones*, chinchillas *Chincilla*, and kangaroo-rats *Dipodomys*.) The House Sparrow and the Wren often dust and preen, etc. after bathing. Other functions in feather maintenance are also likely, including the treatment of ectoparasites (if present) and their discouragement; as with anting and sunning, the absence of such parasites at times when the behaviour occurs does not disprove the theory. Speculation that dusting soothes the skin during the moult by applying heat to the feather tracts seems ill-founded; there seems to be no seasonal correlation, incidental or otherwise, between dusting and moulting and, indeed, moulting *Coturnix* quail have been shown to dust significantly less during the moult than at other times. K.E.L.S.

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(For further references, see COMFORT BEHAVIOUR and SUNNING.)

E

EAGLE: substantive name of large members of the Accipitridae, e.g. *Aquila*, *Haliaeetus* and *Circaetus* (see HAWK).

EAR: see HEARING AND BALANCE.

EAR COVERTS: modified contour feathers which cover the outer openings of the ears (see PLUMAGE; TOPOGRAPHY).

EAR TUFT: a bunch of long feathers towards the top of the head found particularly in owls. They can be erected when the bird is excited or afraid but have nothing to do with the ears or with hearing. An ear tuft may also be called a 'horn'.

EARLY EVOLUTION OF BIRDS: the debate over the origin of birds has been renewed in recent years after many decades of relative quiescence. There never has been any question that the late Jurassic fossil *Archaeopteryx lithographica* is the closest relative of all modern birds, (see ARCHAEOPTERYX), but opinions differ as to which group of archosaurs, the crocodiles, thecodonts or theropod dinosaurs, is most closely related to the avian lineage. The classic work of Heilmann in the 1920s suggested a thecodont ancestry, quite independent of those lineages which led to the crocodiles or to the sauropod and theropod dinosaurs. This traditional view has been challenged by Ostrom, who has argued that the avian lineage (including *Archaeotperyx*) is most closely related to theropods. He cites an impressive list of shared similarities in the postcranial skeleton in support of his claim. A third view is that *Archaeopteryx* and modern birds are more closely related to crocodiles than to theropods. At present the theropod hypothesis is to be preferred, if only because of the greater volume of evidence marshalled by Ostrom (1974, 1976).

With respect to our attempts to understand the biological transformations that took place between 'reptiles' and modern birds, it may not matter which of the above hypotheses we accept, because the most relevant source of evidence for inferring these transformations would seem to be *Archaeopteryx*. But the problem remains: how are hypotheses about the origin of birds to be tested? The structure of *Archaeopteryx* can be reconstructed and inferences can be made about its functional-mechanical characteristics. From this, 'scenarios' about the transformation to the modern avian condition can be created, but must be subject to critical evaluation, i.e. it must be possible to reject them, even if only by challenging the consistency of the arguments, since the chances of testing them empirically are small. Ostrom's hypothesis about the origin of flight is a case in point. He postulates that *Archaeopteryx* and its close relatives were primarily terrestrial predators and in pursuit used their feather-covered forelimbs as 'insect nets'. Such behaviour and morphology, he theorizes, 'pre-adapted' this lineage for powered flight. The traditional hypothesis is that an arboreal *Archaeopteryx* developed the ability to fly by parachuting and gliding between trees or to the ground. *Archaeopteryx* itself does not provide compelling evidence against either hypothesis. The latest interpretations suggest that *Archaeopteryx* possessed moderate aerodynamic capabilities, if not powered flight, but this is consistent with either a terrestrial or arboreal origin of flight. If *Archaeopteryx* is interpreted as arboreal, one could argue that its ancestors were terrestrial and already had the power of flight (Ostrom's hypothesis); if *Archaeopteryx* is interpreted as being primarily terrestrial, acquisition of arboreal habits could still be necessary for the evolution of an aerodynamic capability. Actually, the structure of *Archaeopteryx* does not seem designed exclusively either for a terrestrial or an arboreal existence, further complicating the issue. Any preferred hypothesis could be saved from falsification by shifting the postulated events backward or forward in time. Thus, such narrative-type scenarios on evolution of FLIGHT, homeothermy, origin of FEATHERS or other characteristics can scarcely be scientifically tested. Phylogenetic hypotheses, on the other hand, are rigorously testable in that they can be supported or not by analysis of new characters or new taxa. Some of these hypotheses, and their implications for the early history of birds, are considered below. It must be stressed that opinions on almost any hypothesis differ widely, that few critical evaluations have been published and that space does not permit extensive description of the evidence for or against.

One major lineage, comprising the divers, grebes, penguins, petrels, shearwaters and allies, may be one of the basal groups of birds. The divers, grebes and several Cretaceous diving birds, including *Hesperornis*, share many unique characteristics of pelvis, hindlimb and skull. Relationship of those groups to the penguins is supported by similarities of skull, sternum and pelvis. Pelecaniforms and procellariiforms seem to be good monophyletic taxa and similarities in their skull morphology suggest that they may be sister groups and related to the diving birds and penguin lineage, thus forming a single large aquatic assemblage.

Further, A.C. Wilson and his colleagues have argued that these aquatic groups share a general similarity in their proteins that sets them somewhat apart from other avian lineages. Also it has long been accepted, though without compelling evidence, that penguins and procellariiforms might be closely related.

This hypothesis involves interesting implications. First, this lineage must extend back to the beginnings of avian history. The extinct diving group, the enaliornithids, is related to divers, grebes and hesperornithids. *Enaliornis* is found in lower Cretaceous deposits, which implies that the common ancestors of the lineages leading to the diving birds and penguins on the one hand, and to pelecaniforms and procellariiforms on the other, are older, extending virtually back to the time of *Archaeopteryx*, much further than previously suspected. (This does not mean that the recent families of these orders are as old.)

Secondly, the hypothesis indicates that an early evolutionary line produced an entirely aquatic radiation, thus implying that each did not occupy that environment independently.

Thirdly, the hypothesis implies the loss of reptilian features such as teeth independently in at least two lineages. *Hesperornis* possessed teeth and, if this genus is related to divers and grebes, it can be inferred that teeth were lost in the latter lineage. Likewise *Ichthyornis*, the other late Cretaceous genus known to have teeth, may be more closely related to the charadriiforms than to any other group; this implies a second independent loss of teeth in charadriiforms.

A second group, the 6 orders of ratite birds and the tinamiforms (tinamous) were considered to be very primitive unrelated taxa, with separate ancestral stocks flying to the far-flung southern continents, evolving there in isolation to produce distinct lineages of large flightless birds. But much recent morphological, behavioural and biochemical data indicate that these birds comprise a monophyletic group. One hypothesis unites the South American rheas and African ostriches, on the one hand, with the Australian cassowaries and emus on the other. These 4 groups are related to the elephant birds of Madagascar, and all 5 in turn to the moas and kiwis. Finally, the ratite assemblage is most closely related to the Neotropical tinamous, capable of flight.

Much can be inferred from this hypothesis. First, because of their relationship to the tinamous, and because they possess features (e.g. pygostyle, alula) associated with flight, the palaeognaths were not primitively flightless; this contrasts with the old view that ratites were intermediate between reptiles and 'true' birds. Secondly, the ratites became flightless once, rather than many times independently. Thirdly, large body size evolved only once, soon after the ratite lineage separated from that of the tinamous, the kiwis apparently representing a secondary reduction. Not only are the closest relatives of the kiwis, the moas, of medium to very large size, but kiwis also lay an egg that is the largest relative to body size of any bird.

The hypothesis of ratite monophyly correlates well with what is known about continental drift and the timing of the break-up of the continents. It is thus possible to erect a fairly simple hypothesis regarding the biogeographic history of the ratites, involving continental fragmentation, isolation of once widespread ancestral populations, and subsequent evolution of the various taxa.

To what extent were the ratites and tinamous a part of the basal radiation of birds? A satisfactory answer will come only when an hypothesis has been presented and corroborated regarding their closest relatives among the remaining non-passerine birds. At present there is little or no evidence supporting the earlier view that ratites represent the sister-group of all other birds (although some biochemical data are said to point to this position). Ratites and tinamous seem just as advanced morphologically as other non-passerine groups, and thus it may be they are related to some non-passerine taxon fairly far removed from the basal radiation of birds.

Recently a small number of phylogenetic hypotheses, interrelating avian orders, have been proposed which, if corroborated by further evidence, may give increasing knowledge about the early evolution of birds. Most of these hypotheses are highly controversial and all the evidence has not yet been published. Nevertheless, it is useful to summarize their findings because they provide the best picture we have of avian evolution.

The Charadriiformes (shorebirds, gulls, and allies) are undoubtedly a very old group, extending well into the Cretaceous. Interrelationships within the order are a matter of some dispute and await a well-corroborated hypothesis. The Gruiformes (cranes, rails, and allies) have been considered as related to charadriiforms, possibly on the basis of a general similarity seen between the gruiform bustard-quails and plains-wanderers (Turnicidae) and some charadriiform groups, such as the seed-snipe (Thinocoridae) or the pratincoles and coursers (Glareolidae); and the similarity of the latter family to the sandgrouse and pigeons has suggested a close relationship between columbiforms and charadriiforms. If eventually these 3 groups are seen to have close ties with one another, the relationship very possibly would define one of the major early radiations within birds.

Recently, Feduccia (1976) and Olson (1978) have suggested that flamingos (Phoenicopteridae) are not related to ciconiiforms but to avocets and stilts (Recurvirostridae) within the charadriiforms. This hypothesis is based on some osteological similarities between the 2 groups and on a general similarity in breeding habits between flamingos and the Australian Banded Stilt *Cladorhynchus*. But there are data from osteology, myology, and biochemistry in conflict with their scheme of relationships and consistent with the view that recurvirostrids are advanced charadriiforms and that ciconiiforms comprise a monophyletic assemblage.

Another phylogenetic hypothesis links the ducks, geese, and swans (Anseriformes) and the pheasants, grouse, and their allies (Galliformes). That these are sister-groups is suggested by shared similarities, interpretable as derived, in their skull morphology and behaviour, as well as a general similarity in their biochemical make-up. On the basis of an electrophoretic analysis of egg-white proteins, Sibley and his colleagues (1972) postulated that the Hoatzin (Opisthocomidae) is not related to galliforms but to cuckoos (Cuculiformes). Conflicting evidence, both from morphology and the immunological examination of their proteins, suggests that the Hoatzin may not be related to cuckoos but is instead the sister-group of the other galliforms. Whichever hypothesis about *Opisthocomus* is correct, the relationship between anseriforms and galliforms involves two orders in which the history of the primitive families seems closely tied to the break-up of the southern continents by continental drift. This implies that their ancestry extends back into the Cretaceous. For example, within the galliforms the Hoatzin is South American in distribution; the next most primitive group, the megapodes, is found in Australasia; and the next most primitive group after the megapodes, the cracids, is primarily South American. Within the anseriforms, the primitive sister-group of the ducks, geese, and swans is the screamers (Anhimidae) of South America, whereas the most primitive member of the Anatidae, the Magpie Goose *Anseranas*, is Australian. These relationships imply trans-Antarctic relationships between South America and Australia, a common biogeographic pattern in plants and animals.

There is as yet no compelling evidence to suggest a relationship between the anseriform-galliform lineage and any other order. Several candidates have been suggested, including the ratites and tinamous and also the ciconiiforms. Once a corroborated hypothesis is put forth, it will almost certainly define a major lineage in avian history extending well back into the Cretaceous.

Most of the more 'advanced' non-passerine groups cannot be viewed amongst the earliest of avian lineages, but a consideration of alternative phylogenetic hypotheses and our present knowledge of avian paleontology strongly suggest that most of these orders had their origins in the Cretaceous.

The interrelationships of the diurnal birds of prey (hawks, falcons, and their allies) and the owls (Strigiformes) have been controversial and debated for more than a century. Some well-known 19th century avian systematists, such as T.H. Huxley and F.E. Beddard, believed in a relationship whereas others, such as M. Fürbringer and H. Gadow, thought owls to be closer to the nightjars and their allies (Caprimulgiformes). Some recent workers, most notably M. Jollie, hypothesize that the diurnal birds of prey are an unnatural group, composed of perhaps 4 separate taxa.

There are a number of unique osteological and myological characteristics uniting owls with at least some of the falconiform birds, and there are few similarities between owls and caprimulgiforms. To complicate matters further, some birds of prey, such as the secretary-birds (Sagittariidae) and New World vultures (Cathartidae), show no clear-cut relationships.

The origins of these orders must go back to a time in the Cretaceous. Virtually all of them have fossil representatives in the early Cenozoic, and thus the interordinal common ancestors were older still. Of considerable interest would be the discovery of the groups of non-passerine birds to which diurnal birds of prey and strigiforms, on the one hand, and caprimulgiforms on the other, are related. Such knowledge would help define several very old lineages within birds and provide much information about the evolution of the predatory life-style.

Two orders, the cuckoos (Cuculiformes) and the parrots (Psittaciformes), require brief mention. Both have been perennial enigmas as far as their relationships are concerned. Given the array of their possible relationships to other non-passeriform groups, both must be rather old, very likely Cretaceous.

All workers have recognized the orders Coraciiformes and Piciformes to be the most 'advanced' of the non-passerine birds and have considered the song-birds (Passeriformes) to be related either to one or the other, or to both. There is general agreement that the piciforms and passeriforms each constitute a monophyletic group, and equally that the coraciiforms may be an assemblage of unrelated taxa. Passeriforms have traditionally been related to piciforms but recent work suggests that passeriforms might be related to at least some coraciiform taxa. Moreover, the trogons (Trogoniformes) and mousebirds (Coliiformes) are also possibly related to some coraciiforms. The interrelationships of these groups are being studied by several systematists. In any case, fossil evidence already suggests that the common ancestors of these lineages must have been Cretaceous in age, although many of the recent families, particularly those in the Passeriformes, are almost certainly the results of Cenozoic radiations.

It can be seen from the preceding account that the interrelationships of the avian higher taxa are in a state of flux. Yet, it is equally obvious that this is a period of great excitement within avian systematics and that each year more and more is being revealed about the evolutionary history of birds. Once we have tested and corroborated hypotheses about the phylogenetic relationships of avian taxa, we can begin to answer a number of fascinating and important questions. For example, how many times did foot-propelled and wing-propelled diving evolve? How many different lineages of birds entered an aquatic environment? How many times did raptorial behaviour and morphology evolve?

In addition to these and other questions, phylogenetic hypotheses will also allow us to reconstruct the biogeographic history of avian taxa and relate that history to the paleogeographic and paleoclimatologic changes that took place in the Mesozoic and Cenozoic. One thing is almost certain to emerge from such analysis; avian phylogeny and biogeography are more intimately related to large-scale continental movements and climatic changes than previously realized. J.C.

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EARTHCREEPER: substantive name of *Upucerthia* spp. (see OVENBIRD (1)).

ECDYSIS: see MOULT.

ECHOLOCATION: the ability to detect the presence of nearby objects by emitting sounds and analyzing echoes that return to the ears. This is found in 2 groups of birds: the Oilbird or Guacharo *Steatornis caripensis* (Caprimulgiformes, Steatornithidae) of northern South America and Trinidad, and in cave swiftlets of the genus *Aerodramus* (formerly included in *Collocalia*; Apodiformes, Apodidae) of the Indo-Pacific region (see SWIFTLET).

Uses. All these birds are cavernicolous in habit, using echolocation to find their way into the safety of caves where many of them nest and roost in complete darkness. Echolocation does not appear to be used in finding food. Oilbirds feed nocturnally on fruits and nuts which they appear to find visually, for they fly silently outside the caves. Swiftlets feed on insects, probably by sight, for they fly mainly by day although echolocation allows them to leave or return to the roost during darkness and so to forage much farther afield than would otherwise be possible. Swiftlets have also been observed feeding at night near artificial lights. Measurements of the sensitivity of their echolocation (described below) suggest that they are quite unable to detect targets as small as flying insects by this means.

Sounds. Unlike the very high-frequency (ultrasonic), vocal pulses emitted by most bats, the echolocation sounds of birds are clearly audible to man as a continuous train, or 'rattle', of sharp clicks. Sound frequencies range from 1 kHz to about 12 kHz (peak 2–4 kHz) in *Steatornis* and from 1–2 kHz to 7–16 kHz (main energy 2–7 kHz) in various *Aerodramus* species (Fig. 1). During flight in complete darkness, clicks are emitted continuously at rates of 3–20 per second, the higher rates being used when landing or negotiating an obstacle. The structure of the clicks varies in different species. The clicks of several *Aerodramus* species have been studied in detail and consist of 2 quite distinct sound impulses (Fig. 2a), each lasting for about 1 ms (millisecond) and 15–16 ms apart; the first impulse is of lower intensity than the second. These double clicks somewhat resemble those of the echolocating fruit-bats *Rousettus* (2 impulses of similar intensity, 20–30 ms apart but with sound frequencies of 10–65 kHz). Occasional triple clicks have been reported in *A. vanikorensis granti*. In *Steatornis* and in *Aerodramus maximus*, however, each click consists of a rapid burst of about 5–8 impulses within an interval of 20 ms (Fig. 2b, c). The significance of these different patterns is not yet clear but probably each provides more detailed information about the target than could be obtained from a single impulse.

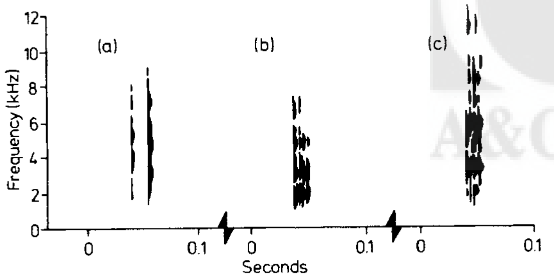

Fig. 1. Sound spectrograms of the echolocation clicks of: (a) the Edible-nest Swiftlet, *Aerodramus fuciphagus*; (b) the Black-nest Swiftlet, *Aerodramus maximus*; (c) the Oilbird, *Steatornis caripensis*.

The mechanism by which the clicks are generated is not known. In the fruit-bat *Rousettus* the double impulse is produced by clicking the tongue and this may also occur in the birds. Other suggestions are that the sounds originate in some part of the respiratory tract, such as the syrinx. However they are produced, the sounds seem to be emitted via the open bill since the echolocating *Aerodramus vanikorensis* swiftlets that incorporate vegetable material in their nests carry it in their feet; the non-echolocating species of swiftlets, *Collocalia esculenta* and *Hydrochous gigas*, carry nest materials in the bill.

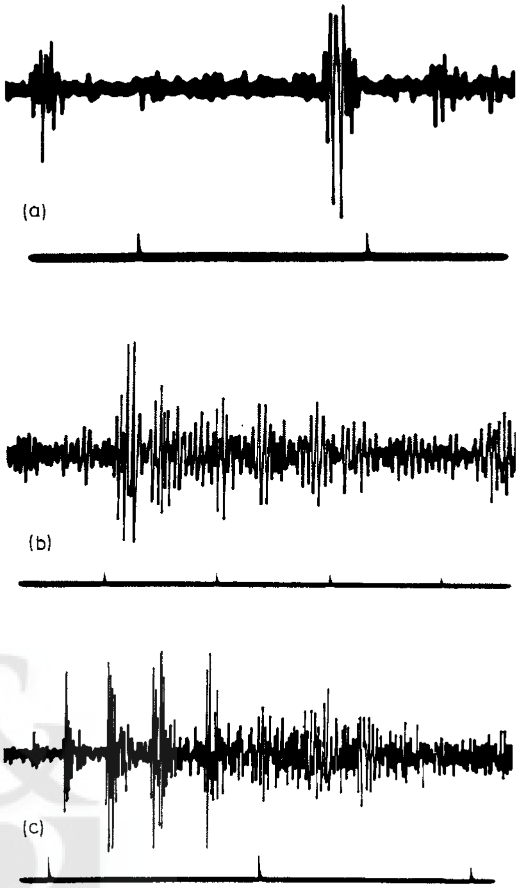

Fig. 2. Oscilloscope waveforms of the echolocation clicks of: (a) *Aerodramus fuciphagus*; (b) *Aerodramus maximus*; (c) *Steatornis caripensis*. All time markers equal 1/100 sec.

Hearing. The ears of echolocating animals form the receiver of the system so the sense of hearing in these species is of special interest. In general birds do not hear high frequencies (unlike most mammals) and recent observations suggest that *Steatornis* is no exception. Both the inner

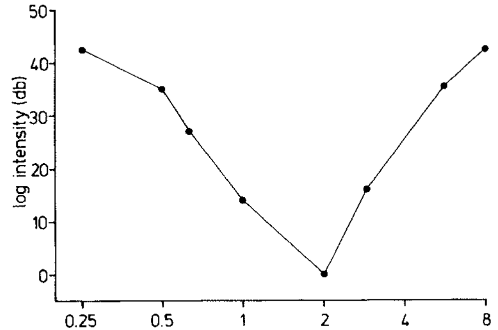

Fig. 3. Characteristic hearing curve of *Steatornis caripensis*. (Derived from Konishi & Knudsen 1979).

ear and the auditory region of the brain show sensitivity extending from 250 Hz to 8 kHz with a pronounced peak at 2 kHz (Fig. 3). This is at the lower end of their click spectrum but coincides with the most intense components. The effective wavelengths used for echolocation are therefore about 17 cm. Nothing is known of the range of hearing in *Aerodramus* although tests of its echolocation acuity (described below) suggest that shorter wavelengths and therefore higher frequencies are used.

It has been suggested that the auditory nerve in birds is able to follow much more rapid changes of sound intensity than is possible in mammals. If this is the case, birds would seem to be pre-adapted for the detection of echoes from emitted clicks. More recent work, however, suggests that the original comparison was not entirely valid and that birds in general are not especially outstanding in this respect. It remains to be seen whether echolocating birds show any special adaptations, as *Rousettus* does when compared with other, non-echolocating fruit-bats.

Acuity. One test of the accuracy and sensitivity of an echolocating system is the ability to detect and avoid fine wires or rods suspended in the flight path. Early work on different species of *Aerodramus* produced rather conflicting results. *A. fuciphagus* was apparently unable to detect wooden rods of 1 cm diameter although *A. vanikorensis* could avoid 6 mm rods. More recent tests on *A. hirundinaceus* with rods of 1 cm or 4 mm and wires of 1.5 mm diameter support the earlier results for *A. vanikorensis* and suggest that even the finer wires were often detected.

Results of tests on *Steatornis* in outdoor aviaries indicate that vision is used in preference to echolocation even on moonless but starlit nights. When blindfolded, the birds clicked continuously but hovered instead of negotiating obstacles. Arrays of plastic discs, with diameters from 5 cm to 40 cm, were then hung in turn in a passageway of the roosting cave. Only discs of 20–40 cm were avoided, suggesting that the acuity of echolocation is very low in this species. Direct comparisons are difficult because flat discs reflect sound in a different way from cylindrical rods or wires. Nevertheless, it seems likely that acuity and sensitivity are higher in *Aerodramus* than in *Steatornis*. The strength and directionality of echoes depend on the sound wavelength in relation to the size of the reflecting object, so it is possible that *Aerodramus* actually 'use' shorter wavelengths from the higher frequencies present in their clicks.

Both groups of birds are far inferior in their echolocation performance to the ultrasonic bats that use centimetre or even millimetre wavelengths and can detect wires as fine as 0.1 mm diameter. This is not surprising for their systems have very different purposes. Whereas many bats have to detect and intercept small flying insects that may be actively evading pursuit, the birds apparently have only to negotiate their presumably familiar caves, find their nests and avoid collision with their neighbours. How they (and bats) manage to do this when enormous numbers are flying in a confined space is still a complete mystery. J.D.P.

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ECLECTUS: former generic name used as English name (otherwise 'Eclectus Parrot') of *Lorius roratus* (see PARROT).

ECLIPSE: a post-nuptial plumage stage occurring in some species. It is characterized by being of much shorter duration than the winter (or non-breeding) plumage in most species that show marked seasonal change, as well as by being dull in comparison with a conspicuous breeding dress. Notably, the males of many of the Anatidae are in full breeding plumage for the greater part of the year but have a dull plumage during the latter part of the summer (while a simultaneous moult of the remiges may render them temporarily flightless)—see DUCK; MOULT; PLUMAGE.

ECOGEOGRAPHICAL RULES: term proposed by Mayr (1956) as a replacement for the less satisfactory term 'ecological' or 'climatic rules', for the 'rules'—used in the sense of generalizations that are widely valid but not without exceptions—relating geographical variation in size, proportions, colour, and other characters of animals to climate and other environmental factors. The best known of such rules in birds are BERGMANN'S, ALLEN'S and GLOGER'S, and the tendency for clutch-size to increase with latitude. (See also ENERGETICS, Climatic adaptation).

Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution 10: 105–108).

ECOLOGICAL ISOLATION: a term used in at least two quite separate ways.

Oceanic islands, or mountain tops surrounded by forest are ecologically isolated, in a purely physical sense from other, similar areas of habitat. Extreme isolation favours the evolution of endemic species.

In an entirely different context, a set of species may be said to be ecologically isolated from one another by virtue of their distributions, feeding or nesting ecologies. The term may be applied either to a set of closely related species from one geographical area, or to a set of species, only some of which are closely related, sharing a habitat.

In both cases, ecological isolation refers to the manner in which each of the species in question differs in its ecology from congeners and/or cohabitants. Species may be isolated geographically, locally between habitats, or have different feeding or nesting ecologies within habitats. The European titmice (Paridae) provide excellent examples of all these methods of ecological isolation.

Lack, D. 1971. Ecological Isolation in Birds, Oxford and Edinburgh.

ECOLOGICAL RELEASE: an increase in the abundance of a species and/or a broadening of its feeding ecology in the absence of a competing species: most often used to describe what happens to the ecology of a species if it occurs on a faunally impoverished island with few competitors.

ECOLOGICAL SUCCESSION: the changes that occur in a habitat over time, due to habitat modification by former colonists (the build-up of humus, for example) and the arrival of new species. Thus bare ground undergoes succession through scrub to woodland, and lakes gradually fill in and become marshes. Many bird species are associated with ecological communities in a particular stage of succession; scrub woodland, second growth forest, or reed-swamps for example, all of which are stages in ecological successions to different habitats.

ECOLOGY: variously defined as the study of plants and animals in relation to their environment; the study of the distribution and abundance of organisms; and the study of the structure and function of nature.

It is well known that each species of bird breeds and spends the non-breeding season, respectively, in characteristic areas of the earth; these areas, which in many instances are the same, form the geographical range or distribution of the species (see also DISTRIBUTION, GEOGRAPHICAL; MIGRATION). Within these areas, the species will occupy only certain habitats, and within the habitat, each species has a characteristic behaviour and abundance. It interacts with other birds, with its food organisms, with its own predators, and less directly with numerous other living things that share its habitat. The search for patterns within these phenomena, and for the principles which underlie them, constitute the main objectives of avian ecology.

Ranges and niches. Evidence for direct climatic limitation of species' ranges is generally poor, but there are some well-documented examples. The further dispersal of the House Sparrow *Passer domesticus* into desert regions of North America may now be limited by daily maximum temperatures surpassing its upper limit of tolerance. The same species is limited northwards by low winter temperatures, except where it makes use of man-made shelters and food. The remarkable northward spread of the Fan-tailed Warbler *Cisticola juncidis* in Europe after 1971 is apparently due to a long succession of mild winters: the limit to this expansion of range may be set by the 5°C January isotherm. Whereas it seems obvious that climate must impose similar limits on the distributions of many other species of birds, most ecological data are anecdotal, and confounded by the effects of climate on vegetation and hence on food supplies. Many species avoid seasonal climatic extremes by migrating, and to this extent climate has profoundly influenced their ecology.

The total geographical distribution of many species is most easily described in terms of a vegetation type: here the effects of climate appear to be indirect, via the plants. Thus, boreal forests that have survived on southern mountains since the last retreat of the glaciers are occupied by outlying populations of typical northern birds. The Redpoll *Carduelis flammea* in Europe and the Blackpoll Warbler *Dendroica striata* in North America are examples. Many species have also extended their ranges over wide extremes of climate by taking advantage of the agricultural habitats created by man (see RANGE CHANGES). In these cases at least it is reasonably clear that the nature of the vegetation rather than the climate governs the distribution of the species.

Ranges can be mapped (see ATLAS; CENSUS) and habitats described by the vegetation, topography and local climatic conditions. A species's 'niche' is a more abstract concept, not helped by the word being used in two different ways. Sometimes it refers loosely to the role or job of the species: Old World vultures (Aegypiinae) and New World vultures (Cathartidae) both fill the 'scavenging niche' in their respective continents. More rigorously, niche refers to the full range of key environmental conditions within which the species can survive: vegetation of particular heights, food of particular types and sizes, temperatures within defined limits, etc. If one species is prevented from occupying or using some particular combination of environmental variables by the presence of a second competitively superior species, it is convenient to refer to the range of environmental conditions which the first species could occupy as its 'Fundamental Niche'; and to the range which it actually does occupy as its 'Realized Niche'.

Local diversity. Four factors, at least, are important in determining the number of species of birds breeding in an area. They are the size of the area, its distance from similar areas, habitat complexity, and latitude. Differences in the richness of local bird communities reflect differences in these four major variables, which also influence broader, geographical patterns in bird diversity.

Size and distance effects. Large areas support more species than small areas. This is true both of real islands surrounded by water, and 'pseudo-islands' isolated by other environments, e.g. the southern isolates of boreal forest, lakes, woods in agricultural land, or urban parks and cemeteries. In virtually all cases, if the logarithm of the number of breeding species (S) is plotted against the logarithm of the size of the area (A), the resulting graph is a straight line with an average slope very close to 0.3 (i.e. $S \propto A^b$ with $b \simeq 0.3$). Slopes in individual studies range from 0.052 for the total bird species found on 'pseudo-islands' in the Southern Venezuelan Highlands, to 0.78 for breeding seabirds on Hawaiian atolls. The steeper the slope, the bigger the difference will be between the species diversity of large and small islands of comparable type.

The conservation implications of these findings are important. As a good approximation, if an island is reduced to one tenth its former size, (e.g. by felling, reclamation, or natural disaster), approximately one half the breeding species will disappear. Which species will be lost is more difficult to predict. As an example, in English broad-leaved woodland, Moore and Hooper (1975) found Nightjars *Caprimulgus europaeus* and Lesser Spotted Woodpeckers *Dendrocopos minor* breeding only in the largest areas (> 100 ha): many species, including Tawny Owls *Strix aluco* and Treecreepers *Certhia familiaris*, were apparently absent from the smallest woods which they censused (less than 0.01 ha). In urban cemeteries in Chicago, only American Crows *Corvus brachyrhynchos* and Chipping Sparrows *Spizella passerina* nested in the smallest plots: large cemeteries (> 100 ha) supported 18 breeding species (J. Lussenhope).

Why should large islands support more species than small islands? *The Theory of Island Biogeography* (MacArthur and Wilson 1967) views the number of species as being set by a rapidly achieved dynamic balance between immigration and extinction (and see DISTRIBUTION, GEOGRAPHICAL). Small populations on small islands have a higher probability of becoming extinct because natural disasters more often wipe out rare species than common ones: and high extinction rates lead to fewer species. Alternatively, and no less likely, the 'Theory of Habitat Heterogeneity' proposes that larger islands contain a greater variety of habitats, and hence more species. Both explanations undoubtedly contribute to the species-area relationship. Differences in slope in species-area relationships presumably reflect, in part, the different rates at which new habitats are added as islands increase in size.

The distance of the island from suitable source areas is also important. Area for area, isolated islands support fewer species than otherwise similar islands nearer to large pools of potential colonists. It is generally agreed that isolation reduces the rate of immigration, and hence lowers the equilibrium species number.

Habitat complexity. Areas of comparable size and isolation may still differ markedly in the diversity of their breeding birds. In a few hectares of habitat, the number of species of breeding land birds is strongly influenced by the amount of foliage at different heights, and to a lesser extent by the variability in these layers from place to place (habitat patchiness). The variety of plant species has little effect: a habitat composed of all sizes of a single tree species will support more birds than a uniformly mature stand of many different trees. Intriguingly, the same foliage profiles generate similar numbers of breeding species in North America and in Australia even though the birds and plants are totally different (H.F. Recher). Less attention has been paid to other types of habitat but, for example, the breeding bird diversity of Swedish lakes is influenced by productivity (S.G. and I.N. Nilsson): area for area, naturally more productive (eutrophic) lakes have more species than oligotrophic water bodies.

When a plot of land is abandoned by man, or is denuded by natural causes, its vegetation undergoes a regular succession usually leading to vegetation resembling that of undisturbed areas nearby. The birdlife undergoes a succession paralleling that of its habitat, some species being present only in early stages of the plant succession and others in later stages. Species abundances also change gradually. Vegetation has a profound effect on which species of birds occur and how many of each there will be. The number of species found at any one point on the successional gradient, however, is determined mainly by the foliage height profile at that point, as already outlined.

Latitude. There are astonishing variations in the number of species breeding in single habitats at different latitudes. The general trend is for species diversity to increase towards the Equator. Thus a few ha of rain-forest in Mexico may have over 100 species of breeding birds, while a comparable forest, with similar foliage profile, in temperate regions seldom has more than 30 species, and in high latitudes far fewer species breed in any single habitat. Two species of heron breed on the coast of Newfoundland, 8 in the vicinity of Long Island, and 12 in southern Florida. What is the cause of the much greater diversity of species in the tropics? One possibility is that evolution (speciation) has proceeded faster or for longer in the tropics and, given enough time, temperate regions will eventually acquire as many species as the tropics have at present. Alternatively, all habitats are saturated or very nearly saturated with species, and the limit is for some reason higher in the tropics. The data available at present are more consistent with the second explanation than the first. Tropical rain forests support numerous birds with very specialized or 'narrow' niches—resident fruit, flower or large-insect feeding species relying on a predictable supply of such resources the whole year round; most of these species could not possibly survive at higher latitudes.

Not all geographical regions or groups of birds show a cline in diversity towards the tropics. In mature eastern deciduous forests of North America, breeding passerine species diversity increases steadily northwards, almost doubling over 16° of latitude (K.N. Rabenold). Long distance migrants (e.g. Parulidae) are the main contributors to this reverse gradient. There are several possible explanations, but no concensus, as to why. In Fenno-Scandinavia, the number of species of breeding waders (Charadrii) (and the proportion of wader species in the total land-bird fauna) increases northwards from a minimum of 7 species in each '100 km' square in the south to 23 in the far north. O. Järvinen and R.A. Vaisanen suggest that this cline is a function of habitat heterogeneity: for example, the presence of more 'seashore' and 'mountain' habitats further north increases the number of wader species by 5–6 and 2–3 respectively.

Two final points about species diversity are worth making. First, a great deal of work has been done on the factors controlling species diversity during, and much less outside, the breeding season. In general the same broad patterns appear to hold throughout the year, although the numbers and kinds of species in particular habitats often change dramatically as migrants come and go (see MIGRATION). Second, diversity can either be described simply by the number of species, S (sometimes called 'Species Density'), or in more sophisticated ways using mathematical 'Indices of Species Diversity'. The latter have two principle advantages. They take into account not only the numbers of species, but also their relative abundances; and most are insensitive to the omission or inclusion of occasional, rare, species. The commonest Index of Diversity in the bird literature is the Shannon-Wiener Index (H′), described in detail by Krebs (1978). In practice, for bird communities, H′ and S are usually highly correlated and can be used interchangeably.

Population dynamics. Within a habitat, different species of birds differ noticeably in their abundances: woodpeckers, for example, are usually much rarer than titmice (see TIT) in woodland. Moreover, providing the habitat does not change, each species-population remains relatively stable from year to year, fluctuating within narrow limts. The long-term sustainable abundance of a species is referred to as its 'Carrying Capacity', denoted symbolically by the letter *K*. Unusually severe winters inflict heavy mortality upon small resident passerines (e.g. Wrens *Troglodytes troglodytes*) pushing their populations well below *K*; recovery follows quickly over the next 2 or 3 breeding seasons. The interesting question is why such populations eventually stop growing and what regulates them.

Some species do, from time to time, show remarkable and sustained population growth, increasing exponentially (that is, by a constant percentage each year) over several years. The colonization of Britain by the Collared Dove *Streptopelia decaocto* and its subsequent dramatic increase is a good example. The population of Shags *Phalacrocorax aristotelis* on the Farne Islands in North-east England grew continuously at a little over 15% a year for over 30 years from 1930 onwards. Indeed all species have the potential to increase exponentially in this way; technically, it is referred to as their 'Intrinsic Rate of Increase', *r* (see also NATURALIZED BIRDS).

Processes of two kinds prevent most populations from growing exponentially for very long. The first are 'density independent' and include natural disasters such as hard winters which kill large numbers, irrespective of initial density. The growth of the Shag *Phalacrocorax aristotelis* population on the Farne Islands was terminated abruptly by an outbreak of 'Paralytic Shellfish Poisoning': 82% of the breeding population died during a few days in May 1968 (see RED TIDE). Limits to population growth are also imposed by processes of a second kind, called 'density-dependent'. The term refers to changes in one or more of the rates of immigration, reproduction, emigration or death in response to changes in population density. Density-dependent processes regulate populations, for example through an increase in the death rate (i.e. the proportion dying) as population density increases; or a decrease in the birth rate (i.e. the number of eggs laid by each female) as density increases; or some combination of the two. Competition for a limited food supply, disease, and predators are all potentially capable of imposing density-dependent restrictions upon population growth. Populations eventually stabilize when births and immigration are balanced by deaths and emigration.

By comparison with many other groups of animals, the number of species of birds for which the key density-dependent processes have been identified is very small (see Krebs 1978: Lack 1966). Female Great Tits *Parus major* in Wytham Woods, near Oxford, lay progressively smaller clutches as the density of the breeding population increases; Weasels *Mustela nivalis* also prey more heavily upon Great Tit nests in those years, and those parts of the wood, where the birds are most dense. Together, these two density-dependent processes control the abundance of this particular population of Great Tits.

Territorial behaviour may provide density-dependent control of some bird populations, by limiting the number of breeding pairs. Experimental removal of territory holders often shows there to be a surplus of birds waiting to occupy vacant sites. It would be a mistake, however, to assume that territorial behaviour evolved in order to regulate population density. Ownership confers considerable advantages on individual territory holders, and natural selection operates on individuals, not on populations. Hence, whilst one consequence of territorial behaviour may be to regulate population density, it is not the reason territorial behaviour evolved (see Krebs and Davies 1978). It is now generally agreed that many other behaviours, such as periodic abstinence from breeding and deferred maturity, have similarly evolved to maximize individual fitness. Whilst they may again have consequences for population dynamics (by reducing recruitment) the hypothesis that they evolved specifically to adjust population recruitment to available resources is not tenable.

Diversity and population stability. A popular belief is that more diverse ecological communities are more stable: a second that they are more stable because they are more complex. Data to support the first contention for birds (or any other organisms) are almost non-existent. The second is certainly wrong.

Unfortunately ecologists use the word 'stability' to mean several different things. Here it refers to the amplitude of the fluctuations in population numbers measured at comparable time-intervals; from one breeding season to the next for example. By comparison with many animals, birds have remarkably stable populations. Occasional spectacular irruptions (see RANGE CHANGES), or precipitous declines to extinction (see EXTINCT BIRDS), are exceptions which prove the rule. Whereas it is quite common for an insect population to change in density from one year to the next by a factor of 100 times or more, a 10-fold change in density for most birds is a very large fluctuation indeed. But within these rather narrow limits, certain patterns are still discernible. It seems likely that tropical rain-forest birds are not only members of extremely diverse communities, but also that their populations are very stable by comparison with temperate forest species; unfortunately really good data are hard to come by. A detailed study using 15 long-term censuses of breeding land birds by O. Järvinen showed that central European and southern Scandinavian communities are made up of fairly stable populations, but, as expected, more northerly populations from species-poor communities fluctuated markedly.

The argument that populations fluctuate more in simple communities because diversity is low appears on theoretical grounds to be misguided. Mathematical models (May 1974; see also Krebs 1978) of simple as opposed to complex communities show quite the reverse; as a general rule, complex systems (with many species, and numerous interactions between species) are less, not more stable than simple ones. Hence, if species-rich systems in nature are more stable than simple ones, it is despite, not because of, their complexity. Present evidence suggests that cause and effect work the opposite way round to popular intuition and belief. Harsh, unpredictable and fluctuating environments are a primary cause both of the lower diversity of northern bird communities, and the greater instability of their component populations. The much more benign and stable environment of a tropical rain-forest supports numerous species with very specialized or 'narrow' niches that could not possibly survive at higher latitudes. Stability begets diversity and not the other way round.

Species interactions and the competitive exclusion principle. In 1934, G.F. Gause wrote: 'As a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of foods and modes of life in which it has an advantage over its competitor'. The ideas embodied in this quotation are often referred to as the 'Competitive Exclusion Principle.' In the terms outlined previously, Gause's principle asserts that two species cannot coexist indefinitely if they are limited in their population sizes by the same density-dependent factor. *Inter alia*, the members of a local bird community, it is argued, must be sufficiently different in their ecological niches to reduce, if not eliminate, interspecific competition and hence avoid competitive exclusion. Since there are likely to be only a limited number of ways of exploiting an environment (a limited number of niches), there must be limits to the number of species which coexist in different communities.

Innumerable studies document such differences in the ecological niches of coexisting species. For example, species may differ in body-size and hence food-size as in the fruit pigeons *Ptilinopus* and *Ducula* of New Guinea lowland rain forest (J.M. Diamond); or in feeding stations, like the antbirds in the genus *Myrmotherula* which differ in their foraging heights in South American rain-forest (J. Terborgh). Less esoteric examples include differences in body-size and hence prey-size and feeding station in tits *Parus* spp. coexisting in European broad-leaved woodland; differences in bill length (and hence maximum probing depth) and leg length (and therefore in the maximum depth of water exploited) in waders sharing a muddy shore; and in the use of feeding grounds at different distances offshore by seabirds from mixed colonies. Lack (1971) provides an outstanding review of numerous examples.

There are two main caveats attached to the admittedly plausible view that such ecological differences necessarily have anything to do with minimizing competition. First, species cannot compete unless something, for example food or nest sites, is in short supply. It is therefore crucial to know when the main periods of resource limitation operate on individual species. If, for the sake of argument, individual populations are mainly controlled by food shortages outside the breeding season, then resources may not be limiting for breeding birds, and differences in their ecology during the breeding season have nothing to do with minimizing competition for food (Fretwell 1972). Second, it is obviously absurd to regard each difference in the ecology and morphology of species sharing a habitat, or indeed any particular difference, as necessarily having anything to do with 'minimizing competition' or 'permitting their coexistence'. It is a difficult matter to decide which, if any, of the observed differences are important. Wiens (1977) argues strongly that competition and 'niche-differentiation' play an extremely small part in structuring most bird communities; others (e.g. Cody and Diamond 1975, and Lack 1971) would certainly disagree.

None of this is to say that the competitive exclusion principle does not operate sometimes: only that in most cases much more rigorous evidence is badly needed. Sometimes, 'natural' experiments are provided. The mainland flycatcher *Elaenia flavogaster* appears to be driving the West Indian species *E. martinica* from the Grenadines, and the Topknot Pigeon *Lopholaimus antarcticus* apparently almost exterminated the White-headed Pigeon *Columba leucomela* in Australia when, due to palm-fruit shortage, both were forced to feed on the same camphor laurels.

Such examples are reasonably convincing. Much more equivocal are distribution patterns which are consistent with the effects of interspecific competition, but which certainly do not prove it. Some species are much commoner on islands than in similar mainland habitats (Northern Cardinals *Cardinalis cardinalis*, Gray Catbirds *Dumetella carolinensis* and White-eyed Vireos *Vireo griseus* on Bermuda for example), possibly due to an absence of competitors on the island (K.L. Crowell). But it is also possible that cases of apparent 'Competitive Release' on islands are due to an absence of predators or disease, a more abundant food supply, or subtle differences in the vegetation. The only way to be really sure is to do experiments, and with birds this is often technically very difficult or ethically unacceptable. But some experiments on competition have been carried out.

Removal of Red-headed Woodpeckers *Melanerpes erythrocephalus* from Illinois woodlands in the winter allowed two previously excluded species to invade, (the Red-bellied Woodpecker *Melanerpes carolinus* and White-breasted Nuthatch *Sitta carolinensis*) and a third (the Downy Woodpecker *Picoides pubescens*) to broaden its feeding niche by foraging higher up the trees (J.B. Williams and G.O. Batzli). And by experimentally inducing Jackdaws *Corvus monedula* to nest in Magpie *Pica pica* territories in Sweden, competition between these two species for food during the nesting season was elegantly demonstrated by G. Hogstedt.

Finally, we should note that if predation or disease play an important part in controlling some bird populations, then competition for limiting resources will again be markedly reduced. The link between population dynamics and the interpretation of community structure is therefore a very close one.

Food chains, food webs and energy flow. Each species of bird in any community is part of a network of feeding relationships encompassing many sorts of organisms. In the simplest case they are members of a 'food chain', with green plants at the base, and one or more bird species as higher members. A typical food chain is:

Sparrowhawk (*Accipiter nisus*)
↑
Great Tit (*Parus major*)
↑
Winter Moth caterpillars (*Operophtera brumata*)
↑
Oak leaves (*Quercus*)

The concept of a food chain is a convenient abstraction; a way of focusing on parts of much more complicated 'Food Webs'. Thus, Great Tits not only take Winter Moth caterpillars, they also feed on a broad spectrum of woodland invertebrates and seeds, each of which in turn is exploited by other organisms. Great Tits also suffer predation from Weasels. Weasels and Sparrowhawks take many other sorts of prey. The resulting web of interactions can be very complex.

One of the interesting generalizations to emerge from food-web studies is this. If we follow individual pathways through a web, the number of steps from bottom to top is typically short, involving not more than 3, 4 or at most 5 levels, from plants (level one) through herbivores (level 2), carnivores (level 3) and carnivores on carnivores (level 4). ('Carnivore' is used here to denote a species which eats other animals: it includes insectivorous and predatory birds). The assignment of individual species to such 'trophic levels' is useful but necessarily simplistic, because most select food from more than one level. Great Tits take caterpillars from trophic level 2, and spiders from trophic level 3, and hence straddle the third and fourth trophic levels. But few would deny that Great Tits feed, on average, lower in the food chain than Sparrowhawks.

A second useful generalization is that species higher in the chain tend to be rarer than species lower down. Dense swards of vegetation support between 10 and 100 voles per hectare; we do not expect to find more than one pair of Tawny Owls on 10 hectares feeding on the voles. At certain times of the year there may be more than 100,000 Winter Moth caterpillars per hectare, but only between 1 and 10 pairs of Great Tits, and one pair of Sparrowhawks per square kilometer.

All organisms require energy to survive. Food chains represent the transfer of energy from the 'primary producers' (plants) which make food energy available by photosynthesis to higher trophic levels (see ENERGETICS). Of the energy consumed by an individual, population or entire trophic level, only a fraction appears as useful production (food) for the next step in the chain. The rest is dissipated in respiration, or lost as faeces. Birds, being warm blooded (endothermic), dissipate a very large amount of energy in respiration. On an annual basis, a typical bird population makes available as production only 1% or less of the energy it consumed. It is not surprising, with such a rapid dissipation of energy at each step in the food chain, that hawks are rarer than their passerine prey and food chains are short. But there may be more to it than this. Food chains are not noticeably longer in more productive communities; nor are chains dominated by cold-blooded animals (which use up much less energy in respiration and hence make more available as production) noticeably longer than those in which birds (or mammals) are important components (S. Pimm and J.H. Lawton). These paradoxes are not fully understood but, as far as birds are concerned, body-size must also constrain the lengths of food chains. Most predators must be bigger than their prey, so that even if enough energy reached the ends of some food chains to support a population of predatory birds at trophic level 6, such 'super-predators' would probably be too large and heavy to fly.

In the total energy economy of terrestrial communities, birds are trivially important. In a Northern Hardwood Forest in New Hampshire, R.T. Holmes and F.W. Sturgess showed that the plants made available over 40 million kilocalories per hectare per year as 'primary production' (1 kilocalorie = 1,000 calories; an alternative way of measuring energy is in joules. There are 4.18 joules in a calorie). Of the 40 million kc, 56 species of birds between them consumed only 0.17% as primary consumers (trophic level 2) and 0.14% as secondary consumers (trophic level 3). In marine communities, the impact of vast seabird colonies may well be more substantial. Fourteen species of seabirds, including Fulmars *Fulmarus glacialis*, Guillemots *Uria aalge* and Puffins *Fratercula arctica* consumed an estimated 29% of the mean annual fish production within a 70 km radius of their colony on Foula, Shetland (R.W. Furness).

As energy flows down food chains, so do a wide range of compounds pass from victim to exploiter and back to the environment. The role of birds in the cycling of key elements, like nitrogen and phosphorus, has received comparatively little attention, except in the case of the accumulation of the vast GUANO deposits from the faeces of the Guanay Cormorant *Phalacrocorax bougainvillei* along the coast of Peru. In one study, the faeces of Rooks *Corvus frugilegus* brought more calcium and potassium into an English woodland in 8 weeks than entered the community in a whole year of normal rainfall (J.S. Weir). How crucial this input was to other members of the community is not clear.

Harmful compounds also pass through food chains and may accumulate in vulnerable top carnivores both of terrestrial and aquatic environments. The havoc wrought by chlorinated hydrocarbons (DDT, Dieldrin and their relatives) on the Peregrine Falcon *Falco peregrinus* and other raptor populations is well known; see e.g. EGGSHELL THINNING; TOXIC CHEMICALS.

Evolutionary ecology. Not all interactions in ecology involve aggression, competition and being killed. A small but important component involve co-operation: the technically correct term is 'Symbiosis', where two species gain mutually in fitness from the interaction. The removal of ectoparasites from the bodies of large African mammals by Oxpeckers *Buphagus africanus* and *B. erythrorhynchus* is one example. Of much more general importance are the roles of birds as plant POLLINATORS, and as agents of SEED DISPERSAL.

Compared with insects, birds are minor pollinators of flowers, but for certain specialized plant species in some communities they are vital. The birds gain by feeding on nectar and the plants by setting fertile seeds. Classical flower-feeders are the hummingbirds of the New World, and the sunbirds and honeyeaters of the Old. Birds and flowers often show a high degree of mutual adaptation or COEVOLUTION; for example typical hummingbird pollinated flowers in North America (e.g. *Penstemon*, and *Ipomopsis*) are red (bees cannot see red, hummingbirds can), with long corolla tubes and copious nectar. In the south-western deserts the Ocotillo or Candlestick Plant *Fouquieria splendens* times its flowering to coincide with the northward spring migration of Rufous Hummingbirds *Selasphorus rufus*.

Reliance on birds as pollinators becomes progressively rarer outside the tropics. The role of birds as dispersers of fruits and seeds, however, is of widespread importance. The sizes, colours, time of ripening and composition (i.e. protein, fat and sugar levels) of many fruits appear highly evolved for the needs of particular species or groups of birds. The marked changes in colour which accompany ripening in numerous fruits serve as conspicuous signals to their avian consumers. Many seeds will not germinate until they have passed through a bird's intestine. A particularly remarkable example may be the Mauritian tree *Calvaria major*. Formerly widespread and abundant on the island, by 1973 only 13 old and dying specimens remained, prompting the suggestion that seeds must have passed through the gut of the Dodo *Raphus cucullatus* before germinating: unfortunately the evidence is at best equivocal (see DODO). The message, however, remains: too close a mutual dependence on other species carries a price as well as evolutionary advantages.

Evolutionary ecologists are concerned not only with coevolution, but also with understanding the whole range of adaptations shown by species to their environments: that is, with questions of how niches are moulded. The habitats chosen by a species are likely to be those in which the individuals have the greatest production of surviving offspring, as the genes of these individuals will be preserved by natural selection. The survival of the offspring will depend upon the adaptations of the bird to life in that area, and upon the number and habits of other species already utilizing the area. From a bewildering variety of specific adaptations several broad generalizations are now emerging.

Average CLUTCH-SIZE, for example, increases with latitude in single species, and within a group of close relatives (like *Emberiza* buntings or stiff-tailed ducks *Oxyura*). The longer hours of daylight further north and seasonal flush of insect food presumably allow birds to produce and rear more offspring, and select for individuals laying larger clutches.

A convenient but necessarily crude distinction, encompassing a whole range of adaptations, is between 'r-selected' and 'K-selected' species. r-selected species (from the technical notation for the Intrinsic Rate of Increase of a population) have high reproductive rates; live in unpredictable environments; suffer high density-independent mortalities; are generally small and short-lived, with good powers of dispersal; and are opportunistic with markedly fluctuating populations. K-selected species (from the technical notation for the carrying capacity of a population) are usually large, but have low reproductive rates; live in predictable environments; suffer low density-independent mortalities; are long-lived and colonize new habitats slowly; they are ecologically restricted and normally have very stable populations maintained close to their carrying capacities by density-dependent controls. Budgerigars *Melopsittacus undulatus* and California Condors *Gymnogyps californianus* lie at opposite poles of the r-K continuum. J.H.L.

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ECONOMIC IMPORTANCE: see PESTS, BIRDS AS; UTILIZATION BY MAN.

ECOSYSTEM: the totality of factors of all kinds that make up a particular environment.

ECOTONE: an area of transition (or the actual boundary) between adjacent plant associations, and hence between the animal communities associated with them.

ECOTYPE: a locally adapted population or race, having characters resulting from the selective pressures exerted by its particular environment.

ECTOPARASITE: a parasite inhabiting the exterior of the host's body, as distinct from an ENDOPARASITE. Apart from the nest parasites discussed below, birds are parasitized by the following groups of ectoparasites: chewing lice (Phthiraptera, 'Mallophaga'), louse-flies (Diptera, Hippoboscidae), fleas (Siphonaptera) and bugs (Hemiptera, Cimicidae) belonging to the Insecta, and ticks and mites belonging to the Arachnida. Not included here are the free-living biting flies (e.g. Ceratopogonidae, Culicidae, Simuliidae, Tabanidae) and leeches, although these can be important vectors of endoparasites such as protozoa and arboviruses.

Chewing lice (Mallophaga). These belong to the insect order Phthiraptera that also includes the sucking lice, and spend the whole of their life-cycle on the body of the host. They live amongst the feathers, with the exception of species of one genus that live in the throat pouches of pelicans and cormorants. They feed on feathers and blood or other tissue fluids; blood may be taken by some species from developing feathers and species of at least one genus feed exclusively on fluids; lice living inside the calamus of the quill feed on the central pith. The eggs are attached to feathers or in a few cases are laid inside the quills. Mallophaga are closely adapted to the environment formed by the feathers of the bird; their pigmentation, size and shape and certain morphological characters of the head are apparently dependent on feather colour and structure. In size and shape they are adapted to the different ecological niches found on the body of the bird; thus, for example, on the head and neck is found a short round-bodied type, and on the wings and back a more flattened, elongate type. A bird is usually parasitized by a number of different species of Mallophaga, some adapted to the different ecological niches on the body of the host; the Rook *Corvus frugilegus*, for example, has 6 species belonging to 5 genera, and some of the tinamous have as many as 12 species of Mallophaga.

The present distribution of Mallophaga suggests that they became parasitic on the class Aves at an early stage and that they evolved with their hosts. Different species of birds do not normally come into contact with one another, so that there is little opportunity for interchange of lice populations; these have, therefore, become strongly isolated, so that in many cases a species of Mallophaga is found on only one host species or a group of related host species. Thus, in general, Mallophaga of related hosts are themselves related; within the order Charadriiformes, for example, there are a number of mallophagan genera common to the 3 suborders, and the species of these genera parasitizing the suborder Alcae are more closely related to each other than to those on the other suborders, Charadrii and Lari.

Thus each order of birds is parasitized by species belonging to one or more genera that are frequently peculiar to it, and the relationship between the species of these genera generally reflects the relationship between the hosts within the order. It is, therefore, usually possible to place a bird correctly in its order, and often in a lower category, if the mallophagan genera parasitizing it are known, and for this reason Mallophaga may be useful evidence in deciding the relationships of birds of doubtful affinities. The affinities of the Mallophaga suggest, for example, relationships between the Struthionidae and the Rheidae, between the Phoenicopteridae and the Anseriformes, and between the Musophagidae and the Galliformes. However, many factors, such as discontinuous distribution of genera and species, parallel and convergent evolution, secondary infestations, and human error in interpretation of the evidence, may obscure the initial relationship between host and

House Martin *Delichon urbica*, with Hippoboscid fly on back, collecting mud for nest. (*Photo: E.J. Hosking*).

parasite, so that evidence from Mallophaga cannot be used as an infallible guide to relationships between the hosts.

Louse-flies (Diptera, Hippoboscidae). The Louse-flies are true flies. They are blood-suckers specialized for living on birds and mammals by being tough, leathery, flattened dorso-ventrally and with strong curved claws. The wings are usually fully developed, but may be reduced and useless for flight. The larvae develop, singly, inside the abdomen of the female; the fully developed larva (prepupa) pupates immediately after its release from the female. In the case of Swifts *Apus apus* and House Martins *Delichon urbica*, which return to the same nest site each year and whose flies are flightless, the next generation of flies is produced from pupae deposited in the nests. In many other species the pupae are deposited away from the nest and the emerging adult must fly in search of a suitable host. There are *c.* 200 species, of which *c.* 150 are recorded from 24 orders of birds. Some species, e.g. *Pseudolynchia canariensis*, are widespread and polyphagous, while others have a much more restricted distribution and host preference, such as *Crataerina pallida* confined to certain *Apus* spp. in the western Palearctic. Some show a distribution more dependent on habitat, such as the *Ornithomya* spp. in Britain: *O. chloropus* occurs on all birds in open, particularly moorland, areas; *O. avicularia* and *O. fringillina* in other areas, the former on thrushes and larger birds, the latter on smaller birds. The Ostrich louse-fly *Struthiobosca struthionis* is much more closely related to the hippoboscids of larger mammals than to the rest of the bird flies.

These relatively large parasites can occur in large numbers—over 30 of the flightless *C. pallida* have been found on one swift and over 40 of the related *C. hirundinis* on one House Martin. They are often accused of weakening birds, but there is little evidence for this and the birds only suffer their attentions for relatively short periods since the flies die before the birds migrate. Very few flies are carried on migrations to or from the breeding site.

Mallophaga and pregnant females of certain mites attach to hippoboscids to aid their dispersal from host to host. These flies are the principal vectors of some trypanosomes and *Haemoproteus* (Protozoa).

Fleas (Siphonaptera). The fleas are blood-suckers; the body is flattened laterally to allow them to move easily through fur or feathers, and their power of jumping enables them to reach a new host or escape capture. Of the more than 2,000 species and subspecies of fleas only *c.* 125 are bird fleas. The entire pre-adult life is passed away from the host, usually in the host's nest, where the larva feeds on organic debris. Bird fleas are found on the body of the bird, but are more numerous and most species are largely resident in their nests. As the flea may spend so much of its life-cycle off the host, it is influenced as much by climatic and other environmental factors as by the host itself. This, together with the fact that in each generation the flea, on emerging from the pupa, may have to find a new host, has generally limited host restriction. There are, nevertheless, a number of host-specific bird fleas, of which *Ceratophyllus rossittensis* on the Crow *Corvus corone* is an example. On the other hand some bird fleas have a restricted geographical distribution; thus *C. borealis* is found in the British Isles almost exclusively on the outlying islands. In others environmental factors clearly influence distribution; for example, there is considerable overlap in the hosts used by *C. garei* and *C. gallinae*, but the former occurs mainly in damp nests on or close to the ground, while *gallinae* occurs mainly in looser built dry aerial nests. Similarly, the House Martin in Britain is host to 5 species of fleas, but 2 species (*Callopsylla waterstoni* and *Frontopsylla laeta*) occur only on nests on cliffs, while one species (*Ceratophyllus hirundinis*) is found only in nests on buildings.

Large numbers of fleas may be found in one nest—up to 2,000 have been recorded.

Bugs (Hemiptera, Cimicidae). Less than a third of the 80 species of the bed-bug family Cimicidae occur on birds, mainly on Hirundinidae and Apodiformes. Most of the others feed on bats. In Britain the Martin Bug *Oeciacus hirundinis* of House Martins and the Pigeon Bug *Cimex columbarius* of domestic pigeons are common. The eggs are fixed on or close to the nests of their host, and the emergent nymphs and subsequent stages feed on blood. They can occur in large numbers in the nests, but they are not well adapted to travelling on their hosts and so are not often found on birds away from the nest.

Mites and ticks (Acari). Some mites ectoparasitic on birds are blood-feeders, for example the Red Mite of poultry *Dermanyssus gallinae* (Dermanyssidae) occurs frequently on both wild and domestic birds. This species feeds at night, passing the day in dark retreats in the nest or roost, except in heavy infestations, when it is found on the host at all times. The widespread macronyssid species *Ornithonyssus sylviarum* (the European Fowl Mite) and *O. bursa* (the Tropical Fowl Mite) complete their life-cycle on the host, feeding by both day and night. *Bakericheyla chanayi* (Cheyletiellidae) has been recorded feeding on the blood of passerines. The chelicerae of blood-sucking mites are generally stylet-like for piercing, and, in some, the shafts are grooved to form a blood canal. The Knemidokoptidae and Epidermoptidae are skin parasites of birds; the former usually attack specific tissues and cause characteristic conditions such as 'scaly-leg' and depluming scabies. Females of some epidermoptid genera are also found on the host's hippoboscid and mallophagan ectoparasites.

Certain larval Trombiculidae ('chiggers') are ectoparasitic lymph-feeders, while representatives of the Rhinonyssidae, Dermanyssidae, Ereynetidae and Cytoditidae inhabit the nasal cavities of numerous birds.

'Feather-mite' species of the Analgoidea, Pterolichoidea and Freyanoidea have adapted to fill the various microhabitats provided by feathers. Modifications chiefly affect body shape and terminal leg setae and are most marked in those mites inhabiting exposed sites, such as the primary flight feathers. Feather-mites remain on their host throughout their life cycle; those living on the feather surface feed on desquamated skin cells and oily secretions from dermal glands, while those found within the calamus utilize quill substances. Species are generally restricted to a particular avian family, host specificity being most marked in sea-birds and least in passerines.

Other mites associated with feathers include members of the Syringophilidae (Cheyletoidea); these are elongate species which live inside the quills. Some 18 genera are reported from 10 bird orders.

Ticks (Metastigmata) comprise a specialized order of large blood-sucking Acari which are all ectoparasites of terrestrial vertebrates. They are an economically important group, being vectors of many disease organisms including rickettsias and spirochaetes.

Ticks are usually confined to the head region of birds, probably due to the efficiency of the beak as a 'de-ticking' instrument. The tick's mouthparts are adapted both to secure it to the host during feeding and to facilitate blood-sucking.

Of the soft ticks (Argasidae), a number are primarily associated with birds. *Argas persicus* and *A. reflexus*, for example, infest domestic fowl and pigeons respectively, although both have also been reported from wild birds. *Ornithodoros capensis* parasitizes sea-birds, while other species of this genus have been found on both avian and mammalian hosts.

Argasids spend most time in the dwelling place of the host. The larvae may remain attached to the host for several days, but the nymphal stages (of which there may be up to 8) and adults only feed during the host's visits to its roost or nest. Due to the rather irregular and limited opportunity for meals, argasids engorge rapidly and can survive for long periods without feeding.

Birds are also primary hosts for a number of hard ticks (Ixodidae), for example *Ixodes rothschildi*, *I. unicavatus* and *I. uriae* are parasites of sea-birds, while *I. passericola* infests passerines. Ixodids associated with birds are often 3-host species; each stage (larva, the single nymphal stage, adult) feeds on a different host before dropping to the ground to moult or lay eggs. In contrast to argasids, hard ticks may take some days (some males even take months) to engorge.

The immature stages of several genera of ticks which normally infest mammals are also found attached to avian hosts, and it has been suggested that bird migration contributes to the spread of mammalian tick-borne organisms.

Nest fauna. Birds' nests may contain a great many animals apart from the rightful occupants (see NESTING ASSOCIATION): 529 different kinds, chiefly arthropods, have been taken from 56 nests in Finland. The groups discussed above are all obligate parasites, that is, they are obliged to spend at least part of their life on or in very close association with their hosts, and receive nourishment directly from the host. Apart from any of these that may be in the nest, probably 20–25% of nest dwellers are actually dependent on the occupied nest, the rest being casual visitors or those that are also found elsewhere in similar microhabitats. Included among those dependent on the nest are certain beetles, moths and flies. It is the blood and tissue-feeding larvae of some flies, e.g. the genera *Protocalliphora* (Calliphoridae), *Philornis* and *Passeromyia* (Muscidae) or *Neottiophilum* (Neottiophilidae), that can be the most dangerous parasites of the young birds, sometimes being responsible for their deaths. *Carnus* species are tiny flies (Diptera, Carnidae) that emerge from the previous season's nests and then fly, if necessary, to an occupied nest, where the wings are shed and the abdomen becomes greatly distended (physogastric). Even then they are only *c.* 2 mm long. They probably feed on secretions of wounds etc and, although often found on unfeathered nestlings, are unlikely to do them much harm. On the other hand, many of the inhabitants of the nest act as useful scavengers and some feed on the parasites, such as beetles and their larvae that feed on flea larvae. The nest fauna is dependent on the type of nest; those in burrows and holes, especially when occupied from year to year, have a richer fauna than open, scantily lined nests, such as that of the Woodpigeon *Columba palumbus*.

Harmful effects. Apart from being vectors of certain diseases (see DISEASE), ectoparasites when present in large numbers may have a debilitating effect on their hosts and may even cause death; heavy infestations of feather mites may practically denude a bird of feathers, and some Mallophaga cause damage to wing feathers by chewing holes in these when in pin. The presence of large numbers of ectoparasites has been accused of causing the host to injure itself by scratching and to interfere with egg production and fattening of poultry. Secondary infections may occur at sites of attachment in particular of ticks. Scaly-leg caused by knemidokoptid mites can deform or cripple the bird. Predation by the host is the main control of ectoparasites and a debilitated or injured bird may accumulate excessive populations; dust bathing may also help in ectoparasite elimination (see COMFORT BEHAVIOUR; DUSTING).

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ECTROPODACTYL: term applied to an unusual arrangement of the toes, found in some Picidae (see LEG).

EDAPHIC: term applied to environmental factors dependent on conditions of the soil or substratum.

EDIBILITY: see PALATABILITY OF BIRDS AND EGGS.

EDIBLE NESTS: the nests of certain species of SWIFTLET (Apodidae), composed largely of saliva or nest-cement, being the mucilaginous secretion of the paired sublingual glands (Bernstein 1859, Marshall and Folley 1956). The salivary glands have no digestive function, but are periodically increased in size in both sexes and solely in relation to nest building. Once dry, the secreted gelatinous nest-material is very difficult to dissolve in water, buffer solutions, or even dilute acid or alkali. This is an ecological adaptation, enabling the bracket-shaped nests to stick to the rock surface even under permanently humid cave conditions. Little is known about the chemical nature and nutritive value of the nest material. The secreted product is a mucoprotein yielding on hydrolysis proteinous compounds and reducing sugars (17%). Because of its rather high carbohydrate content, the product contains polymers of amino sugars, i.e. glycopeptides. Hydrolysis of the proteins yields a high content of amide-N, arginine, cystine and histidine, the last two being S-containing amino acids. An overall analysis showed that the commercial product contained 11% water, 9% nitrogen, 1% sulphur and very small amounts of phosphate. Its mineral (ash) content was rather high, being 2.5% (Wang 1921). Isoelectric focusing of the proteins showed a protein pattern to some extent similar to the blood protein pattern of the same species.

Edible, i.e. sufficiently 'saliva-rich' nests to make commercial harvesting worth while are produced by 3 species of *Aerodramus*:

(1) *Aerodramus fuciphagus*, the Edible-nest Swiftlet, building a white, bracket-shaped self-supporting nest. Its nest-cement is nearly unadulterated as it is only very sparsely mixed with a few downy feathers of the bird's own plumage. It breeds in sea caves in the Malayan and Indonesian Archipelago, also in caves of limestone outcrops far inland and in old buildings, often in Chinese quarters. Usually the caves or colonies are protected and subjected to careful harvesting.

(2) *Aerodramus unicolor*, the Indian Edible-nest Swiftlet, which builds a nest of moderately copious nest-cement intermingled with large feathers (sometimes rectrices and primaries) of the bird's own plumage and vegetable materials. The nest is also self-supporting. This swiftlet breeds in sea-caves on rocky islets off the southern coast of the Indian sub-continent and Sri Lanka.

(3) *Aerodramus maximus*, the Black-nest Swiftlet, makes a self-supporting relatively small, more saucer-shaped nest with saliva hinges of firm nest-cement. In contrast to the foregoing species, the nest-cement is copiously mixed with small feathers of the bird's own plumage. Moreover, in contrast to the first two species which invariably lay 2-egg clutches, the full clutch of this species is one egg. This species is the main occupant of the Great Cave of Niah, Sarawak, N. Borneo (probably the largest single site, with 2 million nests) and other caves in this region. It breeds together with the Edible-nest Swiftlet in inland caves in Indonesia and only sporadically in buildings (Malaysia).

Unfortunately, the species named *Collocalia esculenta*, the Glossy Swiftlet, makes nests of mainly extraneous materials that render them inedible even by Chinese standards.

Edible nests are highly valued by the Chinese as a culinary delicacy, being made into the most expensive food in Asia, 'caviar of the East', namely bird's nest soup. The nutritional value will be that of protein-sugar solution, although its complete amino acid composition has not yet been determined. Eaten alone, it is a practically tasteless gelatinous substance to an untrained palate. Chinese and other Asians esteem it, however, as a tasty, nourishing and even aphrodisiac food. It is also used for convalescents and the aged. Because of their relative tastelessness, bird's nests are often served by the Chinese in soup or jelly mixed with chicken, spices, sauces or sweets. Nests of the Edible-nest Swiftlet are of the highest grade as they are white in colour and contain few feathers. They are generally sold tied up in rows or strings as intact nests. The lowest grade is that of the Black-nest Swiftlet, whose nests require cleaning in order to remove the feathers, as they are sold as powder.

The collecting of edible nests reaches far back into antiquity, probably to pre-historic times, as indicated by remains found in the Niah cave

Edible-nest Swiftlet *Aerodramus fuciphagus* at nest. (*Photo: J.H. Becking*).

(Harrisson 1959). The trade in nests was established in China as long ago as the T'ang Dynasty (AD 618–907), as is evident from figures on pottery. The first written records are from Arabic sources (Idrisi, AD 1154). The trade is mentioned by the Dutch naturalist-surgeon J. Bontius in 1625, referring to edible nest sales in the newly founded Jacatra (now Jakarta), and in records in the Daghregister of Batavia for 1637. Records of harvests from the caves on the southern coast of Central Java (Rongkop) date back to 1743 (Voltz 1905). In 1840 the rights were purchased from the feudal authorities by the Government of the Dutch East Indies for the large sum of Hfl. 130,000, and leased by the government in 1886 for Hfl. 725 and in 1893 for Hfl. 1,495 monthly (Van der Meer 1927). Junghuhn (1853) mentioned that the Chinese paid in 1847 Hfl. 4–5,000 per picul (= 62 kg) of nests and that the total annual revenue of the cave of Karangbolong (Central Java) was *c.* Hfl. 200–250,000. In Malaysia (Penang) in 1978 the yield of a house colony for a 7-month period was 1,200 nests (12 kg), worth £560 (Langham 1980).

Collecting the edible nests in high, dark caves is a hazardous occupation and only done by special collectors, whose skill is often passed on from father to son. The crevasses, chimneys and galleries where the swiftlets breed in dense clusters are normally reached by long sets of single bamboo poles, pinned or socketed together, and (at Niah) reaching up to 130 m in height. One man climbs and balances, wielding a long bamboo to which is attached a beeswax candle above a hoe-like blade with which he scrapes the nests off; on the floor far below an assistant gathers them as they fall. The sea-cave at Rongkop can only be reached by rattan (or rope) ladders. When the sea is rough, its entrance is alternately opened and closed by the rolling waves and the climber (like the swiftlets) has to select the right moment to enter by launching himself into the cave on a swinging rope. Throughout south-east Asia this difficult and dangerous work is falling out of favour with the younger generation, so that the number of nests taken is slowly dwindling. In N. Borneo the bird's nest industry is falling into decay, at least temporarily; this process is assisted by the austerity of recent policy in China, for over a thousand years the prime consumer. However, in other parts of south-east Asia (Malaysia, Indonesia) the industry is still flourishing, as is evident from the high prices for the product and high rents paid by the leaseholders. (T.H.) J.H.B.

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EFFERENT: opposite of AFFERENT (see NERVOUS SYSTEM).

EGG: the development of the female reproductive cell or ovum with additional layers added in the oviduct and then laid by the female.

The avian egg is a complicated structure whose essential components are yolk, albumen, and shell, together with various membranes segregating the constituents (Fig. 1). The relative proportions of the three major components vary substantially between species in response to differing ecological pressures on each.

Yolk. The ripe ovum is richly endowed with yolk, the main nutritive component for the development of the embryo. Essentially a viscous liquid enclosed in a thin elastic vitelline membrane, the yolk nevertheless has a distinct structure of alternating thick layers of yellow fat-rich material and thin layers of white, poorer in fats and pigment. The central core of white yolk is called the latebra and extends outwards in a narrow column towards the vitelline membrane. This it meets in an expansion called the 'nucleus of Pander' enveloping the 'germinal spot' or blastodisc from which the embryo will develop after fertilization. This blastodisc is visible only in unfertilized eggs, as a small opaque white circle containing some vacuoles. Once fertilized, the ovum commences development at the blastodisc, turning it into a blastoderm visible on dissection of a new-laid egg as a wide oval region with a central transparent portion known as the area pellucida; from this the embryo develops.

The yolk of an egg provides the main reserves of food materials for the developing embryo and correspondingly varies between species. Nidifugous species have proportionally more yolk in their eggs than have nidicolous species and the yolk itself is also rich in lipids. Since such eggs are also unusually large for the species body size, the total yolk and lipid contents are substantially above those of nidicolous species. Part of this extra lipid fuels the greater developmental maturity of the nidifugous hatchlings and part provides the food reserve needed until they can find their own food.

Albumen. The albumen or egg-white comprises 4 more or less concentric layers about the yolk, with the innermost layer extending along the long axis of the egg from opposite ends of the yolk to meet the shell membranes and form a protective suspension system for the yolk called the chalaziferous membrane. On this the yolk hangs in a layer of liquid albumen, in turn encased in an albuminous sac, a structural framework of semi-solid mucin fibres whose interstices are filled with liquid albumen. The fibres extend at each end of the egg into the inner shell membrane, thus locking the entire sac in place to form a cushioning shell, isolating the yolk from deformation stresses. The sac is otherwise isolated from the shell membranes by the fourth zone, a thin layer of liquid albumen.

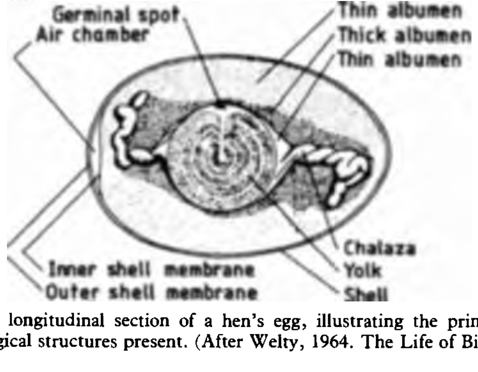

Fig. 1. A longitudinal section of a hen's egg, illustrating the principal morphological structures present. (After Welty, 1964. The Life of Birds).

The main components of the chalaziferous membrane supporting the yolk are the chalazae, a pair of dense spirally twisted cords of mucin fibre attached to the yolk as a fibrous capsule over its surface and interlacing with similar fibres in the albumen at the two free ends (Fig. 1). The arrangement allows the yolk to rotate freely as the position of the egg changes in the nest, resulting in a permanently 'up' position for the developing embryo. The chalazae acquire their twisted dense structure during the rotation of the egg as it descends the oviduct.

Albumin accounts for about 90% of the protein of the albumen, with mucin and globulin contributing about 5% each. It is the main component that provides the viscosity of the egg white. The albumen is secreted by the magnum of the oviduct in response to the passage of the ovum along it.

Membranes. The egg membranes consist of 2 layers of parchment-like texture, separated at the blunt end to form an air chamber (Fig. 1). The inner one is about one-third the thickness of the outer and consists of matted protein (keratin) fibres bound together with an albumin-based 'cement' and penetrated by numerous pores. The outer or true shell membrane contains fewer pores and consists in detail of 3 separate layers, the outermost of relatively coarse, unbranched and flattened fibres of keratin, the inner 2 of much finer and branched fibres of keratin and mucin. Both are laid down in the isthmus of the oviduct.

The air cell does not appear until the egg is laid and subsequently enlarges as the embryo develops. Its function is apparently to conserve the limited water supply of the embryo, by re-condensing respiratory water through a 'cold nose' effect.

Shell. The outer layer of the egg is heavily calcified, its inner surface closely attached to the outer of the shell membrane. In detail its inner structure is of an array of approximately hemispherical knobs, each containing a core of organic material in which shell membrane fibres are embedded. These knobs or mammillae fuse basally, before giving way to an outer 'spongy layer' (so called for its appearance in decalcified specimens) in turn encased in a cuticle of organic material. Numerous pores penetrate the shell, commencing in small surface depressions and terminating between the mammillary knobs, and provide for respiratory exchange of oxygen, carbon dioxide, and water (see also EGGSHELL, ULTRASTRUCTURE OF).

The shell is secreted in the uterus and consists of a basic protein framework heavily deposited with minerals, largely calcium carbonate in the form of calcite. The organic material—which resembles but is not identical with collagen—accounts for about 3% of the shell, calcium carbonate about 94%, and magnesium, sodium and potassium salts accounting for much of the rest.

The shell provides the mechanical strength of the egg and its thickness therefore varies between species. A thick shell provides considerable protection against accidental breakage but imposes a difficult task on an embryo attempting to cut its way out. The shell can, however, be weakened during incubation, for the embryo draws heavily on the calcium for its own skeletal growth and the shell is thus thinner when the embryo is ready to hatch. Shells can also be selectively thicker where they are subject to wear: Guillemot *Uria aalge* eggs are thicker at their narrow end, where they are in contact with the surface of the rocky nesting ledges and are thinner at their broad ends, where the chicks emerge. Conversely, the eggs of megapodes are buried in a mound of rotting vegetation or in sun-warmed soil which provides the heat necessary for incubation; the parents hardly touch them at all, and the shells are correspondingly unusually thin.

Shell thickness has proved particularly susceptible to the effect of certain widely used agricultural chemicals, notably DDT. Birds ingesting high levels of these compounds or their metabolic residues subsequently laid thinner shelled eggs than did uncontaminated birds and consequently suffered reduced breeding success through frequent breakage of these eggs during incubation (see EGGSHELL THINNING).

Shape. Eggs vary greatly in shape but within a species they are similar. Also, related groups of species tend to have similar egg forms. Some broad generalities are possible: owls and kingfishers and a few other groups lay almost spherical eggs and most aerial and fast-flying species—swifts, swallows, hummingbirds—lay long elliptical eggs. Most of the species laying pyriform (top-shaped) eggs lay 4 eggs per clutch, with little intraspecific variation. Such eggs can be closely packed together by arranging the narrow ends to point inwards, thus minimizing the area to be covered by the incubating adult; a compact group also dissipates heat rather slowly. A further correlation is that species breeding on bare ledges tend to have pointed eggs, the small rolling circle of the egg when knocked being adaptively advantageous.

Egg-shape is determined during its passage through the oviduct which exposes it to morphological, physiological and genetic influences. A wide variety of terminologies are in use by oologists describing the resulting variety of egg shape. Some of the major terms are illustrated in Fig. 2.

Colour. Eggs derive their colour from pigments secreted by cells in the wall of the oviduct, particularly of the uterus. The pigments are deposited at different depths in the shell according to the position of the eggs in the oviduct at the time of secretion. Much of the ground colour of an egg is provided by pigments in the spongy layer of the shell and must therefore be secreted at the upper end of the oviduct, whilst the markings, spots, and scrawls of the cuticle must be secreted only shortly before laying. There are major differences between species in this respect; in some raptors and plovers the pigment deposits are purely superficial whilst in the Cassowary *Casuarius casuarius* egg the outside is uncoloured but the inner layer is green.

The shell pigments are derived from two sources, blood haemoglobin and bile pigments, respectively giving red-brown colours based on porphyrin and blue-green colours based on cyanin. In certain regions, notably Australia and parts of southern India with red soil, erythrism (production of reddish eggs) is unusually common. The same phenomenon is also unusually frequent (for unknown reasons) in certain species, for example, in Herring Gulls *Larus argentatus*.

In many species the eggs are uniformly coloured or tinted, as in the blue or blue-green of many thrushes and the pale green of many ducks. But in many other species the ground colour is over-laid with dense patterns of blotches, spots or streaks of one or more colours. The density and intensity of these may vary along the egg, possibly reflecting the pressure applied to the egg in the oviduct. If the egg is still when pigment is applied, a pattern of spots will be generated but if the egg is in motion then lines or streaks will result.

Despite the great variety of markings, the eggs of individual females are often distinctive and therefore under hereditary control. This is also implied by the precision with which European Cuckoos *Cuculus canorus* and other brood-parasites mimic the eggs of their host species (see BROOD-PARASITISM).

Egg coloration shows a number of broad ecological correlates. Most ground-nesting species have cryptic brownish eggs if laying on dead vegetation, lighter, sandy-coloured eggs if nesting on beaches or in deserts, or even blackish eggs if nesting on burnt ground (as with *Cursorius temminckii*). Within the thrush family, ground nesters tend to have relatively cryptic eggs in brown, grey or olive, tree-fork species to have eggs with heavy blotches resembling shadow-marks, crevice nesters to have speckled white or blue or just plain blue eggs and hole-nesters to have pure white eggs. The gradient with nest situation suggests exposed eggs benefit from coloration by making them inconspicuous to predators whilst white eggs are needed in dark situations where the birds risk putting their feet through their own eggs. Both ideas have been confirmed experimentally.

White eggs are also found in those open-nesting species which cover their eggs when leaving the nest, as do various ducks and grebes, or which incubate or cover their eggs from the laying of the first one, as do herons, owls and doves. This also suggests that the ancestral egg was white, with colour an evolved characteristic against predation.

Individual variation in egg markings or colour is most pronounced in those species in which confusion of egg ownership is possible. For most birds, return to their nest is a guarantee of return to their own eggs but in crowded colonies and in species without nests this certainty is reduced. Guillemots have been shown to identify their own eggs on the basis of individual combinations of ground colour and profuse blotch patterns; each bird can thus be certain it has returned to its own egg on the crowded cliff ledges. Individually recognizable eggs have also been reported from Great-tailed Grackles *Quiscalus mexicanus* nesting colonially in crowded coconut palms.

Certain species are particularly prone to the attentions of brood-parasites and egg discrimination is generally higher among these species than among unparasitized species. In general, the former recognize only species-specific characteristics of their own egg, perhaps because the selective costs to the bird of erroneously rejecting its own eggs in attempting individual discrimination would be greater than the costs of occasionally failing to detect parasitization by another species.

Size. The size of eggs laid by birds ranges across 5 orders of magnitude

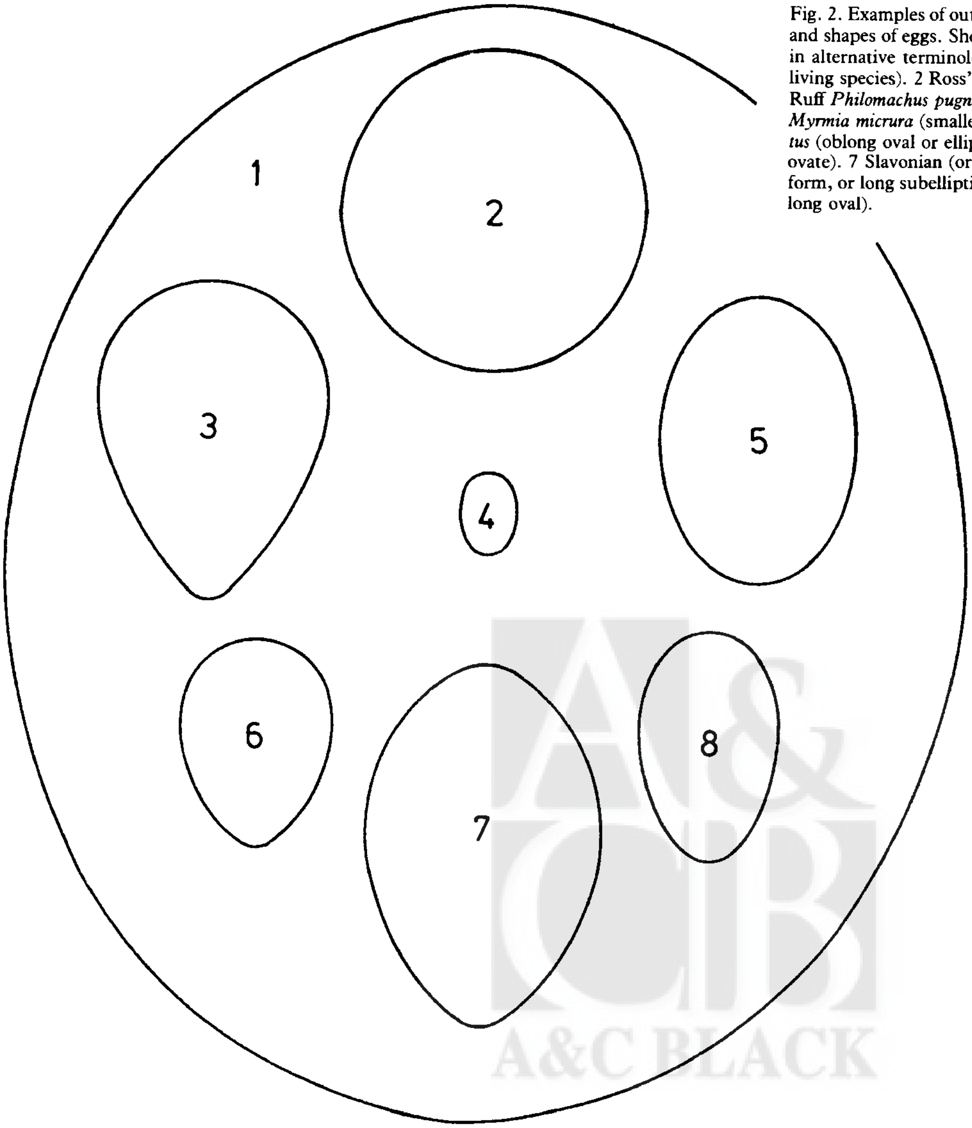

Fig. 2. Examples of outlines (or 'profiles') to illustrate some different sizes and shapes of eggs. Shown in natural size; the shapes here are designated in alternative terminologies. 1 Ostrich *Struthio camelus* (largest egg of a living species). 2 Ross's Turaco *Musophaga rossae* (round or spherical). 3 Ruff *Philomachus pugnax* (pyriform or conical). 4 Hummingbird species *Myrmia micrura* (smallest egg). 5 Coroneted Sandgrouse *Pterocles coronatus* (oblong oval or elliptical). 6 African Thrush *Turdus olivaceus* (oval or ovate). 7 Slavonian (or Horned) Grebe *Podiceps auritus* (bi-conical, fusiform, or long subelliptical). 8 Alpine Swift *Apus melba* (elliptical ovate or long oval).

from a hummingbird's 0.3 g through to the 1,600 g egg of the Ostrich *Struthio camelus*. Egg weight is closely correlated with the weight of the female, however, varying allometrically within each order or family to a 0.67 exponent. That is, if species A weighs twice species B its eggs will weigh $(2.0)^{0.67}$ or 1.59 times those of species B.

Substantial differences in egg-size exist between different orders once body size is allowed for: a 100 g falcon lays a 15 g egg whilst a 100 g dove lays only a 6 g egg. Such differences (which for a 100 g bird range from 4.5 g in the Cuculiformes to 21 g in the Procellariiformes) are associated in part with whether the chick is nidicolous or nidifugous. Precocial chicks must fend for themselves in whole or in part from shortly after hatching and therefore have to hatch from a relatively larger egg. Within a particular development class the extent to which the chick is covered with down at hatching is correlated with egg-size.

Some parasitic cuckoos have unusually small eggs for the size of the female, evidently adaptive for their habits of parasitizing species smaller than themselves.

Even within a single order of birds there may be considerable variation in the size of egg laid by individuals of common size but from different families. In the Passeriformes egg weights from 30 g birds vary from 6.0 g in the Fringillidae through 4.0 g in the Troglodytidae, 3.3 g in the Turdidae, 2.9 g in both Motacillidae and Alaudidae to 2.6 g in the Hirundinidae. The trend suggests that the more aerial species lay relatively lighter eggs for their body size.

Similar differences exist within even a single tribe. In the Anatidae, for example, each tribe has a very similar egg weight to female weight relationship but average egg weights differ between tribes. For a 100 g bird egg weights range from 53 g in the Cairinini through to 101 g in the Oxyurini. Interestingly, the ducks of the Anatini have eggs at the light end of the spectrum (59 g at 1,000 g body weight) whilst the geese of the Anserini are the second heaviest tribe (74 g at 1,000 g).

Within a species egg-weight varies considerably, both between females and between clutches by an individual female. Egg-size is correlated with female size, heavier individuals producing larger eggs. This effect is genetically controlled, so that egg-size is inherited. But egg-size is also phenotypically modified by other factors. Females breeding for the first time generally lay slightly smaller eggs than do more experienced individuals and the very oldest birds may revert to producing smaller eggs. Also, since females of many species have difficulty acquiring enough food for egg-formation even in normal conditions, a scarcity of food during the egg-laying period may result in rather smaller eggs than usual. Small eggs are less successful at producing viable fledglings, however, and the majority of birds with multi-egg clutches produce a smaller number of eggs of near normal size in such circumstances. Species with already low clutch-size (the extreme being single egg species) cannot readily adjust clutch-size in this way and instead take longer to produce each egg. The European Swift *Apus apus*, for example, normally lays 3 eggs at two-day intervals but in bad weather lays only 2

Snares Crested Penguin *Eudyptes robustus* male and clutch. Note larger second egg (29% heavier). (*Photo: J. Warham*).

eggs with a 3 (or even 4) day interval between them.

Differences in egg weight between the eggs of an individual clutch have also been recorded but the pattern varies between species. In the domestic fowl the first egg of a set is often slightly smaller than those following, perhaps because the oviduct stretches slightly with the first egg. Amongst wild birds, however, the most frequently observed divergence from a common egg-size for the clutch is for the last egg to be smaller than the others. This is regularly observed amongst gulls, raptors, herons, and other groups with unpredictable food sources. The small final egg produces a smaller and weaker chick than do the other eggs and it dies quite quickly if the food supplies are inadequate for the entire brood. Were all the young equally sized, all might get equal but inadequate shares of the available food and all might die. In good seasons the last chick survives despite its small size. In other species, including some owls and Coot *Fulica atra*, the later eggs of the clutch decrease in size with laying order so that the resulting young are a graded series with respect to competitive ability and 1, 2, or more of the weaker young die off in turn until brood size and food supply are matched. An extreme form of this type of within-clutch weight-difference occurs in Macaroni Penguins *Eudyptes chrysolophus* (and in other penguins of the genus) in which the first egg (which is smaller, by about 42% than the second egg), is neglected by the parent unless the second egg is lost; it never produces a fledgling if the second egg hatches.

In House Martins *Delichon urbica* unusually small eggs have been shown to result from the depression of aerial insect abundance brought about by bad weather while the females were laying. In other species of medium body size, 'runt' eggs appear in the nest on the final laying day, probably because the female concerned has exhausted her energy (or other) reserves before completion of a normal egg. In these cases, of course, small egg-size is maladaptive.

Since egg-weights are proportional to female body weight raised only to a 0.67 power rather than to a 1.0 power, large species lay relatively smaller eggs than do smaller species. At one end of the range small hummingbirds lay eggs about 25% of their own body weight. At the other Ostriches *Struthio camelus* lay eggs about 1% of their weight. The smallest species thus achieve a remarkable feat of metabolism in the production of each egg. However, many birds produce not one but several eggs as a set (see CLUTCH-SIZE) so that the total egg mass they produce is substantially larger. Clutch-size decreases slowly with body weight, however: for each 10-fold increase in body weight the average clutch-size decreases by 30% amongst the ducks and by 28% amongst the pheasants. Large birds thus do not make the same relative effort in egg production as do small species.

Very few birds produce more than their own body weight in eggs in a single clutch. Some finches reach a mximum of 95–110%, and clutch weights similarly only slightly exceed body weight in even the most productive ducks and pheasants. There may, therefore, be some physiological limit to egg production about this point. R.J.O'C.

See photo BROOD-PARASITISM.

Murton, R.K. & Westwood, N.J. 1977. Avian Breeding Cycles. Oxford.
Romanoff, A.L. & Romanoff, A.J. 1949. The Avian Egg. New York.
Skutch, A.F. 1976. Parent Birds and their Young. Austin.

EGG COVERING: eggs are sometimes covered by adult birds about to leave the nest-site. Grebes (Podicipedidae) provide the best known examples, disturbed birds pulling pieces of nest material over the eggs when mildly alarmed, completing the process and slipping away if further alarmed. If surprised from the nest the bird may return briefly to the eggs to cover them before staying away for a longer period. Many northern ducks and geese (Anatidae) also cover the clutch when leaving it unattended, using a thick layer of the feather or downy lining of the nest for the purpose. Tits *Parus* spp. regularly cover the eggs until the clutch is complete. Egg covering is also observed in warmer climes: at least two African sand-plovers *Charadrius* cover their eggs with sand when driven from the nest by human approach (see also SEEDSNIPE). These cases all probably constitute examples of anti-predator precaution but in other species thermal factors may be more important. Scandinavian Goldcrests *Regulus regulus* build a 'flap' of soft feathers across the entrance to the nest which lessens the circulation of near-freezing air across the clutch when the eggs are left unattended. This flap does not occur in nests in the more southern parts of the species' range.

EGG MIMICRY: see BROOD-PARASITISM.

EGG PROTEIN: see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA.

EGG RECOGNITION: the ability of individual birds to recognize their own eggs. The ability is well-developed in species nesting colonially without substantial nest structures e.g. Guillemots *Uria aalge*—and in species subject to BROOD-PARASITISM. Recognition may be achieved by responses to individually distinctive patterns of colour and markings or by recognizing a foreign egg as 'odd man out' within a clutch. See EGG; RECOGNITION, INDIVIDUAL.

EGG RETRIEVAL: several scrape-nesting species—terns, sandpipers, gulls and others—will retrieve eggs which are accidentally ejected from the nest, provided they are not too far away. Few species will retrieve eggs as much as a metre from the nest site. The retrieval process has been particularly studied in the Greylag Goose *Anser anser* and found to involve a rather stereotyped behaviour pattern. The goose retrieves a displaced egg by stretching the neck towards it, bringing the bill to the far side of the egg and rolling it back into the nest; any wobbling of the egg is compensated by lateral movements of the bill. If the egg is removed experimentally during this process, the backward motion with the bill may be completed even though no egg is present. The lateral bill movements do, however, disappear. The retrieval behaviour thus involves the release of a complex 'action pattern' which runs to completion once released, with only its orientation modified by stimuli from the egg wobble.

EGGS AS FOOD: see PALATABILITY OF BIRDS AND EGGS; UTILIZATION BY MAN.

EGGSHELL DISPOSAL: see PARENTAL CARE.

EGGSHELL THINNING: disease, nutritional deficiency, age, stress and certain drugs can cause birds to lay abnormally thin-shelled eggs. In wild birds, eggshell thickness typically shows a normal frequency distribution around a constant mean for each species, but occasional extra thin-shelled eggs can result from chance adversities to individual birds. In 1966, investigation of an unprecedented increase in frequency of broken eggs in nests of Peregrine *Falco peregrinus*, Sparrowhawk *Accipiter nisus* and Golden Eagle *Aquila chrysaetos* in Britain revealed that it coincided with pronounced and widespread eggshell thinning in those raptors. Large samples of eggshells in egg collections, going back to the 19th century, showed a sharp drop in shell thickness to new means which were, for the above species, 19%, 17% and 10% lower than the previous constants. In the Peregrine and Sparrowhawk the onset of decline was precisely dated to 1946–47. Other species showing post-1947 eggshell thinning in Britain included Heron *Ardea cinerea* 20%, Gannet *Sula bassana* 20%, Merlin *Falco columbarius* 13–22%, Shag *Phalacrocorax aristotelis* 12%, Hobby *Falco subbuteo* 5%, Kestrel *F. tinnunculus* 5%, Crow *Corvus corone* 5% and Rook *C. frugilegus* 5%. Species examined but showing no significant change were Buzzard *Buteo buteo*, Raven *Corvus corax*, Guillemot *Uria aalge*, Razorbill *Alca torda*, Kittiwake *Rissa tridactyla*, Black-headed Gull *Larus ridibundus*, Golden Plover *Pluvialis apricarius* and Greenshank *Tringa nebularia*.
Shell thickness was measured first as an index by the formula

$$\frac{\text{Weight of shell (mg)}}{\text{length (mm)} \times \text{breadth of shell (mm).}}$$

Precise and direct measurements confirmed that this decrease in relative weight of eggshells is the result of decrease in their thickness. Eggshell thinning has been shown to be widespread and pronounced in many North American bird species, mainly raptors and fish-eaters, including the Guillemot. In the Peregrine (10–26% less) the onset was again dated to 1946–47. Shell thinning in Peregrine eggs is reported also from mainland Europe, Siberia, North and South Africa, Arctic North America and Australia.

Correlative and experimental evidence have established repeatedly that the principal cause of the eggshell thinning phenomenon is contamination of the parent females by the environmental pollutant pp′ DDT and its metabolite pp′ DDE, which were sufficiently widespread in 1946–47 to account for the onset then. The subsequent success of DDT as an agricultural insecticide has caused almost global risks of eggshell thinning in vulnerable species. The population effects of DDT/DDE-induced eggshell thinning vary. There appear to be inter-specific differences in sensitivity, with flesh- and fish-eating birds showing the most marked shell thinning. The populations of some species are variably exposed to DDT/DDE contamination because of geographical and ecological factors. The virtual extinction of the Peregrine in the eastern United States and south-east Canada by 1964 is attributed largely to the effect of shell thinning in causing egg breaking and nesting failure, and hence an unfavourable recruitment/mortality balance. Any species' population showing an overall shell thinning of 20% or more is at serious risk of decline, and a general relationship between population status and degree of eggshell thinning for a range of North American birds has been found. As uses of DDT have been phased out in parts of the western world, monitoring has revealed recoveries in shell thickness in certain species.

The biochemical mechanism of DDT/DDE induced eggshell thinning is not precisely known despite much study. Cooke concludes that it may vary between different species, but that in the Peregrine a reduction in shell components in the shell gland during calcification is probably involved, perhaps in response to decreased enzyme activity in the shell gland tissue. D.A.R.

Cooke, A.S. 1973. Shell-thinning in avian eggs by environmental pollutants. Environ. Pollut. 4: 85–152.

Hickey, J.J. & Anderson, D.W. 1968. Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. Science, N.Y. 162: 271–273.

Ratcliffe, D.A. 1970. Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. J. Appl. Ecol. 7: 67–115.

EGGSHELL, ULTRASTRUCTURE OF: composed chiefly of calcite, one of the crystalline forms of calcium carbonate, and a small amount of organic matrix. The calcified layers may be covered by an organic cuticle, as in some Galliformes, and sometimes also by a crystalline layer of vaterite, a form of calcium carbonate, as observed in the 'chalky' cover of the eggshells of certain seabirds, such as gannets and cormorants (Tullett *et al* 1976). Small amounts (usually not over 0.1% by weight) of other inorganic constituents such as phosphorus, magnesium, sodium and potassium are also incorporated in the calcified shell. Phosphorus quantities may occasionally reach *c.* 2.5% by weight in some Galliformes.

The various calcified layers can be revealed by scanning electron microscopy. Usually the calcified eggshell can be subdivided into the following zones: caps, cone layer, palisade layer, surface crystalline layer, and a surface stratum, either organic (cuticle) or crystalline (vaterite). Below the basal caps there are two membranes, which adhere to each other except at the broad pole of the egg, where an intervening airspace is formed. The thickness of the fibres forming the eggshell membrane varies with the size of the egg. For instance in the Double-crested Cormorant *Phalacrocorax auritus* the fibres of the outer membrane are 5.0 µm in diameter, but the same fibres in the Long-tailed Tit *Aegithalos caudatus* measure 0.5 µm in diameter (Becking 1975). The palisade layer is distinguished by the presence of numerous pit-like cavities, which are in fact vesicular holes because they have an organic lining, as is evident by carefully dissolving the calcite with dilute acid. On the outer membrane there are centres of crystallization, called mamillary cores, which are small masses of organic matter adhering to the eggshell membrane. From these, crystals of calcite ('spherulite crystals') grow radially in all directions to enclose the membrane fibres, thus firmly binding the calcified part of the shell to the eggshell membrane. Calcite crystals which grow inward and sideways produce the basal caps, and those which grow outward to meet crystals from other centres of crystallization form the cones.

As is obvious from scanning electron micrographs, the eggshell near the outside is very compact. It shows a lamellate pattern approximately parallel to the surface of the eggshell and at an angle to the lamellae of the underlying palisade layer. The latter lamellar structure is produced by the rhombic cleavage pattern of the calcite crystals. The calcite lattice is, under natural cleavage conditions, a fundamental rhombohedron with an angle of 105° between adjacent faces and each face with plane angles of 102° and 78°. As indicated by measurements, the palisade layer of a radially fractured eggshell has a perfect calcite cleavage pattern. The lower part of the palisade layer shows many holes, the so-called vesicular holes, randomly distributed. These pit-like holes, which appear to be lined with organic matter, are larger and more abundant in the eggshells of tropical birds than in those of Palearctic birds. Nothing is known about their physiological significance, but it may be related to the facilitation of gas exchange, which is hampered by high humidity.

Large pores are sparsely but uniformly distributed over the eggshell surface. Most bird species have a characteristic number (with small variations) of pores per eggshell surface area. The pores provide direct connection between the outside environment and the spaces between the cones. Scanning electron microscopy reveals that the pore entrances at the surface are always situated at the borders of the polyangular fields of similarly orientated crystals forming the columns of the eggshell. Different bird groups show a different size and shape of pore channels. In ostrich and rhea they are branched, whereas in other species, in particular in passerines, they consist of a single more or less straight channel from eggshell membrane (or basal cap) to the surface. Pores regulate the gas pressure through the calcified shell, allow the access of oxygen to the blood vessels of the embryo (chorioallantois) in contact with the inner membrane of the shell, and serve for the discharge of carbon dioxide and water, the waste products of the oxidative metabolism of the embryo (Rahn *et al* 1979). Pore openings may be different in shape and size in different groups of birds. Eggs of Galliformes have large pores filled with plaques showing an irregular surface texture of hair-lines and cracks very reminiscent of mud cracked by drought. Many small passerines show straight pores without filling material at the entrance. Eggs of parasitic cuckoos show pores with a funnel-like entrance which is sealed with granular organic matter material. By this characteristic cuculid eggs can be immediately distinguished from similarly coloured host eggs (see BROOD-PARASITISM); moreover cuckoo eggs have a very compact outer texture with triangular or multiangular raised faces (Becking 1975). The surface texture of eggshells as observed by scanning electron microscopy is different in various bird groups and often characteristic of the group. Passerines (e.g. Sylviinae) have eggshells with many minute pits on the surface, whereas cuculids have rather compact pitless shells. Thus the ultrastructure of birds' eggs allows their classification to a certain group and sometimes even to generic or species level. It is a useful tool for determining the identity of putative cuckoo eggs (Becking 1981), and is also useful for studying the morphological aspects of egg breakage by EGGSHELL-THINNING as the result of dietary intake of DDT or other toxic chemicals. J.H.B.

Becking, J.H. 1975. The ultrastructure of the avian eggshell. Ibis 117: 143–151.
Becking, J.H. 1981. Notes on the breeding of Indian cuckoos. J. Bombay Nat. Hist. Soc. 78: 201–231.
Erben, H.K. 1970. Ultrastrukturen und Mineralisation rezenter und fossiler Eischalen bei Vögeln und Reptielen. Biomineralisation Forschungsberichte 1: 1–66.
Rahn, H., Ar, A. & Paganelli, C.V. 1979. How bird eggs breathe. Scient. Am. 240: 46–55.
Tullett, S.G., Board, R.G., Love, G., Perrott, H.R. & Scott, V.D. 1976. Vaterite decomposition during eggshell formation in the cormorant, gannet and shag, and in 'shell-less' eggs of domestic fowl. Acta Zool., Stockh. 57: 79–87.

EGG TOOTH: a small sharp projection on the upper mandible of the full-term embryos of many species, used in chipping open the egg shell during hatching. It is usually lost from the bill within a few days from hatching. See photo PARENTAL CARE.

Whimbrel *Numenius phaeopus* 2 h after hatching, showing the egg tooth. (*Photo: E.J. Hosking*).

EGG WHITE: see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA; EGG.

EGRET: substantive name of several species of Ardeidae (see HERON). See photos CREST; DISPLAY.

EIDER: substantive name, sometimes 'eider-duck', of *Somateria* spp. and *Polysticta stelleri*; used without qualification for *S. mollissima*; in the plural, general term for the tribe Somateriini (see DUCK). 'Eider-down' is the breast down with which the female *S. mollissima* lines its nest and is in some countries collected commercially.

ELAENIA: generic name used as substantive name of *Elaenia* spp. and *Myiopagis* spp. (see FLYCATCHER (2)).

ELANINAE: see HAWK.

ELBOW: see under MUSCULATURE; SKELETON, POST-CRANIAL; WING.

ELECTROPHORESIS: see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA.

ELEPAIO: *Chasiempis sandwichensis* of Hawaii (for subfamily see FLYCATCHER (1)).

ELEPHANT-BIRD: in the plural, general term for the extinct Aepyornithidae (Struthioniformes). Three genera of these large, flightless, graviportal ratites have been recognized. Four generally accepted species of *Aepyornis* and 3 of *Mullerornis* have been described from extensive skeletal and egg remains from Pleistocene to Recent deposits in Madagascar, though not all of these forms may be valid. *Stromeria fajumensis* is known from an incomplete tarsometatarsus from the lower Oligocene of Egypt; its allocation to the Aepyornithidae is, however, controversial (see FOSSIL BIRDS). The Eocene *Eremopezus* is not now considered to be aepyornithid. Miocene and Pliocene eggshell fragments, tentatively identified as aepyornithid on the basis of microstructure, have been found in Lanzarote (Canary Islands), North Africa, Turkey, India and Inner Mongolia (Sauer 1972, 1976). Thus there is no certain evidence that the family ever existed outside Madagascar. The family appears to have been a primitive member of the ostrich-rhea-emu lineage (see EARLY EVOLUTION OF BIRDS).

The Malagasy forms were massive birds with strong, conical bills and vestigial wings. *Aepyornis maximus*, the largest species, stood 3 m tall and may have weighed 450 kg, rivalling the Moa *Dinornis giganteus* and the Australian *Dromornis* (Dromornithidae) as the largest known bird. The legs of *Aepyornis* spp. were very stout, with relatively short tarsometatarsi, suggesting that these birds were probably slow-moving forest-dwellers (Cracraft 1974). The Ostrich-sized *Mullerornis* spp. were more gracefully proportioned. The feet of elephant-birds were apparently three-toed, the hallux usually if not always missing.

Entire aepyornithid eggs measuring as much as 33 × 24 cm have been found in Madagascar, one containing bones of an embryo (Wetmore 1967). Their average capacity has been estimated at 9 litres. These eggs have been described as the largest known single cells in the Animal Kingdom.

Aepyornis apparently persisted until comparatively recent times. Eggshell fragments have been radiocarbon-dated at 1,000 ± 150 years B.P. (Burger *et al* 1975). Flacourt (1658) recorded Malagasy tales of the Vouron-Patra (or Vorompatra), a large Ostrich-like bird supposedly still extant. These may represent, however, a tradition of a bird by then extinct, reinforced by the eggs, of which well-preserved specimens were locally prized. The legendary Roc (see FABULOUS BIRDS), which, according to Marco Polo, lived on islands south of Madagascar, may possibly be linked with such a tradition. The Malagasy natives probably brought about the final extinction of the elephant-birds by a combination of habitat loss through deforestation, with ensuing drought, and hunting pressure. See also EXTINCT BIRDS; MALAGASY REGION. (A.L.T.) R.O.

Burger, R., Ducate, K., Robinson, K. & Walter, H. 1975. Radiocarbon date for the largest extinct bird. Nature 258: 709.
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Flacourt, E. de 1658. Histoire de la Grande Ile de Madagascar. Paris.
Sauer, E.G.F. 1972. Ratite eggshells and phylogenetic questions. Bonn. Zool. Beitr. 23: 3–48.
Sauer, E.G.F. 1976. Aepyornithoide Eierschalen aus dem Miozän und Pliozän von Anatolien, Türkei. Palaeontogr. Abt. A 153: 62–115.
Wetmore, A. 1967. Re-creating Madagascar's giant extinct bird. National Geogr. 132: 488–493.

EMARGINATION: see FEATHER.

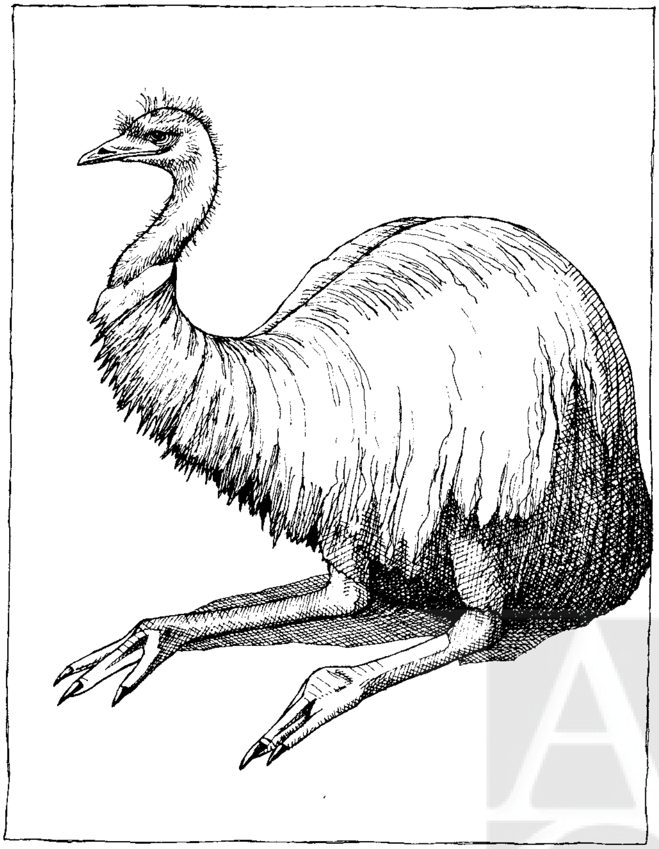
EMBERIZIDAE: a family of PASSERIFORMES, suborder Oscines; BUNTING; CARDINAL GROSBEAK.

EMBRYO: the young bird from the earliest stage of its development within the egg until the time of hatching (see DEVELOPMENT, EMBRYONIC).

EMERALD: substantive name of *Chlorostilbon* spp., *Elvira* spp., and some *Amazilia* spp. (for family see HUMMINGBIRD).

EMIGRATION: term used to describe migration from an area without postulating a return (see MIGRATION).

EMU: name of the sole surviving member of the Dromaiidae (Struthioniformes); in the plural (emus) also general name for the family. The Emu *Dromaius novaehollandiae* occurs over much of Australia, most commonly in sclerophyll forest and wooded savanna. It is rarely found in the centre of the deserts or in the environs of the major cities. In the dense tropical rain-forests of northern Queensland it is replaced by another large ratite species, the Australian Cassowary *C. casuarius* (see CASSOWARY). Smaller island forms of emus, which existed on Tasmania, King I and Kangaroo I (South Australia) were exterminated soon after white settlement. Their respective tarso-metatarsal lengths were (aver-



Emu *Dromaius novaehollandiae*. (*N.W.C.*).

ages) 21, 23 and 27 cm compared to 38 cm for the mainland form; their taxonomic positions are not clear. The mainland Emu is monotypic. Several extinct forms are known from Pleistocene fossils.

Characteristics. The second largest surviving ratite, an adult Emu standing erect is 1.6–1.9 m tall and generally 30–45 kg in weight. On average, females are larger and heavier. No reliable plumage features differentiate the sexes, though during pair formation in late summer females are more recently moulted and often show blacker neck plumes and darker facial skin. The wings are more vestigial than those of other large ratites, lack quills and have no muscular control or part in displays.

Many advanced and derived features of the skeleton are similar to those shown by *Casuarius*, emus and cassowaries being each others' closest living relatives. Other features in common are the double-shafted feathers, lack of an oil gland, inflatable neck sac and coloured facial skin. The types of diet are similar, as are the patterns of breeding biology.

Distribution, populations and movements. Emus remain common over much of Australia, despite persecution in the agricultural zones where birds have caused damage to fencing and growing crops. They drink frequently from sources of fresh water, especially in hot weather; on large rangeland holdings in semi-arid country they have exploited new sources of permanent water provided by dams and troughs. Their populations have probably increased as a direct result of white settlement and provision of water in these areas. The population as a whole is highly mobile and some birds move into marginal areas of the semi-arid and arid interior when rainfall stimulates the productivity of native vegetation. The capture and banding of adults has shown the Emus in Western Australia are truly nomadic and capable of changing their location by up to 500 km in 9 months. Emu-proof fencelines have been built to protect agricultural zones from winter movements of birds attempting to leave unfavourably dry areas. They have had the effect of deflecting seasonal movements of the increased numbers now existing in semi-arid regions. Large concentrations have built up along fences in Western Australia on several past occasions; control measures have been invoked but mostly to little effect.

Food. Emus feed on a great variety of plant material: green herbage; growing tips of shrubs and forbs; fruits; seeds; flowers. Insects and their larvae are also taken. A primitive form of coprophagy occurs, semi-digested particles frequently being consumed from fresh droppings. Coprophagy may have a role in the nutrition of young chicks, which sometimes hatch in a dry, depauperate environment. Geographic and seasonal variations in the availability of food stuffs require that Emus live mainly in low density populations which are seasonally nomadic. The anatomy of the digestive system differs from the general avian type in that there is no crop: the gizzard hangs in the living bird in such a way that the anterior entry and posterior exit are both dorsal, the gizzard extending ventrally as a suspended bag. The caeca are relatively small, bacterial action evidently having little importance in the digestion of a nutrient-rich diet.

Behaviour. Socially there is much aggressive behaviour and display by both sexes, the ontogeny of which is traceable from actions first shown within one week of hatching. During pair formation the larger female is dominant to the male; males accompanying young chicks become aggressive and will attack Emus or other large animals which approach them.

Voice. Both sexes make a variety of bubbling and booming noises, but only displaying females utter single loud, resonant bass notes (referred to as drumming) from an inflated pouch. Males are more inclined to grunt.

Breeding. Wild birds evidently breed in pairs; in captivity 'trios' sometimes occur but pairs are more usual. A clutch of 5–15 blue-green eggs, each weighing 450–650 g, is laid on the ground in autumn and winter at intervals which decline from 4 days or more to 2 days or less over a period of about one month. Females pay little attention to the nest and have no part either in incubation or rearing the young. The male alone incubates the eggs, rising to roll them over once to several times daily. During incubation he does not normally eat, drink, defaecate or leave the immediate vicinity of the nest, but spends his time in nest-building, preening and dozing. The eggs hatch in synchrony after 53–61 days (average 56). Nests of hatchlings are sometimes taken by foxes and dingoes (wild dogs); Wedge-tailed Eagles *Aquila audax* are reported to attack young and occasionally adult birds. Unattended eggs are eaten by Black-breasted Buzzards *Hamirostra melanosternon*, and crows *Corvus* spp.

The young feed themselves and leave the nest with the male when 2–7 days old. Male and chicks maintain close contact and call to each other frequently. The family is solitary and diurnally active, resting in the open at night. Parent-chick bonding loosens after 4 months and family life lasts for 6 months or more; the young grow to nearly adult size and appearance when 1 year old.

Day-old chicks weigh about 1% of adult body weight, can peck at food items on their second day, run and swim competently at one week. They hatch in a thick down patterned with black, white and tan stripes. In 3–4 months this is replaced by a blackish-brown immature plumage consisting of variegated double-shafted plumes. Adult-type plumes appear from 6 months, by which time the young average half adult weight and three-quarters adult height. Sexual maturity occurs from the second year.

Economic use. Attempts to farm Emus intensively in Western Australia have not yet met with success. The skins, from which valuable dress leather can be made, are easily damaged on the living bird. Carved eggs for decoration, subcutaneous fats and Emu meat also have commercial potential if successful husbandry procedures can be devised. See also EMU WAR. (D.L.S.) P.J.C. (2)

Cracraft, J. 1974. Phylogeny and evolution of the ratite birds. Ibis 116: 494–521.

Davies, S.J.J.F. 1967. Sexual dimorphism in the emu. Emu 67: 23–26.

Davies, S.J.J.F. 1976. The natural history of the Emu in comparison with that of other ratites. Proc. XIV Int. Orn. Congr.: 109–120.

Davies, S.J.J.F. 1978. The food of emus. Aus. J. Ecol. 3: 411–422.

Morgan, A.M. & Sutton, J. 1928. A critical description of some recently discovered bones of the extinct Kangaroo Island Emu *Dromaius diemenarius*. Emu 28: 1–19.

Serventy, D.L. & Whittell, H.M. 1976. Birds of Western Australia. Perth.

EMU-TAIL: substantive name of the 2 Madagascar warblers of the genus *Dromaeocercus* (see WARBLER (1)).

EMU WAR: name given to the 1932 'campaign' by an Australian Commonwealth machine gun unit, at the request of the State of Western Australia, to destroy invading Emus *Dromaius novaehollandiae*. It attracted bizarre notice, with front line press despatches. The offensive began on 2 November when an artillery detachment attempted to engage some 20,000 birds, which apparently adopted guerilla tactics and split into small units. This made use of the military equipment uneconomic. The crestfallen field force withdrew after about a month and the method was abandoned in favour of emu-proof fences to check seasonal incursions into the marginal wheat-growing country. D.L.S.

EMU-WREN: substantive name of *Stipiturus* spp. (see WREN (2)).

ENDANGERED BIRDS: any bird species whose numbers are declining can be said to be in some danger of extinction, but the term endangered is usually reserved for those species whose numbers have fallen to a critically low level. Some birds, such as the Mauritius Kestrel *Falco punctatus* and the California Condor *Gymnogyps californianus*, have been reduced to a mere handful of individuals and it is very possible that they will shortly join the list of EXTINCT BIRDS.

Extinction is a natural part of the evolutionary process, which involves the continual replacement of existing species by new ones. It is very difficult, if not impossible, to separate natural changes in the environment from those brought about by humans, but for some endangered species, such as the Kakapo *Strigops habroptilus* of New Zealand, it seems that a decline in numbers was already occurring before the arrival of Europeans accelerated the process. However, throughout the world the last 300 years have been a period of greatly accelerated decline and extinction which has been the result, not of a natural process, but of human activities. It is clear from a geographical and historical analysis of recent extinctions that they have closely followed the spread of industrialized European man as he has colonized various parts of the world. Sometimes the impact of man on birds has been direct, for example when birds are killed for food or clothing or because they are considered to be pests. Of greater importance are man's indirect effects on birds through the destruction or alteration of their habitats.

The history of man as a predator of birds is a mixed one. With some species, such as game birds and wildfowl, he has often avoided over-exploitation. Other species, such as the Eskimo Curlew *Numenius borealis* and the Society Islands Pigeon *Ducula aurorae*, have been driven to the verge of extinction as a result of their nutritive value to humans. The extinct Carolina Parakeet *Conuropsis carolinensis* owes its sad fate to its habit of raiding orchards which caused it to be ruthlessly hunted. Many birds of prey are still shot by gamekeepers on the pretext that they eat game birds, though the impact of birds of prey on gamebird populations is generally minimal.

Probably the most dramatic change in the environment wrought by modern man has been deforestation. This has destroyed or drastically reduced the habitat of many species. The Ivory-billed Woodpecker *Campephilus principalis* still survives in small numbers in Cuba and possibly in isolated pockets of swampland in south-eastern North America. Many species, notably wildfowl, have had their habitat destroyed or reduced by the draining of wetlands to create new agricultural and building land. Another very widespread factor in the decline of many species has been pollution, particularly by pesticides such as DDT (see TOXIC CHEMICALS). These have seriously affected a number of marine and freshwater birds and several birds of prey, such as the Peregrine *Falco peregrinus* and the Osprey *Pandion haliaetus*, which, through eating contaminated prey, absorb and accumulate large amounts of pesticide derivatives in their bodies. Pesticide poisoning causes birds of prey to lay eggs with such thin shells that they are crushed during incubation (see EGG-SHELL THINNING). Another major factor in the decline of many birds has been the introduction by humans of animals such as cats, dogs, rats, sheep and goats to parts of the world where they did not previously exist. These may prey upon indigenous birds or else destroy their habitat. Other indirect human influences on bird mortality are oil spillages at sea, the catching of sea birds such as auks in fishing nets, and collisions with overhead power cables.

Endangered birds may be grouped into 5 categories. These are:

1. Predatory species that occupy an ecological position at the top of a food chain. These are usually large birds that require an extensive area for hunting. Such areas are under constant threat from the expansion of human agricultural and industrial activities. Predators are also the species most prone to pesticide poisoning, and they are adversely affected by a reduction in numbers of any of the species in the food chain of which they represent the highest level.

2. Species with specialized habits. Birds that need a very specific diet or breeding site have difficulty finding alternatives if such resources become scarce. For example, the Everglade or Snail Kite *Rostrhamus sociabilis* of North America has become very rare following the decline in a species of snail which constitutes its sole source of food.

3. Species endemic to small islands. This is perhaps the largest category of endangered species and also includes the majority of those that have become extinct in the last 300 years. Mauritius and the Hawaiian islands have the unhappy distinction of having a greater number of extinct or endangered bird species than any other locality of comparable size. Island species are vulnerable to human influences for two reasons. First, as a result of being isolated from larger and more complex ecosystems for millions of years, many have lost adaptations against predators and competitors. Many island birds have reduced powers of flight, and some, like the Kagu *Rhynochetos jubatus* of New Caledonia cannot fly at all (see FLIGHTLESSNESS). Consequently, they are particularly vulnerable to animals such as rats and cats that have been introduced by man. Second, islands necessarily provide their endemic species with only a very limited range of movement. If islands are heavily exploited by humans, many birds have no alternative refuge.

4. Species that breed in dense colonies. These are particularly vulnerable to direct human exploitation simply because a dense aggregation of many birds in a limited space facilitates the killing of adults or the collection of their eggs and chicks. The Great Auk provides the classic example (see EXTINCT BIRDS). Abbott's Booby *Sula abbotti*, which breeds on Christmas Island in the Indian Ocean, is currently threatened because its one and only breeding colony is also the site of valuable deposits of phosphate fertilizer.

5. Migrants. Migratory species are vulnerable for two reasons. First, since they live in two, often widely separated localities, they may be subject to two quite different sets of hazards. Second, while on migration they often form flocks that fly along traditional flight paths and provide easy targets for hunters. The rarity of the North American Whooping Crane *Grus americana* is largely attributable to shooting along its migration routes.

The first step in the CONSERVATION of endangered birds is to identify those species whose populations are declining and to discover the causes of their decline. In this exercise the work of international agencies such as the International Union for the Conservation of Nature and Natural Resources (IUCN) makes a major contribution. The IUCN publishes the Red Data Book, which is a continually updated list of the world's rare and endangered species. In 1977 and 1979 the Red Data Book listed a total of 167 species and subspecies of birds as endangered. T.R.H.

Greenway, J.C. 1967. Extinct and Vanishing Birds of the World, 2nd edn. New York.

Halliday, T. 1978. Vanishing Birds. London.

King, W.B. 1977, 1979. Red Data Book, Vol. 2, Aves, 2nd edn., revised. Morges, Switzerland.

ENDASPIDEAN: term applied to the tarsal sheath when it has an anterior scutellated segment extending across the inner side of the tarsus; if, on the other hand, this extends across the outer side, the condition is termed 'exaspidean'.

ENDEMIC: term applied to a species or other taxon in relation to a stated area, meaning that it is restricted thereto; also applied to a disease as the antonym of 'epidemic', meaning that it is always present.

ENDOCARDIUM: see HEART.

ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM: in birds, as in all other advanced animals, two complementary control systems exist to co-ordinate the activities of the various tissues within the body. The NERVOUS SYSTEM, based upon nerves running directly to the target organ, has the great advantage of speed and specificity and so is used to control such activities as movement and behaviour. For other functions though, such as growth, metabolism or reproduction, speed and a transient effect are not important and these activities are regulated by the endocrine system. Here, specialized chemical messenger molecules (hormones), produced in small discrete structures called endocrine glands, are poured directly into the blood system and have their effects some distance from where they are manufactured. Not surprisingly, the two systems of communication have great influence on each other. The brain, as the organ which processes information about the outside world, largely controls the endocrine system via the pituitary gland, a good example of this brain-endocrine pathway being found in the way environmental factors regulate seasonal reproduction. An influence in the other direction is seen in the mating and parental behaviour shown by birds during breeding. These activities are products of the nervous system but are not exhibited unless hormones (in this case sex steroids) have primed the necessary brain circuits.

Endocrinology may quite reasonably be said to have been discovered in birds. In 1849 Dr A.A. Berthold of Göttingen published a short article in which he reported that removing the testes from young cockerels prevented the growth of the comb, wattles and spurs but that these were normal in castrated cockerels with testes transplanted back into the body cavity. The effects of castration had been known since ancient times but Berthold had demonstrated that they were reversible and, even more importantly, concluded that something from the testis influenced the secondary sexual characters. Fifty years later his observations were confirmed, but another 30 years were to pass before testosterone was isolated chemically and shown to be the agent responsible for comb growth. The subsequent development of endocrinology means that the basic structure and function of the avian endocrine system is now well understood and probably few new hormones wait to be discovered. In fact, the vertebrate endocrine system is very conservative and a shark possesses virtually the same complement of glands and hormones as a Blackbird *Turdus merula* or a lion. Many of the functions are also similar (e.g. insulin on blood glucose) and where differences do exist it is often the target tissue, where the hormones act, that has changed rather than the actual messenger. For example, in the Salmon *Salmo salar* prolactin changes the permeability of the gills to salts so allowing the fish to migrate from the sea into the river. In ducks the same hormone acts on the brood patch to cause its growth and probably also on the brain to trigger INCUBATION behaviour, whilst in the female mammal prolactin controls milk production in the mammary gland.

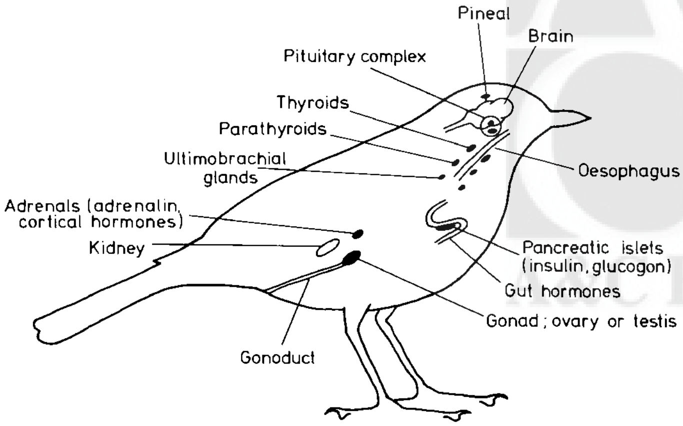


Fig. 1. The endocrine glands in a typical bird. A few other body structures are added as reference points.

Despite the wide range of functions controlled by them, most hormones have relatively similar chemical structures, being either peptides or proteins, or fat-soluble steroids. One implication of this is that the target tissue cells must possess specific receptors that can pick out and bind hormone molecules of only the correct configuration, e.g. the comb of a cockerel binds testosterone but is not interested in the closely related steroid oestradiol that is produced in the hen. If such specificity did not exist the system would obviously fail. Hormones are produced in minute amounts and are very potent molecules: in a laying hen the all-important oestrogens are present in the blood at 100 pg/ml (1 pg is one million millionth of a gram). Hormones also have the tendency to work together rather than individually to induce an effect and so in many cases (e.g. to control blood glucose levels, or growth of the oviduct) more than one is involved. This complicates the story somewhat.

The pituitary gland complex. The endocrine glands in a typical bird are shown in Fig. 1. At the centre of the system lies the pituitary, a glandular complex ($5\ mm^3$ in a chicken) located at the base of the brain. It is this location that gives to the pituitary such a dominant role over the other endocrine organs. The gland consists of two separate areas (Fig. 2). The neurohypophysis is actually part of the brain itself and contains the terminals of many thousands of neurosecretory neurons whose cell bodies lie scattered through the hypothalamus. Neurosecretory neurons play a key role in linking the brain to the endocrine system. In part they act like ordinary nerves, the cell bodies having extensive contact with the rest of the brain, but from their terminals they secrete hormones not neurotransmitters. This dual function allows them to act as bridges linking the brain to the endocrine system. The other part of the pituitary—the adenohypophysis—is entirely glandular and contains cells that produce 7 important hormones. The 2 gonadotrophins (Follicle stimulating hormone or FSH; Luteinizing hormone or LH) control gamete and sex steroid formation in the gonads, whilst thyroid stimulating hormone (TSH) controls the thyroid glands and adrenocorticotrophic hormone (ACTH) steroid production from the adrenal. Prolactin affects various aspects of reproduction. The other 2 hormones—growth hormone and Melanocyte stimulating hormone (MSH)—do not have discrete target tissues and act widely throughout the body. All 7 are protein or polypeptide hormones, LH, FSH and TSH are glycoproteins, containing sugar molecules attached to the protein backbone, and are closely related structurally. The 2 polypeptides (ACTH and MSH) probably derive from a common precursor called lipotrophin.

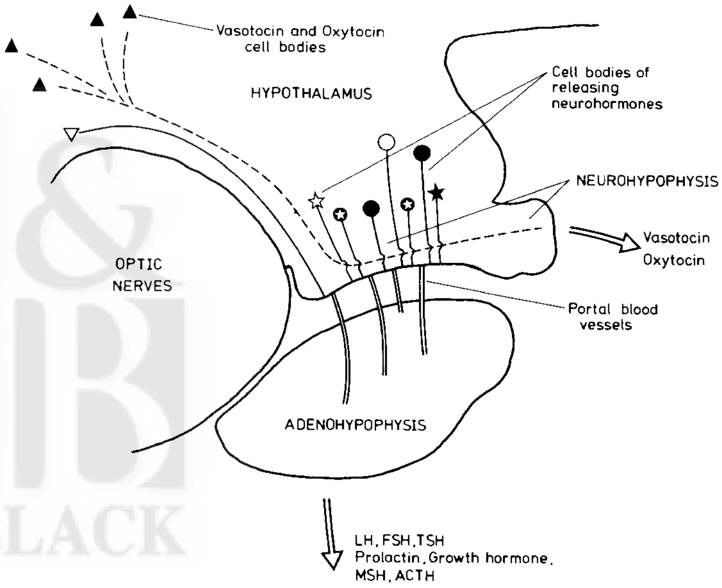


Fig. 2. Diagrammatic representation of the pituitary gland complex. Note that various types of neurosecretory neuron exist in the hypothalamus. The cell bodies are scattered through the hypothalamus but the nerve terminals all end on blood vessels in the neurohypophysis. The releasing hormones travel to the adenohypophysis via a number of special portal vessels. The trophic hormones of the adenohypophysis are secreted into the general circulation.

It appears that for each adenohypophysial hormone there is an equivalent releasing hormone present in the neurohypophysis. Thus, for TSH there is a TRH and for the 2 gonadotrophins (LH and FSH) a gonadotrophin-releasing hormone (Gn-RH). These neurohormones are synthesized within different neurosecretory neurons and released from the terminals into a special blood supply (Fig. 2) that carries them to the adenohypophysis where in turn they cause the release of the appropriate trophic hormone. In this way, the brain controls a wide range of peripheral endocrine functions including reproduction and growth. Some balance is restored to this control by the fact that in many cases the peripheral hormones can feed back on to the pituitary complex and influence its activity. For example, in response to cold there will be enhanced nervous activity in the brain and increased TRH release. The TSH secreted in response to this TRH will elevate thyroxine secretion and so stimulate more heat production. However, to ensure a balance, the thyroxine also acts back on the pituitary to dampen down further TRH/TSH release. Another example of this so-called negative feedback effect is that if the sex steroids are present in excess they depress LH and FSH secretion—a property made use of in the oral contraceptive pill.

Two of the neurosecretory hormones from the posterior part of the neurohypophysis—vasotocin and oxytocin—do not cause the release of other pituitary hormones but act directly on peripheral target tissues. Vasotocin is crucial for preventing dehydration and it achieves this by preventing water loss through the kidney, primarily by acting on the collecting ducts to increase water reabsorption back into the body but also by lowering the rate of filtration through the kidney. Both vasotocin and oxytocin are also involved in egg-laying, acting in concert with prostaglandins to cause waves of muscular contraction along the oviduct so expelling the egg (see LAYING).

The thyroid glands. The thyroids are paired ovoid structures (about 5 mm long in the chicken) lying low in the neck region close to the great veins and arteries. In response to TSH from the pituitary they release 2 hormones—thyroxine and tri-iodothyronine. As their names suggest, these hormones are unique in containing a number of iodine atoms. As in other vertebrates, the thyroid hormones are essential for normal growth and their absence in the young leads to dwarfism. In the adult, the main function is to maintain normal heat production. In addition, the thyroid is somehow involved in feather growth and in the MOULT. Thyroxine stimulates the development of young feathers and in its absence they become elongated and lose their rounded shape. The actual shedding of the feathers (moult) may result from a fall in sex steroids, e.g. at the end of the breeding season, at a time when thyroxine secretion is above normal.

The adrenal glands. The adrenals are small (3 mm^3) paired structures, often orange in colour, that lie just anterior to the kidneys in the body cavity. As in reptiles and mammals, the gland is a composite and contains 2 types of tissue (chromaffin or medullary; interrenal or cortical) which have quite different functions. The chromaffin cells produce adrenaline (and noradrenaline) in response to various stressful situations. This hormone acts rapidly to increase blood pressure and mobilize sugars and fats. As a result the bird is in a better position to take evasive action. Of greater importance, however, are the hormones from the interrenal cells (the corticosteroids, corticosterone and aldosterone) without which life would be impossible. Their secretion is under the control of pituitary ACTH. The corticosteroids have two important sets of functions. Firstly, they are metabolic hormones influencing the long term utilization and storage of carbohydrates, lipids and proteins. At first glance these actions may not appear important but this is deceptive and Cushing's syndrome in man emphasizes the point. In this illness too much corticosteroid is produced and as a result large deposits of fat are laid down. In birds living under natural conditions such intense lipid depositions may actually occur at the beginning of MIGRATION. The second function of the corticosteroids is on salt and electrolyte balance. In most terrestrial and freshwater birds this can be achieved by the actions of the hormones on the kidneys alone but in marine birds which drink seawater the situation is rather more complex. To lose the extra salt many marine birds have nasal salt glands which excrete an extremely concentrated solution of sodium chloride and potassium chloride. Control over this gland is complicated but secretion, having been initiated by nervous stimulation, requires corticosterone for the full activity to be maintained.

Growth hormone and prolactin. These closely related pituitary hormones have widespread effects on growth and tissue development. Growth hormone itself is usually thought to control general body development in young birds. Prolactin appears to have more specific actions. Acting with the sex steroids it is responsible for brood patch development and growth of the female reproductive tract. One of its other classic functions is to cause 'milk' formation in the crop glands of pigeons and doves (CROP MILK). In these birds the tissues in the walls of the crop sac proliferate during brooding and the protein and fat rich cells are sloughed off and regurgitated to feed the young. Prolactin is also involved behaviourally during incubation but its precise role is still unclear.

Hormones of the alimentary tract. Digestion in birds is regulated by both nervous and hormonal influences. It is a complicated process and only recently has it been studied in great detail. Gastrin and cholecystokinin are synthesized in the walls of the proventriculus and duodenum. Gastrin is thought to stimulate acid secretion while cholecystokinin causes gall bladder contraction and pancreatic enzyme secretion. This last function is also stimulated by another peptide hormone from the intestine called secretin (or its related VIP, vasoactive intestinal polypeptide).

The bird's pancreas produces both insulin and glucagon and these peptide hormones (together with adrenalin and corticosterone) are responsible for regulating sugar metabolism. Glucagon increases carbohydrate breakdown so elevating blood glucose and the availability of this sugar to the muscles, whilst insulin acts antagonistically to cause sugar uptake into cells and hence a decrease in blood glucose. In mammals insulin is the dominant hormone in this relationship and its absence leads to high blood glucose and to diabetes. However, in birds the position seems to be reversed and glucagon is the crucial hormone. When absent, blood glucose levels are unnaturally low and it acts to increase the circulating concentrations. Insulin may be primarily responsible for ensuring that levels do not become dangerously high.

Calcium metabolism. It is crucial for life that the various salts and ions are maintained at stable levels. In the case of potassium and sodium the corticosteroids play the key role but for calcium regulation 3 other hormones are involved. Calcium is, of course, particularly important in birds since the eggshell is largely composed of calcium carbonate. It is perhaps best to consider the situation first in the normal bird and then see how this is modified during egg-laying. Blood calcium levels are maintained primarily by 2 hormones acting antagonistically. Parathyroid hormone, a peptide produced in paired glands lying just behind the thyroids, increases blood calcium, whilst calcitonin from the nearby ultimobrachial glands depresses it. Both act in opposite fashions, on resorption of calcium from the bird's bones. A third hormone—1,25-dihydroxycholecalciferol—is also involved. This is produced in the kidney from Vitamin D_3 and acts on the intestine to enhance the absorption of calcium ions from the diet.

Once a bird begins laying its needs for calcium change dramatically. The shell 'gland' or uterus in the oviduct of a chicken has to secrete about 5 g of calcium carbonate in 20 hours to provide the eggshell and thus 2 g of calcium ions must be removed from the blood each day, at the rate of about 100 mg per hour. Since the total circulating quantity of calcium is 400 mg, it is clear that extensive bone resorption must take place each day. However, this cannot continue indefinitely since the bones themselves only contain enough calcium for 10 eggshells and so large quantities of calcium must be obtained from the diet. The end result is to place considerable pressure on the Vitamin D_3 metabolites such as 1,25-dihydroxycholecalciferol that stimulate the uptake of calcium from the gut, and on parathyroid hormone which is responsible for bone resorption. The turnover of bone calcium is so high that birds have evolved a special type of medullary bone which forms in the marrow of the long bones. At times of the day when requirements for eggshell calcium are low the excess is channelled into medullary bone. Later when the bird enters a calcium debt this can be mobilized by parathyroid hormone thus avoiding the need to withdraw calcium from the structural bones. The insoluble calcium carbonate shell is laid down by the cells lining the shell 'gland' in the lower oviduct. These cells contain an enzyme—carbonic anhydrase—which converts CO_2 into carbonate ions. These combine with the calcium ions and precipitate in an ever thickening layer of $CaCO_3$.

The pineal gland. Over the years many functions have been ascribed to the pineal organ, including that of being the seat of the soul! In lower vertebrates and in birds it contains photoreceptors but this function has been lost in mammals. In all it acts as an endocrine gland. The pineal is a small organ (1 mm^3 in chicken) located just behind the cerebral hemispheres on the top of the brain. It is attached by a stalk to the brain but is normally regulated by a nervous innervation from the base of the brain. In birds, as in mammals, it secretes a number of chemical compounds, of which melatonin is the best characterized. Most interestingly, melatonin is not secreted continuously but rhythmically with far more being released at night. In some birds this rhythmic secretion is used as a biological clock to regulate other physiological processes such as locomotor activity and feeding.

Reproduction—endocrinology and physiology. Most birds breed annually, and for three-quarters of the year the reproductive system remains undeveloped. The ecological reasons for this are discussed elsewhere (see BREEDING SEASON). This article concentrates on reproductive physiology, first considering how eggs and sperm are produced and then how these processes are moulded together to produce the offspring at the correct time of the year.

All male birds possess paired testes lying in the body cavity. These increase in size dramatically at the start of the breeding season, often becoming 200 times larger than during the non-breeding part of the year. This change is sometimes known as the progressive or acceleration phase.

The testes are filled with a mass of convoluted seminiferous tubules, each of which is lined by a layer of primary germinal cells. Between the tubules lie clumps of Interstitial (or Leydig) cells which are the source of the male sex steroids (androgens). Growth of the testes occurs as a direct result of increased pituitary LH and FSH secretion. FSH acts on the tubules causing cell division to begin. Within 3 weeks each primary germ cell has divided 5 or 6 times and the tubules are greatly expanded. The production of sperm involves not only ordinary mitotic divisions to increase the total number of germ cells but also a meiotic division to halve the chromosome complement and the transformation of these 'haploid' cells into spermatozoa. The spermatozoa have a characteristic structure with a head containing the nucleus, a middle piece filled with energy-producing mitochondria and a long tail with which to swim up the female tract. How FSH causes all these effects is still unknown but it probably acts not on the germ cells but on the Sertoli cells, which are non-germinal cells also lying within the tubule. In response to FSH, the Sertoli cells are believed to take up testosterone from the interstitium and it may be the sex steroid that actually influences mitosis. The sperm pass out of the testis into a duct (vas deferens) that leads to the cloaca. Near the cloaca this duct is expanded into a storage organ for the sperm. During copulation the cloaca is everted and semen is deposited in the female's cloaca. The volume of semen ejaculated in birds is relatively small (0.2–1.5 ml in the chicken) but it contains many million individual sperm. Artificial insemination is used in the poultry industry and is virtually mandatory in domestic turkeys where the males are now so large that they cannot mate properly. Penis-like organs exist in some birds (e.g. Anseriformes, Tinamidae, Cracidae, and the ratites).

Testosterone, the primary androgen, is secreted when LH acts on the Leydig cells. It has a wide range of functions, all associated in some way with the primary function of fertilizing the egg. Thus, it is responsible for growth of the sperm ducts and storage organs, often for the colourful plumage of the male, and also for much aggressive and sexual behaviour—including song. It also regulates the general level of reproductive activity, since testosterone feeds back negatively to the pituitary complex and suppresses excess LH and FSH secretion.

Most female birds have only a functional left ovary and oviduct, the right being rudimentary. Some of the more bizarre cases of farmyard hens turning into cockerels occur because very occasionally the rudimentary right gonad develops and often turns not into an ovary but into a testis (see OVOTESTIS). Hawks of all the major families (Cathartidae, Accipitridae, Falconidae) can be found that have two functional ovaries. Seasonal changes in the size of the reproductive organs are even greater than in the male. For example, in captive Japanese Quail *Coturnix c. japonica* in winter the ovary weighs 15 mg and the oviduct 20 mg, whereas in the breeding season the respective weights are 6,500 mg and 5,000 mg. In newly hatched birds the ovary contains a mass (a million or more) of minute oocytes. Only a miniscule fraction of these ever develop completely, the vast majority dying at some stage during growth. Each oocyte is surrounded by layers of follicular cells (zona granulosa and theca interna). These produce the sex steroids (oestrogens, progesterone and also some testosterone). During ovarian growth LH and FSH stimulate the follicular cells to secrete oestrogens. These act on the liver to cause the synthesis of yolk, a mixture of proteins and fats. The amounts of yolk produced are quite prodigious—about 15 g every day in a laying hen. In many small birds, e.g. Great Tits *Parus major*, the resources necessary to lay down yolk are so great that breeding cannot be started until there is a sufficient supply of food for the female to manufacture her eggs. In a poor season CLUTCH-SIZE may have to be reduced. The yolk proteins travel from the liver to the ovary in the circulation and are then absorbed by the growing oocyte. Eventually, at maturity, the average bird's ovary contains a hierarchy of about 10 yolky follicles, the largest being the most mature and ready to ovulate. During its final maturation phase this largest follicle appears to stop producing oestrogens (though the smaller ones do not) and instead starts to secrete progesterone. This steroid has a positive feedback effect on the pituitary and triggers a surge of LH secretion. Over the next few hours the LH causes a breakdown in the layers of follicular cells and ovulation of the naked yolk-filled oocyte from the ovary. This is picked up by the open end of the oviduct and fertilized by sperm lying in special crevasses at the top of the oviduct. During ovarian growth the oestrogens, together with progesterone, have also acted on the oviduct to cause its differentiation into an organ capable of investing the oocyte with various protective coats. In birds such as quail and chickens the fertilized oocyte spends about one day in the oviduct. It first stays for about 3 hours in the magnum and acquires layers of albumen (egg white protein). The cells begin to secrete albumen when stretched by the oocyte or by any foreign body in the magnum, even a table-tennis ball. After this the albumen-coated oocyte moves to the isthmus where the shell membranes are secreted. It then travels to the shell 'gland' or uterus and over the next 20 hours the calcareous shell is secreted around the egg (see section above on Calcium Metabolism). Water is also pumped into the albumen, causing it to swell considerably. In the final hour any shell markings are acquired and the egg is then laid as a result of increased oxytocin and prostaglandin secretion causing contractions of the shell 'gland'.

Birds vary widely in their clutch sizes and little is known of how this is controlled physiologically except that in some species ovulation can be stopped prematurely by adding eggs to a clutch. In the chicken, of course, man has learned that ovulation can be sustained for very long periods by regularly removing the laid eggs and well managed commercial strains lay about 270 eggs in 52 weeks. For most species, however, such a trick does not work indefinitely although it is proving valuable in breeding a number of endangered species. Chickens (and other Galliformes) lay to a consistent time pattern. In a few birds ovulation occurs every day at the same time, and the egg from that ovulation is duly laid 24 hours later. This can lead to prolonged sequences, which in one Japanese Quail was continued without a break for 140 days. Such patterns are not common though, and most birds normally lay in sequences containing 2 to 10 eggs, ovulation being restricted to an 8 hour period of each day. Thus, chickens lay their eggs only in the morning and early afternoon. In contrast, quail lay late in the day and early in the night. This periodicity is controlled by a biological clock (see RHYTHMS AND TIME MEASUREMENT).

As emphasized elsewhere (see BREEDING SEASON), environmental factors have to trigger reproductive growth well ahead of the time when the young have to be hatched simply because sexual maturity takes about 2 months to complete. Away from the tropics daylength is used as the main environmental cue heralding the arrival of the breeding season and the way in which photoperiod acts has been extensively studied. Other factors, of course, fine tune the precise time of breeding, but little is known about their physiological effects. One remarkable discovery has been that birds do not use their eyes for photoperiodic light detection. Light floods through the top of the skull and is detected by a photoreceptor lying in the hypothalamus (Fig. 2). Incidentally, the situation is different in seasonally breeding mammals which use their eyes to detect light for the photoperiodic response. Once the light has been detected, day length must then be measured and this requires a clock of some sort. Birds use their circadian clocks for this purpose. It is unclear exactly how this works but possibly there is a daily rhythm of sensitivity to light. For most of the day the bird is insensitive to light but for a period of a few hours, beginning about 12 hours after dawn, it becomes highly sensitive and if light is still present at this time, as occurs for the first time in early spring, then the day is read as 'long'. Experimentally, this means that reproduction can be triggered in birds by day lengths very much shorter than, say, 13 hours provided it can be arranged for some light to fall when the bird is photosensitive. In quail two 15 minute pulses of light set $12\frac{1}{2}$ hours apart mimic a long day and are nearly as effective as a full photoperiod of 13 hours.

If the daylength is interpreted as long by the clock/photoreceptor complex then this leads to Gn-RH release from the neurohypophysis and

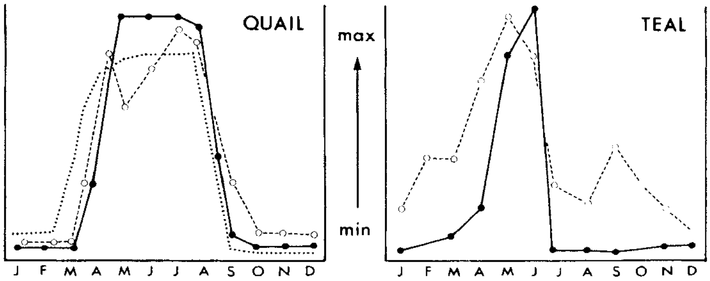


Fig. 3. Annual reproductive cycles (——, testicular size; - - - -, circulating LH and . . . ., FSH) in Japanese Quail *Coturnix coturnix japonica* and Green-winged Teal *Anas crecca* under natural daylengths.

thus LH and FSH secretion from the adenohypophysis, and eventually to the production of sexually mature birds. Each species differs slightly in the timing and duration of its breeding season and this is reflected in the photoneuroendocrine response. Figure 3 shows data for two birds, the Japanese Quail with a long multiple clutch breeding season and the Green-winged Teal *Anas crecca*, a single-clutch species. These graphs emphasize another important feature of bird reproduction: breeding invariably ceases when the days are still long, often even still increasing as in the Teal (and Rook *Corvus frugilegus*). This so-called photo-refractoriness (when the bird is refractory to the influence of long days) is an adaptation to ensure young are not produced too late in the season when food and weather conditions are about to deteriorate. Somehow, the refractory state develops in the brain and suddenly overrides the effects of daylength, cutting off LH and FSH secretion and leading to gonadal collapse. The refractory state is sometimes referred to as the post-nuptial regeneration phase.

Whilst the sex hormones have many actions on the reproductive organs they are also responsible for sexual behaviour. Under their influence, territories are firmly established and courtship begins (see DISPLAY; TERRITORY). The nest is then built and mating begins for by then the sex steroids have acted on the brain to allow copulatory behaviour. During the laying of the clutch the brood patch develops and finally INCUBATION begins. Prolactin and progesterone are involved in this behaviour. Once the young are hatched PARENTAL CARE develops. B.K.F. and A.R.G.

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ENDOGAMY: mating within the group.

ENDOGENOUS: originating from within the body. The converse, 'originating from outside the body', is 'exogenous'.

ENDOPARASITE: a parasite inhabiting the interior of the host's body, as distinct from an ECTOPARASITE. Birds are hosts for a wide variety of endoparasites, but certain genera and families of endoparasites are particularly prevalent, and only these are dealt with here.

With the vast majority of endoparasites there is no direct immediate transmission of infection from bird to bird as occurs, for example, with bacterial and viral infections. A period of development outside the final bird host is usually necessary. Often this is in an invertebrate which is then referred to as an intermediate host, or development occurs directly without the intervention of an intermediate host. Various developmental stages are undergone to produce an infective stage for the final host and, following infection, a further series of developmental stages occurs; these constitute the life cycle of the parasite. Examples of intermediate hosts for bird endoparasites include snails, earthworms and flies.

Evolutionary pressures have led to synchronization of life cycles of parasites with the feeding habits of birds and also with major physiological events in the life cycle of birds. Thus the endoparasites of waterfowl and sea birds use fish and aquatic invertebrates as intermediate hosts, while with insectivorous birds the parasite fauna is largely restricted to those forms that develop in insects. Synchronization of the life cycle with the breeding season ensures transmission of infection to a susceptible chick population, as is exemplified by the increased availability of blood protozoa to expanded populations of blood-sucking flies during the egg laying and nestling season.

Pathogenic effects. When extremely heavy burdens of endoparasites occur, then ill health and death can confidently be attributed to such infection. Nevertheless, it is often difficult to assess the importance of any given parasitic burden as regards the health consequences.

Limited surveys have generally shown that minimal burdens of parasites exist in the natural state, but seemingly heavy burdens sometimes occur without causing any apparent ill health. However, such burdens may become important if the food supply is curtailed or if other diseases occur concomitantly. There are instances when even a very small number of parasites may result in ill health and death, particularly when a vital organ of the body is incapacitated.

Heavy burdens of endoparasites often occur when birds are reared under intensive conditions, without adequate attention to hygiene. Infections may be acquired from domestic poultry, but more usually wild birds introduce infection by faecal contamination into intensive rearing establishments for domestic poultry or game or wildfowl.

The main groups of endoparasites are the unicellular animals (Protozoa), the roundworms (Nematoda), thorny-headed worms (Acanthocephala), tapeworms (Cestoda) and flukes (Trematoda). Only the more important pathogenic or commonly occurring genera or species will be mentioned.

Protozoa. These are single-celled animals, showing a wide variety of forms. Included in this group are the coccidia and the blood protozoa. The most important members of the group in Great Britain are the coccidia. Coccidian parasites of the genus *Eimeria*, for example *E. tenella*, may cause enormous economic loss in domestic poultry but such forms are not transmissible to wild birds, these being parasitized by distinct species. *Eimeria* species usually parasitize the intestine and heavy infections lead to enteritis, which may occasionally be haemorrhagic and fatal. However, immunity to infection is quickly established and usually this prevents the acquisition of overwhelming infections. Geese, Moorhens *Gallinula chloropus*, Kittiwakes *Rissa tridactyla* and cormorants *Phalacrocorax* spp. are among the hosts for such coccidia. A coccidian of the kidney *Eimeria truncata* occurs in geese. In domestic geese it may be highly pathogenic, especially in goslings. Its importance in wild geese is unknown but it is probably pathogenic for goslings.

While the genus *Eimeria* is host specific, the related genus, *Isopora*, common in passerines, is less so: for example *Isopora lacazii* is found in the intestine of about 50 species of birds including House Sparrows *Passer domesticus*, Goldfinches *Carduelis carduelis*, Skylarks *Alauda arvensis*, wagtails *Motacilla* spp. and Chaffinches *Fringilla coelebs*.

All the coccidia are microscopic and live within cells, usually of the intestine. The life-cycle is direct, infection of a bird occurring when it eats the infective stage (oocyst). These oocysts may remain infective on the ground for long periods, and large concentrations of them may accumulate around feeding and watering places. Artificial concentration of birds, e.g. due to hand-feeding in winter, may build up sites of marked contamination.

Lankesterella is related to the coccidia and is a common parasite of House Sparrows and other passerines. Developmental stages are found within cells of the spleen, bone marrow and liver and developmental forms may be seen in the blood. Transmission is probably by the red mite *Dermanyssus gallinae*. Occasionally, the parasite causes congestion and inflammatory foci in the liver and lungs of sparrows.

Previously *Lankesterella* has been confused with *Toxoplasma gondii*, a protozoan which occurs in a wide range of mammals, including man, and the definitive host of which is the cat. Toxoplasmosis, generally, is rare in birds but acute disease of domestic poultry has been recorded in Norway. A survey of *Toxoplasma* in pigeons in Washington D.C. showed 12% to be infected with a strain of organism which was closely related to a human virulent strain. However, there is no evidence that birds infected with *Toxoplasma* constitute an important source of infection for man.

Sarcocystis occurs as cysts, several millimetres long, in the muscles of the heart, legs and breast. It occurs in a range of ducks, grouse etc, though it is not known whether a single or several species of parasite are represented in this distribution. No obvious ill health results from the infection.

Trichomonads are flagellated protozoa. *Trichomonas gallinae* lives in the crops of birds, and in young pigeons it may cause disease and death, infection of the squabs being by contaminated 'pigeon's milk' from the parent (see CROP MILK). Wild and captive birds of prey may occasionally suffer severely from trichomoniasis, apparently from predation on infected pigeons.

Hexamita meleagridis is an intestinal flagellate and is a pathogen of domestic turkeys but may also occur in various wild gallinaceous species, infection in these serving as a source of infection for domestic poultry. *Hexamita columbae* is responsible for intestinal disease in pigeons *Columba livia*, the parasite affecting all parts of the digestive tract. It is distinct from the parasite of turkeys.

Trypanosomes occur in birds, *Trypanosoma fringillinarum* being found in Chaffinches, and *T. avium* in Rooks *Corvus frugilegus* and Jackdaws *C. monedula*. These trypanosomes are not, however, the cause of serious disease, unlike their relatives the trypanosomes of man and animals in Africa. Other blood protozoa include members of the genera *Haemoproteus* and *Leucocytozoon*, both being transmitted by blood-sucking flies. *Haemoproteus* species are found in many species, including thrushes *Turdus*, Blackbirds *T. merula*, Starlings *Sturnus vulgaris*, and birds-of-prey. *H. columbae* of pigeons and doves is transmitted by the louse-fly *Pseudolynchia canariensis*. Clinical signs include anaemia and enlargement of the spleen in young birds. *Leucocytozoon* species are transmitted to ducks by *Simulium* flies. Weakness and dypsnoea occur in heavy infections since cells of the lungs particularly, and the liver and brain, are parasitized. Light infections cause little or no harm.

The protozoan *Histomonas meleagridis* is the cause of the severe and often fatal disease of turkeys known as blackhead. It is transmitted from bird to bird by the caecal nematode *Heterakis gallinarum* (see below). Initially it causes an inflammation of the bowel, but later it affects the liver and produces marked damage and necrosis. Heavy mortality may occur in various species of gallinaceous birds, such as domestic fowl, Quail *Coturnix coturnix*, grouse Tetraonidae, partridges *Perdix* and *Alectoris*, pheasants Phasianidae and especially the Peacock *Pavo cristatus*.

Helminths. These are multicellular forms, generally referred to as 'worms' and include the forms mentioned below, the Nematoda, Acanthocephala, Cestoda and Trematoda. The majority are readily visible to the naked eye, frequently but not exclusively occur in the digestive tract and may require an intermediate host in which development occurs to the infective stage for birds.

Nematoda: Ascaroidea. Ascarids may have a direct or an indirect life cycle. Of those having a direct life cycle, the caecal worms *Heterakis* spp. and the intestinal worms *Ascaridia* spp. are extremely common. The caecal worm of domestic poultry, *H. gallinarum*, may occur also in a wide range of birds, including ducks, pheasants and crows. Infection is acquired by eating infective eggs, which may remain viable in the soil for long periods. Within the caecum of the fowl little direct damage is generally produced, but this parasite is of importance since it transmits the organism of blackhead (see above). Of the other *Heterakis* species, *H. dispar* occurs in ducks, frequently in large numbers, and *H. isolonche* is found in pheasants and causes a nodular disease of the caeca.

The genus *Ascaridia* is widely distributed in birds; *A galli* has a cosmopolitan distribution occurring in domestic poultry and game-birds, while *A. columbae* is a frequent parasite of domestic and wild pigeons. Heavy and sometimes fatal infections with the genus *Ascaridia* may occur in birds that feed in groups. These worms are some of the largest to be found in birds, and infection can be readily detected at post mortem; when in large numbers they may cause impaction of the intestinal tract.

Of the ascarids with an indirect life cycle, the genera *Contracaecum* and *Porrocaecum* are the most common. The larval stages of *Contracaecum* spp. occur in fish, and consequently fish-eating birds (and indeed mammals) are affected by them. *C. spiculigerum* is a very common parasite of the proventriculus and intestine of a variety of sea birds. The genus *Porrocaecum* has a wider host distribution. Some are found in birds of prey, in which case the intermediate stages occur in moles and shrews. *P. crassum* is particularly common in ducks and requires earthworms as its intermediate host, whilst *P. depressum* and *P. ensicaudatum* are widely distributed in many birds, the latter being particularly common in passerines.

Signs of infection include loss of weight, listlessness, loss of plumage and sometimes foamy diarrhoea.

Nematoda: Strongyloidea. The majority of these strongyles have a direct life cycle. The best known are the gizzard-worm *Amidostomum anseris* of geese, the gapeworm of poultry *Syngamus trachea* and the small strongyle of grouse and other birds, *Trichostrongylus tenuis*. *Amidostomum* spp. occur in many different species of ducks, geese and swans. The worms are relatively large and live under the horny coat of the gizzard, causing marked inflammation and severe ulceration that frequently ends in death. Young birds are particularly affected and *A. anseris* may be responsible for heavy mortality on breeding grounds.

The gapeworm occurs in the trachea and bronchi and often causes marked mortality in domestic and game birds, even a few worms leading to respiratory distress. The life cycle may be direct, or invertebrates such as earthworms and centipedes may act as transport hosts, infection being acquired by eating the latter. Earthworms also make the gapeworms of wild birds, particularly those of Rooks and Starlings, more readily transmissible to domestic poultry. It is thought that gapeworms of wild birds—and they occur in many species—are different strains from that found in poultry but the earthworm can modify them so as to produce infection in domestic birds. The gapeworm *Cyathostoma bronchialis* occurs in ducks and geese, and because of their size even one or two of these may occlude the trachea of young birds and cause death.

Trichostrongylus tenuis is a very small worm occurring in the caeca and intestine of ducks, poultry, pheasants, grouse and many other birds. This parasite is of particular importance in the Red Grouse *Lagopus lagopus*, in which it is a well known cause of death. In ducks, too, it may cause severe inflammation of the intestine.

Nematoda: Spiruroidea. All the spirurids require an intermediate host to complete their life cycles, this usually being an arthropod. A wide variety of parasites is included in this group, and they parasitize different sites of the body. One example is the genus *Oxyspirura*, which occurs in the conjunctival cavity of the eye.

One of the most important groups is the Acuariidae, containing several species which parasitize the gizzard or proventriculus of various birds, causing severe damage to the digestive system. *Echinuria uncinata* of ducks and geese may be responsible for heavy mortality in wildfowl kept in captivity; the intermediate host is the water-flea *Daphnia pulex*, which is abundant in stagnant and slow-running waters. Other genera of the Acuariidae include *Cheilospirura*, *Synhimantus* and *Dispharynx*, which occur in a range of galliform and passerine birds; they parasitize the upper digestive tract and have a marked pathogenic capacity.

A remarkable parasite in the Spiruroidea is *Tetrameres fissispina*, found in waterfowl. The female of this species becomes almost spherical and red in colour when mature, and since it lives in the glands of the proventriculus it causes marked dilatation and degeneration of glandular tissue.

Nematoda: Filaroidea. Adult worms live in body cavities and inner organs. They produce larvae, microfilariae, which occur in the blood. These, to complete their life-cycle, are taken up by blood-sucking insects and develop inside them to the infective stage. Infection occurs with the injection of infective larvae into the body of the bird with saliva from the insect.

Nematoda: Trichinelloidea. Capillarids are very thin small worms, difficult to see, but may occur in large numbers in various parts of the digestive tract. One of the commonest is *Capillaria contorta*, which occurs in the crop and oesophagus of domestic and many wild birds. When present in large numbers it causes marked thickening and inflammation of these organs.

Acanthocephala. Thorny-headed worms are small, generally sausage-shaped, and have a large retractable proboscis covered with numerous curved spines. This proboscis is used to anchor the worm to the bowel wall, being thrust into the tissues. The most common is *Polymorphus minutus*, occurring in many kinds of waterfowl, sometimes several hundreds or thousands being found, though in many cases causing no apparent ill health. This species is frequently bright orange in colour and in a heavily infected bird the inside of the bowel may be a continuous orange mass. The intermediate host of *P. minutus* is the freshwater shrimp *Gammarus*. The genus *Corynosoma* utilizes fish as an intermediate host, in addition to an arthropod, and consequently is found in fish-eating birds (and also in seals). In passerine birds the genera *Prosthorhynchus* and *Centrorhynchus* are commonly found.

Cestoda. Tapeworms have an interesting distribution in birds, in that certain groups of birds possess their own particular fauna of them. The family Hymenolepididae is perhaps the largest group occurring in birds, being common in the ducks. Many species occur, and their identification is a matter of great difficulty. The hymenolepid cestodes require intermediate hosts, and these vary from aquatic arthropods to beetles and annelids. Extremely heavy burdens of *Hymenolepis* spp. may occur in birds and are responsible, at times, for severe mortality. One of the commonest species, occurring in a wide variety of ducks and other waterfowl, is *H. anatina*.

The family Dilepididae is also a large group containing tapeworms which occur in a wide range of birds, but especially in the Turdidae and other passerines. Fish-eating birds are commonly infected with tapeworms of this family.

The tapeworm genus *Raillietina* is common in domestic poultry and in game-birds, also occurring in pigeons, sparrows and thrushes. The genus *Anomotaenia* is a large one and occurs in waders, gulls and passerines. The identification of tapeworms requires staining techniques and microscopic examination and is a task for a specialist.

All important species occur in the intestinal tract and the ill effects produced are much the same with all groups being loss of weight, diarrhoea and death in heavy infections.

Trematoda. A wide variety of flukes occurs in birds. Some are extremely small and difficult to see, some may occur in large numbers without causing any obvious ill health, whilst others may be pathogenic in moderate numbers. All undergo development within a snail, and in the majority of cases also require a second intermediate host for the infective stage of the fluke (metacercaria) to be reached, this occurring in a variety of animal life such as fish, snails, insects, crustacea, and annelids. Since many of the intermediate hosts are animals that live in or near water, it is not surprising that waterfowl and sea-birds in general frequently are parasitized by flukes.

The fluke family Echinostomatidae is very common in waterfowl. It is characterized by a collar of spines round the head, and includes some of the largest trematodes of birds and also some of the most highly pathogenic. *E. revolutum* is a common fluke of the intestines of ducks and geese, whilst the genera *Echinoparyphium, Hypoderaeum, Echinochasmus,* and *Himasthla* are common groups in water birds.

Members of the family Microphallidae are frequent in birds feeding on mudflats, saltings, and the seashore. These are very small flukes, and several thousand may be found in the intestine of a single bird. The family Plagiorchidae is chiefly found in sparrows, Starlings and Rooks, and one genus, *Prosthogonimus*, is found in the oviducts of such birds. There are other specific sites for flukes than the intestine; for example, in the gall bladder of passerines *Lyperosomum longicauda* is often found; the genus *Renicola* occurs in the kidneys of gulls; the genus *Clinostomum* occurs in the nasal passages of gulls and herons; and even the skin is affected by the genus *Collyriclum*, which causes cysts in such birds as warblers (Sylviinae), wagtails (*Motacilla* spp.) and sparrows.

One interesting group is the Schistosomatidae, the worms occurring in the vein draining the intestine. Birds such as ducks and swans, grebes, and gulls are parasitized by schistosomes. Infection of birds is produced by the infective stages (cercariae) penetrating the skin. Human bathers may be attacked by these cercariae, when a dermatitis called 'swimmer's itch' is produced. E.J.L.S.

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ENDOTHERMY: (= warmbloodedness, homoiothermy, homeothermy). The ability of birds and mammals to maintain a high, and usually near-constant, body temperature by the internal production of heat (see ENERGETICS; HEAT REGULATION; METABOLISM).

ENDYSIS: renewal of plumage after moult (ecdysis)—see MOULT.

ENERGETICS: a term broadly used to describe the various aspects of intake and utilization of energy. In practice the word is applied to the energy requirements of some phase of avian life history (e.g. egg-laying, moult, migration) or to basal or total energy utilization of a species under specific conditions, but the units measured are actually power units. Historically, avian energy utilization has been expressed in kilocalories per day either on a whole bird basis, or per unit body weight, or in relation to surface area. The International System of Units (SI system) suggests that the appropriate units to be used are joules ($j = 0.239$ cal) and watts ($859.8\,\text{cal}\cdot\text{hr}^{-1} = 1\,\text{j}\cdot\text{sec}^{-1}$ or $0.860\,\text{Kcal}\cdot\text{hr}^{-1} = 1\,\text{kJ}\cdot\text{sec}^{-1}$).

A variety of energy measurements have been used which focus on different levels of energy utilization. *Basal metabolism* is the minimum energy requirement of unfed, inactive birds at nonstimulatory temperatures. *Standard metabolism* is similar to basal metabolism but includes costs of thermoregulation. *Existence energy* is the energy requirement of caged birds in which activity is minimized but costs of thermoregulation and food utilization are included. *Metabolized energy* is similar to existence energy but includes possible energy requirements of moult, reproduction, growth, fat deposition, activity and other productive phenomena.

Basal metabolism. Basal metabolism, better termed standard thermoneutral metabolism, is the rate of energy utilization within the zone of thermal neutrality (i.e. at temperatures which do not stimulate metabolic rates) under certain standard conditions. Functionally, such values are determined by means of indirect calorimetry in which the oxygen consumption or carbon dioxide production of unfed (post-absorptive) birds is measured in unlighted chambers. Rate of oxygen consumption or CO_2 production can be converted to energy or power units by multiplying the volume of gas by the appropriate caloric equivalent (Table 1). The caloric equivalent to be used is judged from the *respiratory quotient* (RQ) which is the ratio of CO_2 produced to oxygen consumed and hence is an indication of the substrate (lipid, protein, carbohydrate or a mixture) that is being oxidized.

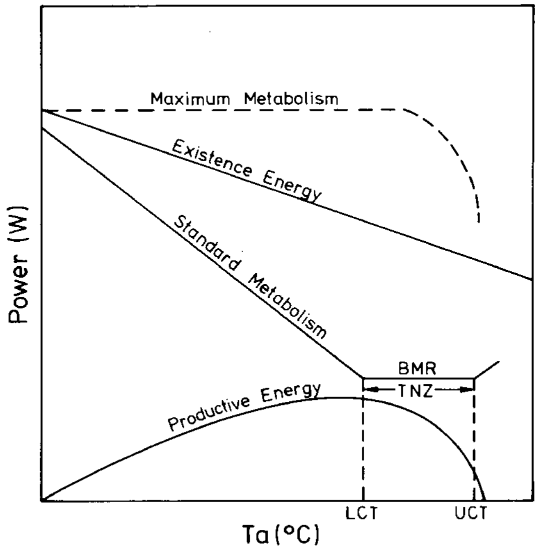

Fig. 1.

Use of oxygen consumption rather than carbon dioxide production as a measure of metabolism is usually preferred. A relatively large residual amount of carbon dioxide is usually present in the bodies of many organisms and this pool may easily increase or decrease, giving a false measurement of CO_2 production. Another problem is that the caloric equivalent of a litre of CO_2 varies widely with the type of substrate being oxidized; the equivalents of oxygen utilization vary less severely. It appears that birds undergo little anaerobic catabolism of energy substrate in comparison with other vertebrates and therefore do not usually accumulate significant 'oxygen debts'.

Allometry of metabolism. The relationship between body weight and standard thermoneutral metabolism is a curvilinear relationship such that the 'best fit' equations are exponential functions of the form:

$$M = aW^b \quad \text{or} \quad \text{Log } M = \text{Log } a + b \text{ Log } W$$

where M is $\text{Kcal}\cdot\text{day}^{-1}$ and W is in kg. Such equations are of considerable biological interest as the exponent or slope (b) of the equation reflects relative response of metabolism to increased body weight and the coefficient (a) indicates the relative magnitude of metabolism. These equations may therefore be used to compare metabolic rates of different phylogenetic groups.

Two principal equations have been presented that describe the relationship between body weight and basal metabolism (Lasiewski and Dawson, 1967). These are:

$$M = 129\,W^{0.724} \text{ (passerines)}$$
$$M = 78\,W^{0.723} \text{ (non-passerines)}$$

According to the Lasiewski-Dawson equations, the metabolic rate of a passerine bird can be expected to be 65% higher than that of a non-passerine bird of the same weight. It is obvious that individual species deviate from these 'best fit' lines, but the metabolic rate of several species or taxonomic groups is noteworthy. For example, metabolic rates of Accipitriformes, Falconiformes, Galliformes, and Strigiformes are lower than predicted by the non-passerine equation, while Apodiformes, Piciformes, Ciconiiformes, Anseriformes and Columbiformes are higher. In general 'primitive' birds with low body temperatures relative to other species have exceptionally low metabolic rates. This is particularly true of ratite species such as the Ostrich *Struthio camelus*, Rhea *Rhea americana*, Emu *Dromaius novaehollandiae*, and the kiwis (Apterygidae).

The allometry of metabolism may have more extensive significance than phylogenetic comparison (see Energy limits on body size, below). Since birds depend upon their territories for food and as energy needs vary allometrically with weight, it is logical that territory size will be an exponential function of size of the bird. Although specific exceptions must be considered, it appears that such a relationship generally exists. In addition, since some energy is lost in the exchange from one trophic level to the next, it is to be expected that carnivores (obtaining their food less directly from primary producers than herbivores) would have larger territories than primary consumers or herbivores. Exponential curves predicting territory size from body weight have exponents greater than 1.0, e.g. all birds, 1.09; carnivorous birds, 1.31 (Schoener 1968), and differ significantly between birds occupying different trophic levels.

Basal metabolism may be influenced by several factors that are not controlled or eliminated by the methodology. This involves measuring rates of oxygen consumption of individuals which have not recently been fed, are inactive and being held at temperatures in the thermal neutral zone (see Fig. 1). Cyclic differences in metabolic rates over the diurnal cycle, seasonal and sexual variations and ecotypic/climatic adaptation may all be influential in modifying the results obtained in particular tests. Before discussing the effects of such phenomena upon metabolism, metabolic rates obtained outside the zone of thermal neutrality must be examined.

Standard metabolism. The rate of energy utilization measured under the same conditions as basal metabolism but at temperatures that stimulate the production of heat is called standard metabolism (see Fig. 1). As ambient temperature decreases within the zone of thermal neutrality, increased heat loss is prevented by greater insulation provided by fluffing of feathers, reduced peripheral circulation and postural modifications. Below the ambient temperature (T_a) at which such physical insulation is at a maximum (the lower critical temperature), standard metabolism increases with decreased temperature, since increased heat loss must be replaced by metabolic heat production; alternatively body temperature (T_b) must drop in order to maintain a positive energy balance (see torpor below). The increase in metabolism is in proportion to $C(T_a - T_b)$ where C is 'conductance' (= the reciprocal of insulation) or the heat transfer coefficient. Minimum rates of heat transfer are largely a function of physical insulation provided by thickness of feathers. Although thickness of the plumage is difficult to measure, weight of feathers (F, in g) increases with body weight (W, in g) according to the equation:

$$F = 0.68\,W^{0.959}$$

This is nearly a direct relation of feather weight to body weight as the slope of the equation is not statistically different from 1.0. However, since surface area increases less rapidly than body weight, feather weight per unit surface area increases significantly with bird weight. As a result, the heat transfer coefficient decreases with body weight in an exponential fashion. From metabolic data this relationship has been determined to be:

$$C = 4.08\,W^{-0.51}$$

where C is in $\mathrm{cal \cdot g^{-1} \cdot hr^{-1} \cdot {}^{\circ}C^{-1}}$ and W is weight in g.

The heat needed to maintain constant body temperature is generated mostly from muscular activity. Shivering is the major source, but locomotor activity and specific dynamic action (see below) also contribute to a varying degree. Non-shivering thermogenesis, well known in mammals, apparently does not occur in birds.

The upper critical temperature marks the upper end of the thermal neutral zone. Above this temperature, the bird is no longer able completely to resist increases in ambient temperature by evaporation of moisture from respiratory surfaces. Standard metabolism increases as body temperature becomes elevated and heat death usually ensues quickly. At high ambient temperatures evaporative water loss increases sharply in a curvilinear fashion such that heat dissipation increases rapidly near upper critical temperatures. The heat of vaporization (H_v) is relatively large and therefore evaporation carries away substantial quantities of heat. H_v increases with the temperature at which evaporation takes place; the commonly used physiological constant is $580\,\mathrm{cal \cdot g^{-1}}$ water at 35°C (at 40°C, a temperature that more closely approximates the body temperatures of many birds, $H_v = 573\ \mathrm{cal \cdot g^{-1}}$). Water loss decreases to low levels at temperatures below thermal neutrality. This is energetically advantageous in that evaporative heat loss in cool environments would require energy and be of no benefit.

Birds that have fed shortly before metabolic tests have higher rates of energy utilization. For this reason, measurements of absorptive individuals under conditions of standard metabolism are termed resting metabolism. The calorigenic effect of food, usually called specific dynamic action, does not appear to vary with body size or species. Specific dynamic action is related to chemical composition and amount of food eaten. For example, pure protein elevates metabolism 20–45% in some species, while the effects of carbohydrate or fat may be significantly less. The calorigenic effect is associated mostly with the viscera and tests indicate that the heat arises from the catabolism of food, rather than increased activity of the digestive organs themselves. The apparent heat produced in specific dynamic action may vary with ambient temperature and appears partially to substitute for the heat produced in thermoregulation in the cold.

Energy demands may be modified by a variety of behavioural adaptations. Species which exhibit huddling or clumping together in tight groups may save significant amounts of energy during periods of inactivity at low ambient temperatures. Individual surface area and heat loss are reduced by the contact with conspecifics. Wrens (Troglodytidae), creepers (Certhiidae) and several other small passerines are particularly noted for huddling together at extremely low ambient temperatures. Use of cavities, winter nests, burrows and other protective sites may likewise conserve significant amounts of energy. Basking in sunlight may increase body surface temperatures and conserve energy by reducing heat loss from deeper in the body. A number of large, dark birds are known for their basking behaviour in which they may spread their wings and direct their ventral surfaces into the direction of the sun. American vultures (Cathartidae), cormorants and several diurnal birds of prey are among those noted for such behaviour. There is evidence that some of these species may deliberately overheat while basking, perhaps in an attempt to rid themselves of ectoparasites. Many other species also bask, often in a less obvious fashion.

Colour of the bird may be important in the amount of heat collected during exposure to solar radiation; in birds that vary in colour or have been artificially coloured, dark individuals may demonstrate energy savings of up to 20% over the energy requirements of light forms. GLOGER'S RULE states that, within endothermic species, black pigments increase in races from warm, humid areas, reds and yellow-browns tend to prevail in arid climates and pigments become generally reduced in cold regions. While much of this colour modification is probably a result of selection for individuals that more closely match background substrate and hence avoid being taken by predators, lighter colours may reflect greater amounts of solar radiation and reduce the tendency to overheat in arid environments. Darker colours conversely may more efficiently absorb solar radiation which assists in maintaining body temperature and reduces the energetic costs of thermoregulation.

Existence energy. The use of the bomb calorimeter in measuring the caloric intake and its utilization by birds was pioneered by S.C. Kendeigh in the late 1940s and gave rise to a means of making long-term evaluations of the energy balance of caged birds. The technique involves measurement of the caloric content of food and excreta of birds maintained under controlled or monitored temperatures, humidities and photoperiods. The term *metabolized energy* is applied to the energy utilized by birds not in a steady-state energy balance (i.e. those birds not maintaining constant weight or which are showing extensive activity other than simple maintenance processes). Functionally, metabolized energy (ME) is calculated as gross energy intake (GEI) minus excretory energy (EXE). GEI is the energy content of ingested food while EXE is the caloric content of the excreta (faeces + urine, since the two are difficult to separate in birds). The ratio (100 ME/GEI) has been variously termed coefficient of utilization, assimilation efficiency or energetic efficiency. The last is preferable, as 'cofficient of utilization' is misleading and assimilation is not being measured. The caloric contributions of faeces and urine are not experimentally separated in most tests. The faeces have not been assimilated but the calories in urine represent wastes that have undergone assimilation and catabolism. Energetic efficiency varies among species and with ambient temperature, photoperiod and composition of food. The effect of temperature and photoperiod may be a function of feeding rates and amount of activity. Energetic efficiency is usually lower at extreme cold temperatures and short photoperiods. Effects associated with composition of food are related to digestibility and the amount of specific dynamic action produced by the food. In general, carnivores have higher energetic efficiencies than seed-eaters or herbivores.

Existence energy is the metabolized energy utilized by individuals maintaining constant weight and which are expending negligible amounts of energy in activity or productive processes such as moult or egg-laying. The form of the relationship between existence energy and ambient temperature is similar to that of standard metabolism (Fig. 1) except that a thermal neutral zone appears to be lacking. Existence energy is usually greater on long photoperiods (i.e. light phase longer than dark phase). Equations that predict existence energy (EE) in $\text{Kcal} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$ from bird weight in g are significantly different for passerine and non-passerine birds (Kendeigh, 1970).

$$\begin{aligned} \text{EE} &= 1.572\,\text{W}^{0.621} \text{ (passerines, 30°C)} \\ \text{EE} &= 0.540\,\text{W}^{0.755} \text{ (non-passerines, 30°C)} \\ \text{EE} &= 4.337\,\text{W}^{0.530} \text{ (all species, 0°C)} \end{aligned}$$

In the zone of thermal neutrality, existence energy exceeds standard metabolism by 31% in passerines and 26% in non-passerines. The difference between existence energy and standard metabolism represents specific dynamic action and costs of activity.

Productive energy. The difference between maximum sustained rates of metabolism and existence energy is defined as productive energy (Fig. 1). It is generally assumed that maximum rates of metabolism are limited only by difficulties in heat dissipation as ambient temperature approaches body temperature, or by exhaustion of energy reserves or decreases in body temperature due to negative heat balance at low ambient temperatures. There are species-specific variations in the magnitude of metabolic maxima. Metabolic scope, an index of the capacity of organisms to mobilize energy, is expressed as a function of maximum metabolic rates as compared to minimum metabolic rates under standard conditions. Birds have metabolic scopes that range from approximately 10 to 20 times basal metabolic rates. As existence metabolism increases with decreased ambient temperature, lower lethal temperatures should be reached when existence metabolism is near or at the maximum sustained rate (i.e. productive energy = 0). If this model holds, then egg-laying or other productive activities would cease at some predictable temperature above the lower lethal limit and also increased physical activity would reduce the ability to survive low temperatures. These predictions have been confirmed by several independent investigations.

Table of combustible energy, oxygen consumption and carbon dioxide production for various foodstuffs.

	Kcal/g	$\text{cal} \cdot \text{ml O}_2$	$\text{cal} \cdot \text{ml}^{-1}\text{CO}_2$	RQ
Carbohydrate	3.8–4.3	5.1	5.0	1.00
Protein	4.3–5.7	4.8	5.8	0.83
Fat	9.0–9.5	4.7	6.7	0.71

Energy stores. Avian energy reserves consist largely of bodies of fat stored in masses beneath the skin and around the viscera. These so-called depot fats are composed of triglycerides. Upon hydrolysis, triglycerides yield fatty acids which may be oxidized (β-oxidation) with a relatively high yield of energy per g of fat (Table 1). Fatty acids provide the substrate that supports all prolonged avian activity. Carbohydrates such as glucose and glycogen are utilized in activities of short duration; the first few minutes of flight are fuelled by carbohydrates but, as flying continues, fatty acids become the major energy source. Fat is an advantageous energy store because of the high energy yield per unit weight. Not only is the caloric content greater, but deposition of fat depots requires little, if any, concomitant storage of water. Conversely, the storage of 1 g of carbohydrate is accompanied by additional storage of approximately 3 g H_2O.

Diurnal rhythms. The Lasiewski-Dawson equations presented above compare basal metabolism in passerine and non-passerine species and do not recognize significant differences that may occur between metabolic rates during the day and night (i.e. between activity phases and resting phases of the daily body temperature cycle). Separation of the relationship between weight and basal metabolism into activity (light or daytime) and rest (dark or nighttime) phases has produced the following equations (Aschoff and Pohl, 1970):

$$\begin{aligned} \text{Activity phase: } M &= 140.9\,\text{W}^{0.704} \text{ (passerines)} \\ M &= 91.0\,\text{W}^{0.729} \text{ (non-passerines)} \\ \text{Rest phase: } M &= 114.8\,\text{W}^{0.726} \text{ (passerines)} \\ M &= 73.5\,\text{W}^{0.734} \text{ (non-passerines)} \end{aligned}$$

Day-night variations in existence energy over the diurnal cycle need not be considered, as existence energy measurements are carried out over several days.

Daily cycles of body temperature and metabolism in birds have been known for many years. Highest body temperature and metabolic rate occur during the bird's activity period and are lowest during the rest phase of the diurnal cycle. These levels are reached independently of actual activity; measurements of basal metabolism are usually carried out with birds in darkened chambers and activity is usually negligible. Daily differences between high and low body temperature and metabolic rate in most species amount to only a few °C. However, a variety of species exhibit extensive decreases in body temperature and standard metabolism under conditions of low ambient temperature, darkness and/or shortage of food. Body temperatures below normal are termed hypothermia. Prolonged, severe hypothermia accompanied by relatively large decreases in heart, respiration and metabolic rates is referred to as torpor. The dividing lines between normal diurnal decreases in body temperature, moderate hypothermia and torpor are sometimes difficult to determine. However, the decrease in body temperature is reflected in an energy saving that is a function of the difference between active body temperatures and those of hypothermia. Reheating the body after a period of pronounced hypothermia or torpor may account for a substantial portion of the total energy demand of the period.

Climatic adaptation. Several widely distributed species are known to demonstrate intraspecific geographic variation in energy utilization probably as an adaptive response to local climate. In general, it appears that northern races and those from high altitudes are better insulated and less sensitive to cold than southern and low altitude races. For example, during the winter, the House Sparrow *Passer domesticus* in North America tends to be more heavily insulated in the northernmost part of its range and at high altitudes. The greater insulation found in northern birds results in smaller increases in metabolic rates with decreased ambient temperature and also results in lower critical temperatures that are shifted downward. Both modifications of metabolic response may contribute to a significant saving when northern individuals are compared with those from further south. Conversely, climatic adaptation may also be reflected in the ability of birds to produce heat; basal and standard metabolic rates may be slightly elevated in northern or arctic species but reduced in southern, tropical or desert forms.

Within many polytypic species of birds there are clines of increasing size northward (BERGMANN'S RULE) and/or decreasing appendage length (ALLEN'S RULE) which are functions of latitude or altitude or both. These ecogeographic rules may have thermoregulatory or energetic implications although considerable controversy has risen concerning the interpretation of the data. Such trends often are significantly correlated with isophane (an index of regional temperature regime calculated from latitude, longitude and altitude) or other measures of regional temperature. Increased size usually results in decreased sensitivity to low temperature; larger birds tend to be better insulated than small birds even when both have equivalent plumage thickness. However, larger birds also have greater overall energy requirements and it is difficult to demonstrate how natural selection might favour increased size in environments that demand more energy. Increased size probably produces other selective advantages such as increased foraging range, greater diversity of food items (as a result of increased bill size) or greater amounts of storage energy which permits survival of short periods of extreme energy demand.

The energetic implications of Allen's Rule lie in the use of extremities in the dissipation of heat. The extremities most important in avian heat loss are the legs and feet. Many species are capable of shunting blood flow to the legs under conditions of heat stress or may reduce blood flow to extremities in the cold. Temperate zone or arctic species may have tarsus and foot temperatures that are quite low in the cold; these may occasionally be as low as 1°C or less in the toes or webbing between them. Several species either extend the legs (sometimes in flight) or fully expose them when under heat stress. Herons wade in the water while panting and fanning themselves with their wings and the Wood Stork *Mycteria americana*, Turkey Vulture *Cathartes aura* and some Sulidae even squirt excrement on their legs and feet to increase the cooling rate. Obviously, increased length of extremities aids in heat loss. At the other extreme, at low ambient temperatures many species sit on their legs or hold them, one at a time, up within the body plumage to prevent heat loss. Several northern species have feathered tarsi which presumably reduce heat loss. In accordance with Allen's Rule, decreased leg length would serve the same purpose to a more limited extent.

Climatic adaptation may also be detected in comparisons of higher

Chestnut-banded Sandplover *Charadrius pallidus* illustrating heat loss by evaporative cooling while panting and by radiation from legs. (*Photo: J.F. Reynolds*).

taxonomic groups (e.g. in interspecific comparisons). Such studies have seldom indicated adaptive modification of basal metabolism when corrected for differences in body weight, except in interphyletic comparisons, but insulation and cold tolerance are often greater in northern members of related species.

Energy limits on body size. The evolution of passerine from non-passerine species has been accompanied by evolution of a higher rate of metabolism. As a result, the range between maximum and minimum size limits has been reduced (Kendeigh 1972). Difficulties in maintaining energy balance probably determine the minimum size limit in birds (about 5 g in passerines and 3 g in non-passerines such as hummingbirds). Minimum size becomes costly for small birds as the exponential relationship between body weight and metabolic rate per g increases sharply at very small sizes while the muscle mass necessary to produce heat becomes relatively small. Although they are also subject to similar limitations, hummingbirds have lower rates of metabolism and conserve energy by heterothermy (temperature regulation by recourse to external sources of heat). This apparently allows them to reach smaller sizes than passerines. Although the data are not unequivocal, it has been suggested that passerine species may have a limited potential for mobilizing energy; costs of existence energy and standard metabolism may be similar at low weights, suggesting that productive energy becomes severely limited. Maximum size in passerines may be limited by their inability to dissipate heat at high ambient temperatures. Non-passerines have lower metabolic rates and maximum size is not as severely restricted.

Seasonal variation in energetics. A variety of adaptive patterns of seasonal adjustment of metabolism are known. Acclimation refers to compensatory adjustments in response to maintained deviations of single environmental variables in the laboratory. Commonly, metabolic rates of birds that have been exposed to low temperatures (cold-acclimatized) in the laboratory are compared to rates obtained from birds maintained at warmer temperatures. Acclimatization is used to describe similar natural adjustments in response to complex deviations such as are found in seasonal changes in environment. Winter-acclimatized birds are often compared with summer-acclimatized individuals. As a result of cold exposure under natural conditions there is an increase in the ability of temperate zone and arctic species to sustain high levels of energy expenditure. This may be accompanied either by greater feather weight and/or subcutaneous fat or by tissue insulation, associated with reduced peripheral blood flow. Lower critical temperatures are theoretically shifted downward and slopes of metabolic curves below the lower critical temperature are more shallow in winter-acclimatized birds. Metabolic rates of species showing such adaptations usually take the configuration illustrated in Fig. 2A. In laboratory studies, there is metabolic adjustment in which rates of heat production after cold exposure are higher and insulation is not adjusted. Cold exposure for short periods of time appears to stimulate the capacity to produce heat and even the basal metabolism of cold-acclimatized individuals is usually enhanced (Fig. 2B). In fact, some students have maintained that enhanced survival in the cold is dependent upon development of a greater capacity to produce heat. However, studies of the plumage of wild birds under natural conditions indicate that natural winter acclimatization rarely if ever occurs without at least moderate increases in both insulation and some aspect of heat production.

Sexual variation in metabolism. In species that are dimorphic in body size there is usually a significant difference in basal and standard metabolism as a consequence of the allometry of metabolism associated with body weight. In monomorphic species the sexes are often metabolically indistinguishable outside the breeding season. Winter ranges of the sexes of dimorphic species in the temperate zone may only partially overlap for energetic reasons. In several North American finches, the males tend to winter further north and are apparently more cold-tolerant than the smaller females, probably because of their greater energy reserves. The separation of range would likewise decrease competition for food in which the larger males should dominate. If the birds tested in metabolic comparisons have previously experienced stimulatory photoperiods, then females may have higher basal and standard metabolic rates as a result of the costs of egg production.

Energy budgets and costs of free activity. Ornithologists have long desired to measure the costs of free existence in birds, but the technical difficulties involved have been hard to overcome. Three basic techniques currently exist that promise to solve this problem. These are time-energy budgets, measurement of metabolism by means of radioactive tracers (particularly doubly-labelled water), and telemetry.

Time-energy budgets are models of daily energy expenditure constructed from schedules of time spent at various activities. Each activity is converted to energy terms by assigning estimates of power costs. Few comprehensive budgets (i.e. constructed throughout the annual cycle) are available and seldom has the accuracy of the budgets been testable. A major difficulty is the assessment of many environmental factors, notably microclimatological ones; these should be included in the model and their effects evaluated upon each recognized activity. The instrumentation required and the complexity of the calculations needed become prohibitive for most researchers.

Doubly-labelled water, more precisely named deuterium oxide or D_2O^{18}, also provides a method for measuring total daily metabolism or costs of specific activity in free-living birds. As the oxygen of respiratory CO_2 is in isotopic equilibrium with the oxygen of body water, injection of D_2O^{18} allows us to monitor turnover rates of both hydrogen and oxygen. Since oxygen-18 is lost in CO_2 and H_2O, while deuterium is lost mainly through H_2O, CO_2 production can be calculated by measuring the difference between the turnover rates of deuterium and oxygen-18. Rate of oxygen consumption can also be computed if Respiratory Quotients (RQs) are known. Metabolic rates are then computed as described above

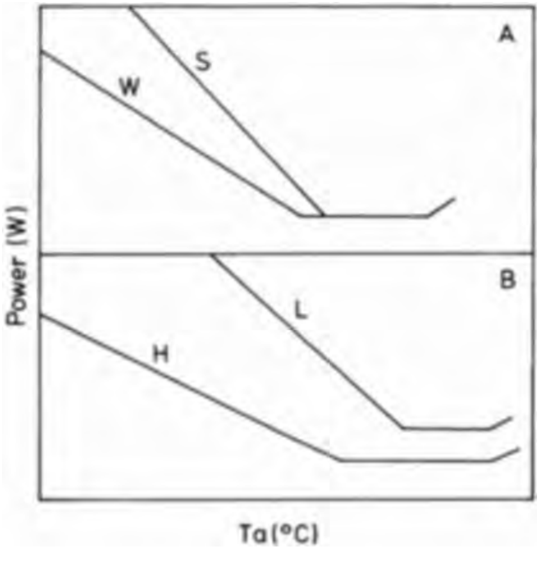

Fig. 2.

for other forms of indirect calorimetry; volume of CO_2 or oxygen must be multiplied by appropriate caloric equivalents indicated by the RQ (see above). In practice, RQs for free-living birds have not been measured and 'best estimates' (e.g. usually RQ = 0.8) have been used. Costs of activity or free existence measured by the D_2O^{18} technique are usually quantified as a function of basal metabolic rate. Estimates of metabolism under laboratory conditions by conventional calorimetry and the D_2O^{18} method are usually in close agreement and estimates of energy expenditure of free-living Purple Martins *Progne subis* from D_2O^{18} studies and a time-energy budget are quite similar. Other radioactive substances, such as phosphorus, iron, or more complex molecules, have not been used to any great extent for the measurement of avian metabolism. Because such substances may be potentially harmful, the difficulties in handling them and the dangers in releasing birds containing them have prohibited their use.

Various telemetry devices which transmit data on body temperature, heart rate or respiratory rates have been constructed and attached to or implanted within birds. Correlation of metabolic rates measured under controlled conditions with such variables could provide a means for estimating energy utilization by free-living birds. In one such experiment, the 'cost of free existence' of pinioned, free-living Blue-winged Teal *Anas discors* was an inverse function of ambient temperature and amounted to 0–18% of existence metabolism at ambient temperatures of 25° to −15°C.

Energetics of flight and migration. The energy demands of flight are a function of bird size and flight speed. Energy expended in flight increases with body weight, but larger birds have lower relative transportation costs (i.e. power needed to transport a unit weight over a given distance) than small birds. Both aerodynamic theory and empirical data indicate that power demands for flight at intermediate velocities are less than costs of slow flight (e.g. hovering) or more rapid flight (Fig. 3). Pennycuick (1969), in highly elegant quantitative analyses, has demonstrated the physical principles involved. In general, the power costs involve various aspects of drag, including the power needed to support the bird's weight in the air (induced power), to overcome friction and drag (parasite power) and the power requirements for overcoming the drag of flapping wings (profile power). Induced power costs decline with flight velocity, while parasite power increases and profile power remains proportional to the sums of induced and profile power. At intermediate speeds the power required is at a minimum since the sums of the power components are minimized.

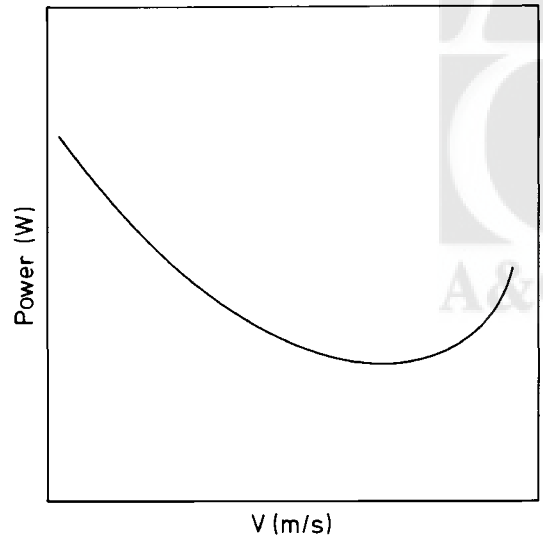

Fig. 3.

A variety of techniques have been used to measure the energetics of flight. Early successful attempts utilized indirect respirometry to measure metabolism of hummingbirds hovering in sealed containers. Tucker (1971) devised an ingenious technique in which birds are trained to fly in a wind tunnel while attached to respirometry equipment. Costs of flying at various velocities can be measured by changing the speed of the air passing through the tunnel, and Tucker has empirically confirmed many of the aerodynamic predictions of Pennycuick. Finally, the D_2O^{18} technique has been used to measure the costs of flight over known distances.

From studies of the cost of flight, a wide variety of observations and predictions about the costs of migration has been generated. For example, with increased body mass, minimum transportation costs occur at higher velocities. Larger birds should therefore migrate more rapidly than small birds. Additionally, the velocity of migration of individual migrants should slow near the end of migration as migratory reserves are depleted and weight drops. Larger birds with relatively similar reserves of premigratory fat should be able to make longer flights than small migrants. The major costs of migration are those of flight, but the temporal pattern and magnitude of deposition of depot fats are important features of energy utilization. Species making long, non-stop flights deposit large amounts of energy, in some cases amounting to several times the caloric content of their bodies, in a few days. The costs of fat deposition have not been extensively investigated, but undoubtedly exceed the caloric content of the fat itself (9.0–9.5 Kcal/g).

Energetics of moult. Energy demands during the moulting process are complex, as increased food demands are brought about by several factors. First, loss of feathers decreases insulation and metabolic rates must be elevated to replace heat loss. Secondly, the energetic requirements of synthesizing new plumage are superimposed upon the increased heat production. Finally, sufficient food must be processed to supply nutrients such as amino acids for the production of feathers. Although only a few studies are available, it appears that total costs of moult (E) vary with avian weight (W, in g) as:

$$E = 8.38\,W^{0.96}$$

or the energy costs of moult are very nearly a linear function of body size.

Reproductive energy. The energetics of reproduction may be divided into several components, including costs of reproductive activities such as territorial behaviour and nest-building, energy invested in production of sex cells and the costs of incubation and feeding of young (King, 1973; Ricklefs, 1974). The ability of the species to generate sufficient productive energy for these activities is a crucial central theme for avian biology. For example, below certain ambient temperatures, accumulation of sufficient productive energy may not occur; egg-laying is limited or ceases entirely. In some cases the geographic distribution of individual species may be limited by their ability to accumulate sufficient productive energy for reproduction.

Costs of egg formation. The energy content of eggs, expressed either as a function of adult body weight or basal metabolic rate, varies greatly among species. Passerines generally invest relatively small amounts of energy (45% of one day's basal metabolism); eggs of ducks (180%), shorebirds (226%) and gulls and terns (320%) contain relatively large amounts of energy. A similar ratio has not previously been calculated for the Brown Kiwi *Apteryx australis*, which lays eggs that weigh between 400 and 435 g. Since the adult weights only about 2,200 g this represents a considerable energy expenditure (rough calculations indicate the energy content = 1,162–1,337% of one day's basal metabolism).

In birds laying more than one egg, the caloric investment per ovum is spread over several days as yolk deposition may simultaneously take place in several ova. Energy requirements probably reach a maximum near the energy content of one egg at approximately the day that egg-laying begins. Production of eggs is inhibited by low ambient temperatures, probably as a result of increased costs of thermoregulation and the resulting decrease in productive energy.

Energy costs of incubation. The heat of incubation comes from the environment, the parents (except the megapodes) and the embryo itself. No complete energy budget exists for both eggs and parents during natural incubation, but it appears that the costs of incubation to the parents may be fairly large. In birds of small body weight, relative costs are probably highest and costs should increase with clutch-size and incubation temperature. Incubation costs also increase with decreased ambient temperature as heat losses from the eggs and nest increase, and must be replaced from increased heat production. Costs of incubation have been calculated or measured as amounting to 11–22% of adult resting metabolism in Zebra Finches *Poephila guttata*, 10–22% in the House Wren *Troglodytes aedon*, and 13–32% for Herring Gulls *Larus argentatus*. In some cases, the contribution of the eggs to their own incubation may be significant. Metabolism of avian embryos increases throughout incubation, but in a pattern that differs between altricial and precocial species. Rate of oxygen consumption of eggs of altricial birds increases exponentially throughout incubation. The metabolism of precocial birds increases through about 75% of incubation and then remains constant until hatching when metabolism again becomes elevated. During the latter stages of incubation, the embryos of the American Kestrel *Falco sparverius* may contribute 19–25% of the total heat required for incubation. In some shorebirds the contribution amounts to 35–40% or approximately 5% of the total energy required during the entire incubation period.

Nest structure and position are important factors in the energy costs of incubation and are usually related to degree of development of young at hatching. Nests of precocial species are often simply constructed and poorly insulated. Nests of altricial birds are more complex and probably provide better heat retention. Within both nest styles, species which have larger clutches usually build nests with greater insulative capacities.

There are very few data for assessment of the energetics of parents feeding young. Relatively crude calculations indicate that in some species the costs may amount to 50% or more of the total productive energy.

Energetics of growth. Increases in body weight from hatching to adulthood are energetically complex. As growth and maturity progress, the composition of young birds changes in a consistent fashion. Altricial species have low caloric contents per g body weight (caloric density) shortly after hatching and caloric density increases with growth mainly because of decreased water content of mature tissues and deposition of energy-rich materials such as lipid. The young of precocial species may have higher caloric densities at hatching, a generally slower growth rate, and smaller increases in caloric density as they develop towards maturity (Fig. 4). See photo HEAT REGULATION. C.R.B.

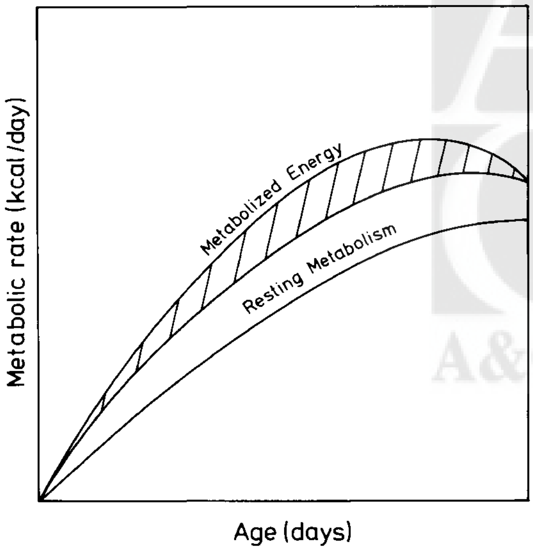

Fig. 4.

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ENICURINAE: see THRUSH.

ENZYMES, DIGESTIVE: see ALIMENTARY SYSTEM.

EPAXIAL: see MUSCULATURE.

EPHTHIANURIDAE: family of the PASSERIFORMES, suborder Oscines; CHAT, AUSTRALIAN.

EPICARDIUM: see HEART.

EPIDEICTIC: term applied by Wynne-Edwards (1962) to communal displays and manoeuvres, particularly those that occur at special times such as dawn or dusk, the supposed function of which is to indicate to its members the numbers of a local population and therefore provide the feed-back enabling the level of the population to be adjusted.

Wynne-Edwards, V.C. 1962. Animal Dispersion in Relation to Social Behaviour. Edinburgh.

EPIDERMIS: the outer layer of the SKIN.

EPIDIDYMIS: in male birds, a compact body lying on the median side of each testis, consisting of convoluted tubules, in which the mature spermatozoa are accommodated before passing down the vas deferens to the cloaca.

EPIGAMIC: term applied to characters or actions tending to promote reproductive behaviour (see DISPLAY).

EPIGENETICS: the analytical study of the developmental process (ontogeny), a term implying the interaction of genetic factors—see DEVELOPMENT, EMBRYONIC; GROWTH.

EPISEMATIC: term applied to appearance or behaviour aiding recognition, applied particularly to coloration. 'Antepisematic' implies a threat; 'proepisematic' refers to social recognition; 'pseudepisematic' involves deception, e.g. the eggs of parasitic cuckoos (Cuculinae) may in a sense be protectively coloured in their mimicry, but the role is fundamentally aggressive. Compare APOSEMATIC; and in general see COLORATION, ADAPTIVE; RECOGNITION.

EPITHELIUM: see SKIN; TISSUE.

EPIZOOTIC: see DISEASE.

EQUILIBRATION: see HEARING AND BALANCE.

EREMOMELA: generic name used as substantive common name of *Eremomela* spp. (for subfamily see WARBLER (1)).

ERNE: archaic and poetic name, in Britain, for the Sea Eagle *Haliaeetus albicilla* (see under HAWK).

EROLIINAE: synonym of Calidritinae (see SANDPIPER).

ERROR, STANDARD AND PROBABLE: see BIOSTATISTICS.

ERUPTION: same, but in relation to area of origin, as IRRUPTION (see also MIGRATION).

ERYTHRISM: see PLUMAGE, ABNORMAL.

ERYTHROCYTE: see BLOOD.

ERYTHRURINI: see ESTRILDID FINCH.

ESOPHAGUS: American spelling of OESOPHAGUS (see ALIMENTARY SYSTEM).

E.S.S.: acronym for 'evolutionarily stable strategy', a term introduced by J. Maynard Smith in 1972. A strategy is simply some specified act, or trait, and an evolutionarily stable strategy is defined as a strategy that, if adopted by nearly all the members of a population, cannot be bettered by an alternative strategy.

The concept of the evolutionarily stable strategy was introduced for thinking about adaptations which have frequency-dependent fitnesses. Frequency-dependent FITNESS means that the number of offspring left by an organism adopting a particular strategy depends on the frequency of that strategy in the population. If the fitness of a strategy is negatively frequency-dependent, then an organism using the strategy when it was rare would leave more offspring than one doing so when it was commoner. The crucial idea in solving which strategy will be the ESS is that of evolutionary equilibrium. At equilibrium the fitnesses of all the strategies in the population are equal, so that natural selection is not altering the frequencies of any of them. Natural selection will cause the population to evolve until an equilibrium is reached, whence the population will be evolutionarily stable and the organisms of the population will be using the ESS. If all members of the evolutionarily stable population use the same strategy, it is called a pure ESS; if more than one strategy exists at equilibrium, it is called a mixed ESS.

Models of evolutionarily stable strategies have mainly been studied to clarify how natural selection might be expected to affect particular traits. For these purely theoretical studies, the strategies and their fitnesses (called 'pay-offs') are conceived by the modeller. One simple model by Maynard Smith, for example, showed how restrained fighting could be an ESS even though vicious fighters always beat animals that ran away. The reason for this result is the frequency-dependence of the fitness of vicious fighters. When vicious fighters are rare they do well because they usually meet animals they can beat; but when they are commoner they usually meet each other, inflicting detrimental injuries, so that animals that run away without fighting have higher fitness.

ESS models can also be used to find out equilibrial frequencies of real strategies in real populations. This has rarely been done so far, however, both because the models were only recently developed and because measuring the fitnesses of the animals requires large amounts of data.

M.R.

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Maynard Smith, J. 1978. Optimization theory in evolution. Annual Review of Ecology and Systematics 9: 31–56.

Maynard Smith, J. 1982. Evolution and the Theory of Games. Cambridge.

ESTRILDIDAE: a family of PASSERIFORMES, suborder Oscines; ESTRILDID FINCH.

ESTRILDID FINCH: in the plural used for members of the Estrildidae (Passeriformes, suborder Oscines) which include the waxbills, grassfinches, and mannikins (not to be confused with the manakins); alternative name is weaver-finch. In addition, various special substantive names have been used such as 'parrot-finch', 'sparrow', and 'weaver'. They have been included in the family Ploceidae (weavers), for their outermost primary is reduced as in the true weavers, and the egg-white protein patterns of the 2 groups are similar (Sibley 1970). Other research has shown, however, that not all 'finches' are necessarily a monophyletic assemblage. There are marked differences, to name a few, between the estrildid or weaver-finches and true weavers in their plumage and egg coloration, clutch-size and nest construction, gape pattern of young, courtship behaviour, mode of parental care and begging of the young, and structure of the digestive tract.

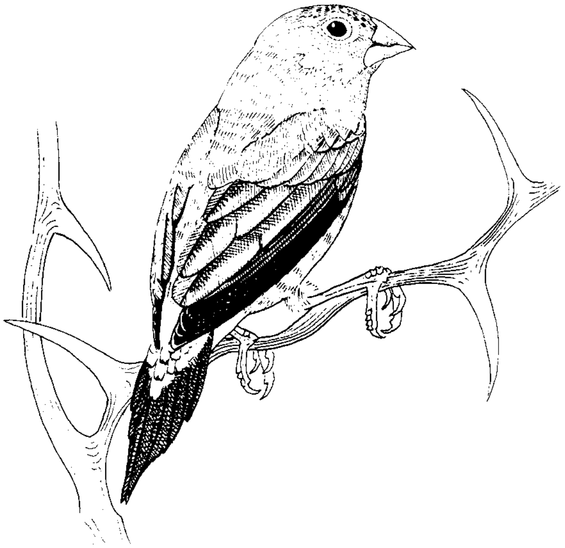
The number of species and genera that are recognized varies among authors. The latest revision (Goodwin 1982) recognizes 137 species and 27 genera. The family consists of 3 main groups, the waxbills, grassfinches and mannikins. Within the waxbills there is considerable adaptive radiation. There are about 60 species currently placed in either 16 or 17 genera by most authors. Some of the genera are poorly differentiated and those with few species, other than the monotypic genera, either form natural species-groups or superspecies (Hall and Moreau 1970). Many of them, particularly those in the genera *Estrilda, Lagonosticta*, and *Uraeginthus*, are small (length 90–108 mm); others, in the genera *Spermophaga* and *Pyrenestes* are larger (length 130–135 mm); and others, in the genera *Nigrita* and *Parmoptila*, are arboreal and eat insects instead of seeds. In all waxbills the juvenile palate markings consist of a series of spots, the commonest pattern consisting of 5 black spots (the so-called domino pattern). The grassfinches, length 100–130 mm, are a rather heterogeneous group and include the majority of Australian members of the family. The juvenile mouth markings range from a number of spots to a single continuous line in the shape of a horse-shoe. Finally, the mannikins are, in general, heavier looking than the others (length 95–120 mm), and the mouth markings in many consist of either one or two horse-shoe shaped lines.

Characteristics, habitat and distribution. The true waxbills, apart from 4 species, are confined to the Afrotropical Region where they are mostly found in open savannas and clearings within the forest areas. The Common Waxbill *Estrilda astrild* is widespread south of about 5°N and its range in East Africa extends northwards into Ethiopia. In addition, it has been introduced to many oceanic islands, to the South American mainland, and Portugal. It is distinguishable through the bright scarlet patch round the eye, also present in 3 other closely related species, but differs from these in having the lower abdomen and under tail-coverts black and the tail dark brown. Its place in West Africa and eastwards to Ethiopia is taken by the Black-rumped Waxbill *E. troglodytes* which has an essentially black tail and white under tail-coverts. Another attractive and common bird of forest clearings and swampy areas is the Orange-cheeked Waxbill *E. melpoda* which is found throughout West and Central Africa. The bright orange patch round the eye and on the cheek distinguishes it from other closely related waxbills. South of its range to about lat. 15°S and east of its range, its place is taken by the Fawn-breasted Waxbill *E. paludicola*. The males of all 9 species of fire-finch *Lagonosticta* are grey or brown, suffused in varying degree with red or pink, and some feathers on the breast and flanks are tipped white; the females are duller. Two of the most widely distributed are the Dark Fire-finch *L. rubricata* and the Red-billed Fire-finch *L. senegala*. The latter is more common, being found in towns and villages and frequently entering houses, whilst *rubricata* inhabits bush, woodland or forest edge. All 5 species of *Pytilia* are striking birds and usually found in thorny thickets and undergrowth in open savanna. The Melba Finch *P. melba* has a wide distribution and is probably the most beautiful. The male has an olive-green back and wings, crimson tail, grey head, barred underparts and brilliant red on the forehead and throat, merging into yellow on the breast. Some waxbills are forest species. Four crimson-wings *Cryptospiza* are found only in montane forest in East and central-southern Africa. The most widespread of these is the Red-faced Crimson-wing *C. reichenovii*. The male has an olive-brown head and underparts, blackish tail and wing, and bright scarlet on the flanks, upper tail-coverts, mantle and facial patch surrounding the eyes. The negro-finches (*Nigrita* with 4 species), and the flower-peckers (*Parmoptila* with 2 species) are both found in primary and secondary lowland forest. Although the negro-finches are not brightly coloured they are markedly different from each other, 2 having black, one white, and one chestnut underparts. The Red-fronted Ant-pecker *P. rubrifrons* also has chestnut underparts and the forehead and fore-crown are bright red.

Of the Asian waxbills, the Green Avadavat *Amandava formosa*, an endemic of India, is unique in being olive-green above and yellow underneath from chin to tail. In contrast, the male Red Avadavat *Amandava amandava* in breeding dress is crimson below spotted with white, red to brown above, and has brown wings. It is the only estrildid that moults into a duller non-breeding dress. It occurs throughout India, West Pakistan and southern Nepal, and its range extends eastwards to Cambodia, Saigon, and the lesser Sunda islands. It has been introduced into numerous islands such as Mauritius, Fiji, Sumatra, Singapore and the Philippines.

The grassfinches are predominantly found in Australia (15 species, placed in 7 genera). Most of them are birds of open grasslands and savannas, usually in the vicinity of water. Four species, however, occur in specialized habitats: the Blue-faced Parrot-finch *Erythrura trichroa* at the forest edge in northern Queensland; the Red-eared Fire-tail *Emblema oculata* in dense eucalypt forests in south-west Australia; and the Painted Finch *Emblema picta* and Zebra Finch *Poephila guttata* in semi-deserts in central Australia. In plumage they are extremely diverse. The parrot-finches *Erythrura* have iridescent green (unique in the family), reds or blues in their plumage; the Painted Finch has brilliant crimson, black, white, and brown in its plumage; and the Zebra Finch, in contrast, lacks bright colours and is pale brownish grey above and white below with a black band across its breast and black tips to the white feathers on the face. The parrot-finches (12 species) are widespread in the Philippines, Borneo, New Guinea and various islands in Melanesia, some of which have endemic species.

The mannikins are sombre coloured, mainly brown or nearly black with bars or shaft streaks, but some have large bold areas of black, white and brown. Five African species belong to the genus *Lonchura*, the Indian Silver-bill *L.* (= *Euodice*) *malabarica* also occurring in India and Sri-Lanka. Many more mannikins occur throughout the Oriental and Australian regions. There are 12 species in New Guinea, one of which, the Chestnut-breasted Finch *L. castaneothorax*, also occurs in Australia.



Indian Silverbill *Lonchura malabarica*. (*M.W.*).

On Madagascar is found the Bibfinch *Lepidopygia nana*, a species of uncertain affinity and considered by some to be closer to *Estrilda*. The largest of the group and best known is the Java Sparrow *Lonchura* (*Padda*) *oryzivora* which is believed to be native to Java and Bali but which has been introduced to many tropical areas including Hawaii, Seychelles and Tanzania. It is a popular cage bird as are many of the estrildids. Included in the mannikins are 2 African species (*Amadina*), the most widespread being the Cut-throat *A. fasciata*, but they differ from typical mannikins in having heavier heads, brighter colours and some differences between the sexes.

Movements. Estrildid finches are largely sedentary, but local movements may occur in the drier parts of their ranges. In Nigeria the Cut-throat migrates southwards in the dry and returns northwards in the wet season. Northern populations of the Aurora Finch *Pytilia phoenicoptera* and the Melba Finch *P. melba* in Nigeria, probably also have regular north-south movements. In Australia, the Zebra Finch is known to undertake large-scale, but irregular, nomadic movements during extended periods of drought.

Food. Estrildid finches are predominantly granivorous, feeding mainly on half-ripe and ripe grass seeds, which they either pick up from the ground or pull directly from the stalk. During the breeding season many of the granivorous species take insect food, and some of the parrot-finches also take fruit. The forest species of *Nigrita* and *Parmoptila* are apparently insectivorous throughout the year.

Several species of grassfinches, mainly in the genus *Poephila*, drink by sucking as do pigeons and doves. This is almost unique among passerines. The birds suck for several seconds at a time; up to 21 s has been observed in the Long-tailed Grassfinch *Poephila acuticauda*.

Behaviour. Estrildid finches seem to form very stable pairs and probably pair for life. Courtship behaviour shows great interspecific differences. It consists mainly of the male courtship dance, the basic movement of which is a vertical up-and-down bob, achieved by alternate stretching and bending of the legs. In some species the male, with rather stiff legs, actually leaves the branch, returning to the same spot each time; in others, rapid swings from side to side or combinations of both these vertical and lateral motions are involved. The ornamented areas of the plumage are usually erect and shown off. In many species the male may carry a piece of grass in his bill, and in most the male utters his courtship song while dancing.

Successful copulation is nearly always initiated by the solicitating female. In passerines this usually involves quivering of the wings, but in the estrildids the soliciting display involves the tail. Female cordon-bleus *Uraeginthus* adopt a horizontal posture and quiver or tremble their tails, which are usually slightly raised. At very high intensity the tail may make lateral and vertical movements up to an angle of 40° to the horizontal. In the grassfinches the quivering occurs in the vertical direction only.

Forest estrildid finches seem to be rather solitary, living in pairs or small parties. Open country species, on the other hand, may form big flocks, at least outside the breeding season, sometimes to pest proportions (the Spice Finch *Lonchura punctulata* and White-backed Munia *L. striata*). Some species, especially those inhabiting the arid parts of Australia, retain their sociability even during the reproductive season and tend to breed in loose colonies. Several times, each day, members of a colony, often joined by members of other colonies, gather together for 'social meetings' during which they feed together, bathe together, rest drowsily or preen each other. Special behaviour patterns such as social calls, peering behaviour (see below) and greeting ceremonies may serve to hold the group together.

Voice. Estrildids possess a considerable variety of calls, the largest number being found in the most sociable species. In the Australian genus *Poephila*, a number of different calls have been identified, including loud 'lost calls', low contact calls, mate and group greeting calls, as well as agitation, alarm, distress, fleeing, nest, copulation, and juvenile calls. They also have a song, not territorial in function nor used in aggression, but used mainly during courtship when it probably serves to attract and stimulate the female. In addition the males of many species utter a so-called 'undirected song' or 'jingle' the function of which is not entirely clear but which may contribute to maintaining the pair-bond. In some species, mainly in the genus *Lonchura*, other birds of a group sometimes respond to the 'jingle' song of a male by flying towards him and standing either beside or in front of the singer whilst peering into his face. If the singer edges away, he is followed by the other. This 'peering behaviour' has been noted in males and females, young and old, and its biological significance is not clear. In a few species, mainly African, the female also possesses a song phrase.

The songs of the estrildid finches are not loud, sometimes being inaudible only a metre away. They consist of high-pitched short and rather melodious phrases (some waxbills), of 'toy trumpet' notes (some grassfinches) or of unmelodious clucks, faint whistles and slurs (many mannikins).

Breeding. The reproductive season differs from species to species as well as between different climatic regions. It coincides with those parts of the year when half-ripe seeds and/or insects are most readily available. In the southern parts of Australia and South Africa, where winter temperatures are low and summers are very dry, estrildids breed mainly in spring but also at times in the autumn. In subtropical, semi-arid areas, they tend to breed during the second half of, and shortly after, the annual wet season(s). In tropical latitudes the breeding season is much more prolonged; thus nests of the Red-billed Fire-finch have been found in each month of the year in West Africa, and over a period of 9 months for the Dark Fire-finch. Finally, in the arid parts of central Australia and central southern Africa, where rainfall is somewhat erratic, estrildids are opportunistic breeders, reproducing whenever environmental conditions permit, the best known examples being the Australian Zebra Finch and the Red-headed Finch *Amadina erythrocephala*.

Most estrildids nest in bushes or small trees. Some, like the Red-eared Firetail, nest in the tops of tall trees, others among tall grass and reeds or right on the ground. A few species, like the Australian Gouldian Finch *Chloebia gouldiae* and the African Cut-throat, do not construct their own nests but use tree-holes or abandoned nests of other species respectively. The nests are domed, with a side-entrance and, in most cases, an entrance tunnel. In most species, the nest is a rather untidy structure, never woven in the manner of true weavers. Some species use feathers or other soft material for lining. Both sexes share in nest construction, the male usually collecting and carrying the material while the female sits inside the nest and builds it in. Some species build roosting nests outside the breeding season, often a co-operative task of several birds which use the roost nest together; others roost on twigs or use empty nests. Roosting behaviour is species-specific.

The clutch-size is usually 4–6. Larger clutches (sometimes as high as 9) have been recorded and are probably due to 2 females laying in the same nest. The eggs of all species are pure white. Both sexes incubate, with individual shifts of from 1.5 to 2.0 h. Incubation data for some genera are as follows: *Estrilda* 11 days, *Lagonosticta* 10–11 days, *Uraeginthus* 11–12 days, *Pytilia* 12 days, *Lonchura* 10–12 days, grass-finches 12–14 days. The nestling periods of those genera studied are: *Estrilda* 17 days, *Lagonosticta* 14–18 days depending on brood size, *Uraeginthus* 16–19 days, *Lonchura* 15–17 days, Australian grass-finches 21 days (very long for a small passerine bird). After the young leave the nest they are fed for another 1–2 weeks. During this time, some species lead their young back into the nest for roosting. Both parents feed the young by regurgitation.

In most species there is no specialized method of nest sanitation; the nestlings defaecate on the walls of the nest, and the faeces rapidly dry and stick there, so that the nestlings are not fouled.

The begging posture of estrildid finches is unique among passerine birds. The head is kept low and the neck is twisted to one side so that the beak is directed upward. The mouth is opened wide revealing the species-specific mouth markings of the nestlings (see above). The edge of the gape usually has white or black and white swellings, and in some species there are highly reflective spots at the base of the bill which presumably help the adults to locate the mouth in the dark cavity of the nest. The mouth markings are displayed conspicuously through lateral waving movements of head and tongue. Young estrildid finches mature very quickly and may breed at an age of a few months; mature gonads have regularly been found in 10-week-old Zebra Finches. This has been seen as an adaptation to the irregular climatic conditions in central Australia. Many African estrildids are parasitized by whydahs (*Vidua*); for details see WHYDAH (1). K.I.

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ESTROGEN: same (American usage) as OESTROGEN; see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

ETHIOPIAN REGION: see AFROTROPICAL REGION.

ETHOLOGY: the scientific study of BEHAVIOUR.

ETIOLOGY: see AETIOLOGY.

EUPETES: substantive name sometimes used for the 3 New Guinea species of the genus *Eupetes* (see RAIL-BABBLER).

EUPHONIA: generic name used as substantive name of *Euphonia* spp. (see TANAGER).

EURING: the European Union for Bird Ringing, founded in Paris in 1963 as a loose federation of European ringing schemes—of which there are more than 30. Its aims are to promote and facilitate the exchange and use of ringing data and to this end it has established an international Data Bank of recoveries, currently located at Arnhem, Netherlands.

EUROPE: see under PALEARCTIC REGION.

EURYLAIMIDAE: family of PASSERIFORMES, suborder Deutero-Oscines; BROADBILL.

EURYOECIOUS: occupying a wide range of the habitats available in an area, i.e. showing 'wide habitat-tolerance'—contrasted with STENOECIOUS.

EURYPYGAE; EURYPYGIDAE: see under GRUIFORMES; SUNBITTERN.

EUSTACHIAN TUBE: see HEARING AND BALANCE; PALATE; and under SKULL.

EUTAXIS: see WING.

EUTROPHIC: rich in plant nutrients, usually referring to fresh water. Eutrophication can occur naturally or can be caused by residues of fertilizers draining into the water from farmland. The opposite term, referring to nutrient-poor waters, is 'oligotrophic'.

EVOLUTION: the theory that the present diversity of living organisms has originated from a much lesser diversity of organisms that existed in the past, by a process of gradual change from generation to generation. The original organisms are generally considered to have arisen from non-living materials. The development of this theory as part of modern science occurred mainly during the first half of the 19th century, particularly under the influence of Lamarck and of geologists concerned with the history of rocks and fossils. The theory was soundly established by Darwin, who not only marshalled a huge array of evidence for the theory but also, with Wallace, proposed a plausible mechanism for the process (see NATURAL SELECTION).

The fossil record provides good evidence for evolution—that is, it provides evidence which cannot be explained by alternative hypotheses except by special pleading, case by case. Thus, a general feature of the fossil record is that organisms tend to appear in the record in the order of their morphological similarity. A simple case of this is presented by Archaeornithes, which are not only morphologically intermediate between archosaurian reptiles and modern birds but which also make their first appearance in the fossil record in between the appearances of these two groups (see FOSSIL BIRDS). For groups of organisms that have been well-preserved in the record, detailed evolutionary lineages may be traced, with general consistency of the evidence of morphological similarity and that of position in time.

Systematic biogeography also provides evidence that is difficult to reconcile with hypotheses other than the theory of evolution, except by special pleading. Within a single geographical region, it is easy to recognize and delimit species in most animal groups: the species are distinct. But this is not so if one adopts a geographically broader approach. One then finds every gradation from species that are widespread but show little regional differentiation, through species that show gradual variation from place to place, species that show well-marked subspecies which interbreed freely, arrays of morphologically distinct forms that replace each other geographically and which hybridize only in a restricted region, groups of species which hybridize only occasionally even when sympatric, to groups of species which never interbreed (see SUBSPECIES, CLINE, SUPERSPECIES, SPECIATION). Geographically replacing populations will often hybridize freely with neighbouring populations but not with more distant ones, even though they are connected by a chain of hybridizing populations. Secondary overlap of the ends of such chains gives rise to RING-SPECIES. Such phenomena are to be expected if organisms have arisen by progressive diversification but not otherwise.

Biogeography also provides evidence of convergent evolution, the process by which species of unrelated and dissimilar groups in different parts of the world come to resemble each other because their evolution has been moulded by similar ecological circumstances. Thus although the diving petrels *Pelecanoides* belong to the order Procellariiformes and the small auks, e.g. *Plautus*, belong to the Charadriiformes, these birds look extremely similar and share many characters that are directly correlated with their way of life: swimming on the sea, diving deeply to feed, and using their wings for both submarine and aerial propulsion. There can be no doubt that the same ecological niche has been filled by evolution from two quite different stocks—the auks in the northern hemisphere, the petrels in the southern.

The biogeography of remote islands and archipelagos provides further evidence. The organisms of such places typically belong to fewer families and genera than do the organisms of equivalent continental areas. Yet the number of species is not reduced in proportion, because some of the families and genera have unusually large numbers of species. Furthermore, although these species are sufficiently similar to be placed in the same family or genus, they may inhabit a range of ecological niches that would be inhabited by species belonging to many different families in an equivalent continental area. The Geospizinae of Galapagos and Drepanididae of Hawaii are well-known examples (see DARWIN'S FINCHES, HAWAIIAN HONEYCREEPER). Selection favours individuals that are able to use empty niches so that, in this situation, it results in the rapid evolution of a diversity of species, each suited to one of the available niches. Since the original array of empty niches was great, the species are ecologically diverse, even though they are taxonomically similar.

Comparative studies show that animals that appear related, judged on general similarity or on the fossil record, tend to share basic underlying plans of parts of their anatomy, physiology, and behaviour. For example, the basic structure of the limbs is the same in amphibians, reptiles, mammals, and birds, even though that plan is modified to give an array of different types of limb, suiting the uses to which each is put. This is what one would expect if the theory of evolution was true. However, it may be that the similarities are explicable wholly in functional, rather than historical terms. Taking tetrapod limbs as an example, it may be that the similarities occur because there are certain basic similarities in the functional requirements for limbs in all tetrapods. We do not know enough about functional anatomy to be able to rule out this possibility. Thus comparative studies provide evidence that is fully consistent with evolution but which does not prove evolution, since there are other hypotheses which can be used to explain the data.

The same is true of the evidence provided by embryology. The early developmental stages of similar animals are generally more similar than the adult stages. If evolution has occurred by gradual change, this is to be expected. Genetic changes that affect processes occurring during the early stages in development are likely to have greater effects on the adult organism than changes that do not have any effect until late in development. Random changes in highly integrated systems, such as mutations in living organisms, are likely to be catastrophic if their effect is large. Thus most of the genetic changes incorporated during evolution will have been of small effect and, therefore, will tend to have been those affecting the later stages of development. Once again, however, functional constraints alone may be used to explain the greater similarity of embryos than of adults. It may be, for example, that the functionally best way of beginning the development of any vertebrate animal, given the similarity of the starting point in all species (the egg), is to proceed through the basic pattern of embryogenesis that the vertebrates display.

Biologists have no doubt that the theory of evolution is correct. Recently, it has come under attack mostly on philosophical and religious grounds. The main thrust of this attack has been that it is not a normal (i.e. hypothetico, deductive) scientific theory because it cannot be proved wrong. This is a mistaken view arising from three sources. One is that predictions of evolutionary theory are predictions about sets of individual phenomena, rather than about those phenomena themselves. For example, in east Asia we find forms of *Larus* gulls intermediate between *L. fuscus* and *L. argentatus*, the Lesser Black-backed and Herring Gulls. The theory predicts that we should find such transitional forms, but it does not allow us to predict which particular species pairs will display them: the prediction is about the whole set of species, not about particular species. Commentators used to the sciences of the laboratory bench have sometimes mistakenly concluded that such general predictions are not scientific predictions at all.

The same confusion about the scale of predictions is partly responsible for the second source of error. Evolutionists have proved ingenious at explaining away exceptions to the general predictions they make, resulting in the charge that the theory can explain anything and that its predictions are therefore unfalsifiable. However, although a few exceptions do not falsify a general evolutionary prediction, if the exceptions are abundant, then the prediction is falsified.

The third source of difficulty is that the major predictions that evolution makes are already known to be true. However, this was not true when Darwin established the theory. He was, for example, embarrassed by the apparent paucity of the transitional forms which the theory predicted and which were later discovered to be abundant. Furthermore, evolution theory continues to provide predictions which are testable in the standard way: many recent advances in the studies of feeding behaviour and social systems have resulted from making predictions based on Darwinian theory.

The modern theory of evolution, established by Darwin, goes further than the basic idea that organisms have evolved: it includes the belief that evolution has been mainly a result of NATURAL SELECTION. Various alternatives to this theory have gained considerable support in the past and some do so today. The theory of Lamarck was rejected when one of its premises, the inheritance of acquired characters, was found to be incorrect (except in some peculiar cases of little general significance). The theory of orthogenesis was shown to be inconsistent with the facts. This theory was that lineages became stuck in an evolutionary groove, evolving in a particular fixed direction, sometimes even developing characters to an extent that was detrimental and resulted in their extinction. However, the fossil record shows no long-continued unidirectional trends and it shows that organisms with so-called detrimental characters often persisted for millions of years.

A common misunderstanding of evolution, related to the orthogenetic view, is that evolution is goal-directed, that organisms evolve some character because they need it. Were natural selection exactly analogous with the artificial selection imposed by man on domestic animals and plants, this would be correct. Natural selection, however, does not occur in order to bring about the evolution that results from it, but simply because ecological circumstances lead to some genotypes reproducing or surviving better than others.

A common result of an evolutionary change, naively interpreted as the reason for evolutionary changes, is that the probability of the species' survival is increased, since characters increasing the survival of individuals are likely to increase the survival of the species to which the individuals belong. However, this is by no means always true. There may even be some characters which, although they decrease an individual's inclusive fitness (see NATURAL SELECTION), raise the viability of the population. For example, producing fewer offspring will often reduce an individual's inclusive fitness but, because a less rapidly growing population is less likely to overstretch the available food resources, reproductive restraint may increase the probability of the population surviving. It has been argued that such characteristics are found in some species and that, since natural selection cannot account for them, selection at the level of whole populations (group selection) must be invoked. This argument is not widely accepted because the existence of such 'self-sacrificing' characteristics is doubtful and because group selection appears to be generally incapable of prevailing against natural selection. The basic reason for this is that the rate of an evolutionary change under natural selection depends on the rate of turnover of generations of individuals (as well as on the strength of selection), whereas the rate of change under group selection depends on the rate of turnover of populations, i.e. the rate at which populations become extinct and are replaced by others. Since populations usually persist for many generations, evolution under group selection will be slower than under natural selection, so if the two forces are in opposition natural selection will prevail.

A more widely accepted alternative to the theory of evolution by natural selection is that most evolutionary change has come about through chance differences in survival of different genotypes ('the neutral mutation and random drift hypothesis'). The replacement of one genotype by another as a result of such chance differences requires that their fitnesses (see NATURAL SELECTION) differ by no more than one part in ten thousand, unless the species numbers less than a few thousand individuals. For characters that have been carefully studied, fitness differences more than one hundred times greater than this have commonly been identified. Because of this, the role of chance differences in survival appears to be limited.

Closely related to the neutralist hypothesis is the view that organisms have characters that are not selectively advantageous in themselves but are side-effects of other characters. Thus vertebrate blood may be red not because the redness is advantageous itself but because haemoglobin is an efficient oxygen-carrier for vertebrates and it happens to be red. Other characters may exist because, being advantageous in the past, they have become an integral part of the organism's constitution and so persist even though no longer useful. While it is undoubtedly true that some characters may exist as mere side-effects or historical hangovers, the recognition of this should not be taken as a licence to explain away any characters of which the selective importance cannot be demonstrated. Experience shows that the failure to demonstrate the selective importance of a character has usually been the result of human incapacity rather than the true lack of such selective importance.

If some characters are selectively neutral, their pattern of occurrence could be of great value in working out phylogenetic relationships, since their occurrence is not affected by the way of life of a particular species at a particular time. For this reason, phylogeneticists have commonly sought such characters. They have, of course, usually chosen those whose functional significance was obscure, biochemical characteristics having been especially popular recently. An approach that is more consistent with evolutionary theory is to consider the evidence as a whole, interpreting the data of comparative anatomy, biochemistry, embryology, palaeontology and biogeography in the light of the ecological circumstances that might have given rise to natural selection for particular characters. J.J.D.G.

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EXASPIDEAN: see under ENDASPIDEAN.

EXCREMENT; EXCRETA: see DROPPINGS; GUANO; GUANO, CAVE; and ALIMENTARY SYSTEM; EXCRETORY SYSTEM.

EXCRETION, EXTRARENAL: excretion, by the nasal (salt) glands, of excess salt present in ingested food and sea-water. The avian kidney possesses only limited ability to excrete sodium chloride and consequently excessive salt intake is harmful, or even fatal, to most birds. Obvious exceptions are those marine birds which are able to tolerate the high salt intake associated with their feeding habits, and Schmidt-Neilsen and his co-workers (1957) demonstrated that the nasal glands were not only particularly well developed in all marine species but were able to excrete salt in high concentration. Normal salt levels were therefore maintained in the blood and tissues of these birds even when large amounts of salt were consumed.

The nasal gland is present in all birds and consists of two or more lobes which lie on the skull above or anterior to the orbit (Technau, 1936). In terrestrial species the gland is small and inactive but correlation between degree of exposure to a marine environment and increasing activity of the gland in members of the Charadriiformes indicates that adaptive and, possibly, acclimative changes can occur (Staaland, 1967).

During secretory activity the duct of each lobe conveys the concentrated salt solution to the nasal cavity, whence it flows through the external nares to the tip of the bill. In some species of birds (e.g. cormorants *Phalacrocorax* spp. and gannets *Sula* spp.), the external nares are closed in the adult and the fluid then trickles from the internal nares in the roof of the mouth to the tip of the bill. Unlike the kidney, which functions continuously, the nasal gland is only active when the need to eliminate salt arises. There are, therefore, periods of intensive activity, e.g. after feeding at sea, interspersed with periods of quiescence.

The almost unique capacity of the salt gland to excrete a concentrated saline solution has interested many investigators and there is now an extensive literature on the physiological mechanisms involved in the secretory activity of the gland (see Peaker and Linzell, 1975). Most of this work has been done on the domestic duck *Anas platyrhynchos* and domestic goose *Anser anser* because these species are easy to handle and their nasal glands secrete readily when excess salt is administered.

The salt gland is derived from the nasal epithelium and consists of numerous tubular lobes each of which contains several thousand branched tubules radiating from a central duct. The distal portion of each lobule contains peripheral cells; these develop into the more numerous, and structurally more complex, secretory cells which occupy the remainder of the tubules. Conversion of peripheral cells to secretory cells appears to be dependent on a salt-water environment (Ernst and Ellis, 1969). The extensive blood supply to the tubules is so arranged that the blood flow in the capillaries is countercurrent to the direction of tubular secretion and probably facilitates the transfer of salt from the blood to the lumen of the gland.

Excessive salt intake by the bird results in increased salinity of the blood and subsequent passage of water from the tissues to the blood to maintain osmotic balance. The change in blood composition and the increase in blood volume have both been regarded as stimulants to nasal gland secretion but it is now clear that it is the former that is primarily responsible. Specialized nerve endings, sensitive to changes in blood tonicity, have been located in the large blood vessels close to the heart and messages from these structures are conveyed, via the brain, to the nasal glands where they initate secretion (Peaker and Linzell, 1975).

K.J.H.

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Technau, G. 1936. Die Nassendruse der Vogel. J. Orn. 84: 511–617.

EXCRETORY SYSTEM: the organs responsible for excreting waste material containing nitrogen from the bird's blood and passing it out of the body, i.e. the paired, elongated kidneys each consisting of 3 main lobes in most birds; but 4 lobes are found in Ciconiiformes and Charadrii, while kiwis *Apteryx* spp. have 5. The kidneys lie symmetrically (except in Gaviidae and Podicipedidae) on the dorsal aspect of the body cavity below the synsacrum. The caudal lobes of the two kidneys are fused in the middle line in the Grey Heron *Ardea cinerea*, Chestnut-bellied Heron *Agamia agami*, Puffin *Fratercula arctica* and penguins (Spheniscidae), and may frequently be so in many other birds. Each kidney lobe is supplied with blood from a renal artery and a branch of the renal-portal vein (see VASCULAR SYSTEM). The subdivisions of the renal-portal veins (the interlobular veins) serve, together with the urine-collecting ducts that accompany them, to subdivide the kidney tissue into numerous lobules; the vessels run round the periphery of each lobule, and in the central region of each lobule there is a relatively large intralobular vein. The kidney tissue proper consists of a large number of convoluted and looping uriniferous tubules, which at one end join the peripheral urine-collecting ducts and at the other terminate in a Malpighian body or glomerulus, each tubule and its Malpighian body being known as a nephron. The Malpighian bodies encircle the intralobular veins: they are very small and very numerous in birds compared with mammals, varying from 400 per mm^3 in some African weavers (Ploceidae) to about 90 per mm^3 in the Rook *Corvus frugilegus*—whereas in mammals there are only about 4–15 per mm^3. The total number of nephrons present in both kidneys may vary from nearly two million in ducks (Anatidae) to some 30,000 in small passerines; the kidneys tend to be larger in aquatic and marsh birds than in others. The renal arteries break up into fine intralobular arteries that entwine the uriniferous tubules and ultimately join the interlobular veins. Capillaries from these veins also ramify amongst the uriniferous tubules and enter the intralobular veins, which in turn finally unite to form the renal vein.

The fluid extracted from the blood by the nephrons—the urine—passes into collecting ducts that unite to form the ureters, and through them the urine reaches that part of the cloaca known as the urodaeum, to be voided by the bird to the exterior (see ALIMENTARY SYSTEM; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM). There is in birds no urinary bladder as there is in mammals.

Avian urine, although subject to considerable variation, is normally cream-coloured and rich in mucoid substances and urates. The high concentration of urates (uric acid) accounts for over 60% of the total nitrogen excreted and is highly characteristic. After some resorption of water in the cloaca, uric acid is deposited as whitish crystals that are frequently seen mingled with the faeces of birds (see DROPPINGS; GUANO).

For elimination of salts by the nasal glands of marine birds see EXCRETION, EXTRARENAL. E.T.B.F.

EXOCCIPITAL: a paired bone of the SKULL.

EXOCRINE: see under ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

EXOGENOUS: see ENDOGENOUS.

EXOTIC: applied to species, etc., meaning that these are in the natural course alien to the area under reference.

EXPECTATION OF LIFE: see AGE.

EXPLOITATION: see UTILIZATION BY MAN.

EXTERMINATION: see EXTINCT BIRDS.

EXTEROCEPTIVE: the senses involved when what is perceived is external (see HEARING AND BALANCE; SMELL; TASTE; TOUCH; VISION).

EXTINCT BIRDS: for the purposes of this article, restricted to species or subspecies that ceased to exist after 1600 AD, the boundary date for historic extinctions accepted by the IUCN Species Survival Commission. Except for rock drawings and preserved feathers of some moas (Dinornithidae; see MOA), we have no evidence of the external appearance of species that died out before that date. See also EARLY EVOLUTION OF BIRDS; ENDANGERED BIRDS.

Of the birds that have become extinct within the span of ornithologically recorded history, the Dodo *Raphus cucullatus* of Mauritius, last recorded in 1662, is the proverbial example. The Passenger Pigeon *Ectopistes migratorius* of eastern North America, whose population of hundreds of millions declined to extinction in less than a century, is perhaps the most spectacular. Other well-known vanished birds are the flightless Great Auk *Pinguinus impennis* of the North Atlantic; the Labrador Duck *Camptorhynchus labradorius*, which became extinct before its breeding range could be discovered; the Carolina Parakeet *Conuropsis carolinensis*, the only parrot native to eastern North America; and the Huia *Heteralocha acutirostris* of New Zealand, in which the sexes differed remarkably in bill shape (see WATTLEBIRD (2)).

Systematic survey. The accompanying table lists all species extinct after 1600 for which tangible remains have been preserved. Although skins survive for most, some are known only from subfossil bones. These can often be correlated with travellers' descriptions. A number of species are known from descriptions or illustrations only. Although some of these, such as a macaw from Jamaica, undoubtedly existed, most must be considered hypothetical. A rail from Tahiti (*'Rallus pacificus'*) and an unidentifiable passerine from Raiatea (*'Turdus ulietensis'*) were named from inadequately described specimens long since lost. Other birds, such as a megapode from the Kermadec Islands, vanished before specimens could be collected, and remain unnamed.

With the loss of the species listed, 29 genera (19 non-passerine, 10 passerine) and the families Aepyornithidae (see ELEPHANT-BIRD), Dinornithidae (see MOA), Raphidae and Pezophapidae (see DODO), and Turnagridae (see THRUSH, NEW ZEALAND) have ceased to be represented among living birds. Of surviving families, the ducks (Anatidae), rails (Rallidae), pigeons (Columbidae), parrots (Psittacidae), starlings (Sturnidae) and Hawaiian honeycreepers (Drepanididae) have lost heavily in representation.

This list is probably incomplete. Some species not seen for many years may already be extinct, although their disappearance has not been confirmed. These may include the Glaucous Macaw *Anodorhynchus glaucus* of South America, last seen (in captivity) before 1905; the Uluguru Bush Shrike *Malaconotus alius* of eastern Tanzania, unrecorded since 1961; and possibly Semper's Warbler *Leucopeza semperi* of St Lucia, West Indies, last seen in 1972. One species, the Socorro Dove *Zenaida graysoni* of Socorro I., Mexico, is extinct in the wild but survives in captivity (Jehl and Parkes 1983).

Other species, listed here as extinct, may prove to survive. In the past, several birds have been confidently recorded as extinct, only to be brought back from the dead by new explorations or more extensive field surveys. Well-known examples are the Takahe *Porphyrio mantelli*, a flightless gallinule from New Zealand, unrecorded between 1898 and 1948; the Seychelles Scops Owl *Otus (magicus) insularis*, lost between 1906 and 1959; the Noisy Scrub-bird *Atrichornis clamosus* of Western Australia, last collected in 1889 and, despite a report in 1920, presumed extinct until its rediscovery in 1961; and the Eyrean Grasswren *Amytornis goyderi* of the central Australian deserts, unseen from 1875 to 1961. The Cahow or Bermuda Petrel *Pterodroma cahow* was rediscovered in 1916, having gone unnoticed since its populous days in the early 17th century. Recent rediscoveries include the White-winged Guan *Penelope albipennis* of Peru, the Fiji Barred-wing Rail *Nesoclopeus poecilopterus*, the Night Parrot *Geopsittacus occidentalis* of Australia, and the Long-legged Warbler *Ortygocichla (Trichocichla) rufa*, also of Fiji. The Molokai O'o *Moho bishopi* was apparently found again in 1981, not on Molokai where it had last been seen in 1904 but on Maui, where no species of O'o has ever been collected.

In addition to full species, over 60 subspecies and many unnamed populations have become extinct since 1600. Perhaps the best known of these is the Heath Hen *Tympanuchus c. cupido*. Despite concerted conservation efforts, the last bird died on or after 11 March 1932, on Martha's Vineyard, Massachusetts, USA.

Extinction dates. For most of the vanished birds listed here, the 'extinction date' is actually the date of the last reliable record. For the 3 moas (Dinornithidae), it is the most recent radiocarbon date. Many of these birds may have survived for years afterwards, particularly those 10 species observed or collected only once, or at most by a single expedition. The Cook Pacific voyages recorded at least 5 birds that were never seen again (nos. 32, 47, 75 and 2 subspecies), and Kittlitz found 3 in the Pacific in 1828 (24, 63, 73).

For some species, the date of extinction can be determined exactly. What were probably the last survivors of 4 species (11, 39, 50, 53) died in captivity. The last Passenger Pigeon died in the Cincinnati Zoo, probably at 1 p.m. (local time), 1 September 1914. Although they were not in captivity, the hour of doom of the last pair of Great Auks is known almost as exactly—the afternoon of 3, or, more probably, 4 June 1844 (though there are later, doubtful, sight records).

Causes of extinction. Extinction is invariably the result of a species' inability to adapt to changes in its environment. Species whose initial populations are small, either because of large home ranges or specialized habitat requirements, are particularly vulnerable to extinction (Diamond and May 1976). So are colonial species having large, concentrated populations, and species dependent on intermittently available resources, rendering them subject to drastic population fluctuations (see ENDANGERED BIRDS). Birds confined to oceanic islands have proved highly prone to extinction; 80 of the 90 species listed here were island dwellers, and some island groups, such as Hawaii, the Mascarenes, and the Bonins, have lost large proportions of their land bird faunas. Among birds with similar feeding behaviours, the largest species have tended to disappear first. In the Hawaiian Islands, 5 of the 7 largest nectar-feeders surviving into historic times (67, 68, 69, 88, 89) have become extinct. The largest, the Kioea *Chaetoptila angustipluma*, was among the first to disappear.

Man's effect on avian extinction certainly goes back far beyond 1600. Hunting has been implicated in the extinctions of the moas and of 5 subfossil species of waterfowl in New Zealand (Williams 1964), and of the flightless scoter *Chendytes lawi* of western North America, which died out about 3,700 years ago (Morejohn 1976). Habitat destruction by the Malagasy probably was responsible for the extinction of the Elephant-birds. Recent discoveries of the subfossil remains of at least 45 species of birds on the Hawaiian Islands suggest that perhaps 2/3 of the original Hawaiian avifauna may have disappeared as a result of human activity before the arrival of Europeans. The vanished species include at least 7 flying and flightless geese, 2 flightless ibises, 7 flightless rails, 3 owls and at least 15 Hawaiian honeycreepers. The Polynesians hunted, introduced dogs, rats and pigs, and, perhaps most fatally, destroyed much of the lowland forest for agriculture (Olson and James 1982).

In historic times, the spread of western civilization to the remotest parts of the world has had a catastrophic effect. The worst period for recorded extinctions since 1600 was the late 19th and early 20th centuries, when many oceanic islands were rapidly developed and altered. Between 1885 and 1907 approximately 21 species became extinct, 8 from the Hawaiian Islands alone. Most of the 10 extinct continental species vanished in the early years of the 20th century. All but one of these lived in North America (including Mexico), India and Australia, areas greatly altered by western settlement in the preceding decades.

But human activity is not solely to blame for all historic extinctions. On rare occasions, a catastrophic natural event has wiped out a population. The unnamed Kermadec megapode and the San Benedicto Rock Wren *Salpinctes obsoletus exsul* disappeared after volcanic eruptions destroyed their habitats, in 1876 and 1952 respectively. More often, however, a variety of factors, both natural and human-induced, has contributed to each extinction. The European population of the Waldrapp *Geronticus eremita* (see IBIS) appears to have been restricted in both range and numbers by climatic deterioration after the mid-16th century, rendering it more vulnerable to the human interference which presumably wiped it out by 1621 (Schenker 1977). Banks (1977) has proposed that a shift in the prevailing winds in the early 19th century may have forced the Eskimo Curlew *Numenius borealis* to alter its migration route, bringing much of the population over New England where hunters brought it to the point of extinction. On the other hand, hunting drove the Auckland Island Merganser *Mergus australis* from most of its New Zealand range, but is not directly responsible for its disappearance from Adams Island, its final refuge (Williams 1964). Similarly, although the precipitous decline of the Passenger Pigeon was largely due to overhunting, its final disappearance cannot be so simply explained. It may have been so specialized for colonial breeding that, after its once immense flocks had been reduced below some critical size, it became unable to fledge enough young to maintain its numbers (Halliday 1980).

The human factor. The most severe effects of man on the extinction of birds have been:

Direct hunting pressure. This has affected mostly the large edible species, such as pigeons, parrots and the hapless Dodo. The last Great Auks were pursued by scientific collectors. The Guadalupe Caracara *Polyborus lutosus* is perhaps the only bird to have been deliberately exterminated, by goat-herders who claimed it took kids.

Introduction of predators and diseases. Feral cats, rats and pigs prey on both nests and adults, and have probably been chiefly responsible for the extinction of several flightless rails and other ground-nesting island species. Black Rats *Rattus rattus* released by a shipwreck on Lord Howe

Island in the Tasman Sea, in 1918, may have wiped out one endemic species (no. 66) and 4 subspecies of song-birds, most of which were ground- or hole-nesters. Ground-nesting birds are particularly vulnerable. Feral cats on Socorro Island, Mexico, probably killed off the endemic dove *Zenaida graysoni* and have driven the endemic mockingbird *Mimodes graysoni* to the brink of extinction. Both birds are ground-nesters. Tree-nesting birds on the same island have not been affected (Jehl and Parkes 1983). In the Hawaiian Islands, introduced mosquitoes possibly contributed to extinctions of birds by spreading avian pox, avian malaria and other diseases to which the endemic birds had lost immunity (Warner 1968).

Introduction of potential competitors. Introduced species may be able to out-compete residents for food or other limited resources. They may even destroy such resources. Rabbits, introduced on Laysan in the Hawaiian Islands in 1903 or 1904, destroyed almost all of the island's vegetation over a 20-year period. During this time, 3 of the 5 resident land birds—a rail, a warbler, and a Hawaiian honeycreeper—disappeared. The rail (no. 22) survived until 1944 on Midway, where it had been introduced.

Habitat destruction. Habitat destruction, particularly the cutting of mature forest, has been the major contributing factor in the extinction of many species. It has meant doom for many island endemics unable to adapt to secondary growth of vegetation or man-made conditions. On the Philippine island of Cebu, which was almost completely deforested in the 19th century, 16 of the 26 resident forest species had disappeared by 1947. These included 9 of the 10 endemics (no. 65 and 8 subspecies). The only surviving endemic, the Black Shama *Copsychus niger cebuensis*, has apparently adapted to secondary growth (Rabor 1959).

Island vulnerability. The particular vulnerability of island endemics has been explained by their long isolation from predators and competitors, with a correlated loss of both defence mechanisms and adaptability. The extinction of almost 20 flightless island species, including 11 of the 18 known flightless rails, provides a classic example.

Subtler factors may, however, be involved in island extinctions. Island endemics are often sedentary, confined to mature forest and other restricted habitats. Species diversity is directly related to the area of available habitat. Therefore, partial destruction of an area of mature forest may lead to loss of some of its bird species even if the remaining area is undisturbed. If the patch of forest is isolated, the species lost may not be able to recolonize it (Diamond and May 1976; but see Boecklen and Gotelli 1984). Despite its relatively undisturbed condition, Barro Colorado Island has lost 16 rain-forest bird species since its isolation by the Panama Canal (Willis and Eisenmann 1979). Even if island endemics could survive by adapting to secondary growth, the rapid spread of introduced birds already adapted to such habitats may prevent the residents from doing so. This may be true even if the endemics are perfectly able to out-compete the new arrivals in their own habitats.

These factors have, until now, had their most drastic effect on the small populations and localized habitats of island endemics. They are, however, increasingly important for the conservation of birds elsewhere. As continuing destruction of natural areas reduces continental habitats to a series of island-like pockets, mere preservation of remaining patches is unlikely to save all species. It is particularly unfortunate that tropical mature forest, the habitat with the largest number of bird species, many of which are highly sedentary, is today the subject of rapid destruction everywhere. A wave of extinctions of continental species much greater than the 19th century wave of island extinctions may be difficult to avoid. James Fisher wrote in 1964: 'It certainly seems likely that an insurance man can give a better quotation for a species' life now than he could at any time in the last graceless quarter of a millennium.' It is difficult now to be so optimistic (see King 1980). (J.F.) R.O.

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Full species of birds believed to have become extinct since 1600. Only those species for which specimens survive have been included. Modified from Greenway (1967), Luther (1970), and King (1979), and other sources (including H.D. Pratt). See Greenway (1967) for hypothetical species.

Species (with approx. date of extinction)	*Range in historic times*
AEPYORNITHIDAE	
1. *Aepyornis maximus*[1] F (*c.* 1649?)	Madagascar
DROMAIIDAE	
2. *Dromaius minor* (*diemenianus*) F (1803–36)	Kangaroo and King Is., Australia
DINORNITHIDAE	
3. *Megalapteryx didinus*[1] F (1785)	South Island, New Zealand
4. *Euryapteryx geranoides* (*gravis*)[1] F (1640)	New Zealand
5. *Dinornis torosus*[1] F (1670)	South Island, New Zealand
HYDROBATIDAE	
6. *Oceanodroma macrodactyla* (1912)	Guadalupe Island, Mexico
PHALACROCORACIDAE	
7. *Phalacrocorax perspicillatus* (*c.* 1852)	Bering Island, USSR
ARDEIDAE	
8. *Nycticorax* (?) *megacephalus* F? (*c.* 1730)	Rodriguez, Mascarene Is.
ANATIDAE	
9. *Cygnus sumnerensis*[1] (*c.* 1590–1690)	Chatham Is., New Zealand
10. *Tadorna cristata** (1943; 1964?)	North-east Asia
11. *Rhodonessa caryophyllacea** (1944)	Indian Subregion
12. *Camptorhynchus labradorius* (1875)	Eastern North America
13. *Mergus australis* (1905)	Auckland Is., New Zealand
FALCONIDAE	
14. *Polyborus lutosus* (1900)	Guadalupe Island, Mexico
PHASIANIDAE	
15. *Coturnix* (*n.*) *novaezelandiae* (1875)	New Zealand
16. *Ophrysia superciliosa* (1868)	Himalaya Mountains
RALLIDAE	
17. *Gallirallus wakensis* F (1945)	Wake Island, Pacific
18. *G.* (*philippensis*) *dieffenbachii* (*c.* 1842)	Chatham Island, New Zeland
19. *G. modestus* F (*c.* 1900)	Pitt and Mangare Is., New Zealand
20. *Tricholimnas lafresnayanus** F (1904; 1961?)	New Caledonia
21. *Atlantisea elpenor*[1] F (1656)	Ascension Island
22. *Porzana palmeri* F (1944)	Laysan, Hawaiian Is.
23. *P. sandwichensis* F (1884)	Hawaii, Hawaiian Is.
24. *P. monasa* F (1828)	Kusaie, Caroline Is.
25. *Aphanapteryx bonasia*[1] F (*c.* 1675–1700)	Mauritius, Mascarene Is.
26. *A. leguati*[1] F (*c.* 1730)	Rodriguez, Mascarene Is.
27. *Porphyrio albus* F? (*c.* 1834)	Lord Howe Island, Tasman Sea
28. *Gallinula* (*n.*) *nesiotis* (1861)	Tristan da Cunha
29. *Pareudiastes pacificus* F (1874)	Savai'i, Western Samoa
30. *Fulica newtoni*[1] (*c.* 1863)	Mauritius (and Reunion?), Mascarene Is.
GLAREOLIDAE	
31. *Cursorius bitorquatus* (1900)	Andhra Province, India
SCOLOPACIDAE	
32. *Prosobonia leucoptera* (1777)	Tahiti and Moorea
ALCIDAE	
33. *Pinguinus* (*Alca*) *impennis* F (1844)	North Atlantic
COLUMBIDAE	
34. *Ptilinopus mercierii* (1922)	Nuku Hiva and Hiva Oa, Marquesas Is.
35. *Alectroenas nitidissima* (1830)	Mauritius, Mascarene Is.
36. *A. rodericana*[1] (*c.* 1670)	Rodriguez, Mascarene Is.
37. *Columba versicolor* (1889)	Nakondo Shima and Chichi Shima, Bonin Is.
38. *C. jouyi** (1936)	Ryukyu Is., Japan
39. *Ectopistes migratorius* (1914)	Eastern North America
40. *Microgoura meeki* (1904)	Choiseul, Solomon Is.
RAPHIDAE	
41. *Raphus cucullatus* F (1662)	Mauritius, Mascarene Is.
PEZOPHAPIDAE	
42. *Pezophaps solitaria*[1] F (1791)	Rodriguez, Mascarene Is.
PSITTACIDAE	
43. *Charmosyna diadema** (1860; 1970?)	New Caledonia
44. *Nestor* (*meridionalis*) *productus* (*c.* 1851)	Norfolk and Philip Islands, Tasman Sea

45. *Psephotus pulcherrimus** (1927)	Eastern Australia
46. *Cyanoramphus zealandicus* (1844)	Tahiti, Society Is.
47. *C. ulietanus* (*c.* 1773–74)	Raiatea, Society Is.
48. *Lophopsittacus mauritianus*[1] F (1638)	Mauritius, Mascarene Is.
49. *Necropsittacus rodericanus*[1] (1731)	Rodriguez, Mascarene Is.
50. *Mascarinus mascarinus* (*c.* 1834)	Reunion (and Mauritius?), Mascarene Is.
51. *Psittacula* (*eupatria*) *wardi* (1881)	Mahe and Silhouette, Seychelles
52. *P.* (*krameri*) *exsul* (1875)	Rodriguez, Mascarene Is.
53. *Conuropsis carolinensis* (1914; 1938?)	Eastern North America
54. *Ara tricolor* (1864)	Cuba (and Isle of Pines?)
CUCULIDAE	
55. *Coua delalandei* (*c.* 1834–37; 1930?)	Madagascar
STRIGIDAE	
56. *Sceloglaux albifacies** (1914; 1950? 1982?)	New Zealand
57. *Athene murivora*[1] (1730)	Rodriguez, Mascarene Is.
CAPRIMULGIDAE	
58. *Siphonorhis americanus* (1859)	Jamaica
ALCEDINIDAE	
59. *Halcyon miyakoensis* (1887)	Miyako Shima, Ryukyu Is.
PICIDAE	
60. *Campephilus imperialis** (1958)	Mexico
ACANTHISITTIDAE	
61. *Xenicus lyalli* F? (1894)	Stephen I., New Zealand
TURDIDAE	
62. *Turdus ravidus* (1938)	Grand Cayman, W. Indies
63. *Zoothera terrestris* (1828)	Chichi Shima, Bonin Is.
SYLVIIDAE	
64. *Acrocephalus* (*f.*) *familiaris* (1916)	Laysan, Hawaiian Is.
DICAEIDAE	
65. *Dicaeum quadricolor* (1906)	Cebu, Philippines
ZOSTEROPIDAE	
66. *Zosterops strenua* (1918)	Lord Howe I., Tasman Sea
MELIPHAGIDAE	
67. *Moho nobilis* (1934?)	Hawaii
68. *M. apicalis* (1837)	Oahu, Hawaiian Is.
69. *Chaetoptila angustipluma* (1859)	Hawaii
CALLAEIDAE	
70. *Heteralocha acutirostris* (1907)	North Island, New Zealand
TURNAGRIDAE	
71. *Turnagra capensis** (1955; 1963?)	New Zealand
STURNIDAE	
72. *Aplonis pelzelni** (*c.* 1930–35)	Ponape, Caroline Is.
73. *A. corvina* (1828)	Kusaie, Caroline Is.
74. *A. fuscus* (1925)	Lord Howe and Norfolk Is., Tasman Sea
75. *A. mavornata* (*c.* 1774)	unknown (Pacific)
76. *Fregilupus rodericanus* (1832)	Rodriguez and Ile-au-Mat, Mascarene Is.
77. *F. varius* (*c.* 1862)	Reunion, Mascarene Is.
PLOCEIDAE?	
78. *Neospiza concolor* (1888)	São Tome, Gulf of Guinea
FRINGILLIDAE	
79. *Chaunoproctus ferreorostris* (1890)	Chichi Shima, Bonin Is.
DREPANIDIDAE	
80. *Paroreomyza flammea** (1964)	Molokai, Hawaiian Is.
81. *Hemignathus* (*Loxops*) *sagittirostris* (*c.* 1900)	Hawaii
82. *H. obscurus* (*c.* 1895)	Hawaiian Is.
83. *H. procerus** (*c.* 1968–69)	Kauai, Hawaiian Is.
84. *Rhodacanthis palmeri* (1896)	Hawaii
85. *R. flaviceps* (1891)	Hawaii
86. *Chloridops kona* (1894)	Hawaii
87. *Ciridops anna* (1892)	Hawaii
88. *Drepanis pacifica* (1898)	Hawaii
89. *D. funerea* (1907)	Molokai, Hawaiian Is.
ICTERIDAE	
90. *Quiscalus palustris* (1910)	Mexico

[1] known from subfossil remains, or from subfossil remains and travellers' descriptions

* possibly extant

F flightless

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EXTRALIMITAL: occurring only outside the boundaries of the area under consideration.

EYAS: special term (also 'eyass'; plural 'eyasses') for a nestling falcon or hawk, used especially of those species taken by falconers for training (see FALCONRY).

EYE: see VISION.

EYELASH: a bristle (modified feather) resembling a mammalian eyelash (hair) in situation and appearance; such eyelashes occur in a few groups of birds, e.g. conspicuously in hornbills (Bucerotidae), many species of cuckoos (Cuculidae), eagle owls *Bubo* spp., and the Ostrich *Struthio camelus*. See also PLUMAGE.

EYREAN: see AUSTRALASIAN REGION.

EYRIE: term (also 'eyry', 'aerie', 'aery') for the nest of a bird-of-prey, often an eagle *Aquila* sp., etc. (see also under FALCONRY).

F

FABULOUS BIRDS: kinds of birds that the human imagination has conjured up as religious, magical, or poetic symbols. This is apart from the role played by real species of birds in folklore, heraldry, witchcraft, and totemism (see FOLKLORE; HERALDIC BIRDS; OMENS, BIRDS AS).

The concept of fabulous birds, as of all zoological symbols, originated in primitive man's personification of the forces of nature. As his mind evolved he became increasingly aware of his aloneness in a mysterious and often hostile universe. Abstract concepts of a god or protecting power were at this time beyond his range, and it was thus natural that he should take the familiar creatures of his environment as the basis of elaborate symbols representing the good and evil powers that ruled his life. The more sinister zoological symbols, such as the dragon, belonged to the earth, and especially to the dark subterranean world of evil spirits. Birds, on the other hand, belonged to the sky—an ethereal region of purity and light. Fabulous birds were thus generally symbols of hope and regeneration, representing benevolent forces and the highest aspirations of mankind.

The first fabulous birds of any importance appeared in the Middle and Far East. The chief was Garuda, a gigantic bird-of-prey who, in Hindu mythology, was believed to bear the sun-god Vishnu on his daily journey across the sky. The earliest concepts of Garuda were almost certainly purely avian, and it seems probable that he was a composite symbol derived from observations of such real birds as Pallas's Fishing Eagle *Haliaeetus leucoryphus*, the Crested Serpent Eagle *Spilornis cheela*, the Lämmergeier *Gypaetus barbatus*, and the Brahminy Kite *Haliastur indus*. Later, however, he began to be depicted with human arms and legs, the avian characters being restricted to a white face, a golden body, and red wings. Garuda was a relentless enemy of serpents, which were a symbol of evil, and he was also supposed to carry elephants and tortoises to the summits of high mountains to devour them. The cult of Garuda spread eastward from India and he became a much venerated symbol in Indo-China, Siam, and Cambodia. In Malaya he was known as Gerda, and according to Ingersoll the men of Perak still say when a cloud obscures the sun; 'Gerda is spreading his wings to dry.' The cult of Garuda even reached Japan, where he was variously known as Gario, Bingacho, or Karobinga; but here he changed his sex and became half woman, half bird, a sort of feathered angel with the legs of a crane.

Westwards from India several bird-gods and demi-gods shared affinities with Garuda, and many have been descended from him. The most important was the early Persian Senmurv, half bird, half mammal, which was regarded as an elemental connecting link between heaven and earth. The wings, body, and tail of the Senmurv were those of a bird, but it was also supposed to have teeth; and the female of the species was believed to suckle its young. Like Garuda, it was an enemy of serpents and a benefactor of mankind, making its home in a tree of which the seeds would cure all evil. Every time the Senmurv alighted in the tree its branches used to shake and thousands of these seeds were scattered through the world.

In later Persian mythology the Senmurv was replaced by the Simurg. This was a giant bird which made its nest on Mount Alburs, on a peak that touched the sky. It was regarded as a symbol of strength and wisdom, a friend of the sick and the poor, and a comforter of mankind. Some beliefs concerning the Simurg show affinities with the Phoenix legend. For instance, it was reputed to live 1,700 years, and when at the end of that time the young was hatched, the parent of the same sex (some versions of the legend say the opposite sex) burnt itself to death. The Simurg may also be identified with the Anka of Arabic lore, and it shares some of the characters of the Rukh or Roc. The latter was a huge bird which inhabited an island in the Indian Ocean (usually identified with Madagascar), and was reputed to carry off elephants in its claws. The fronds of the exceptionally large palm *Sagus ruffia* were once regarded as the feathers of the Rukh, and the giant eggs of the extinct Madagascan bird *Aepyornis maximus*, each of which will hold over 10 litres of liquid (see ELEPHANT-BIRD), may also have played a part in the development of the legend as recounted in the *Thousand and One Nights*, the second and fifth voyages of Es-Sindibad of the Sea.

The most famous and poetic of all fabulous birds is the Phoenix. Pliny describes it as being the size of an eagle, with a gold neck, purple body, azure tail, and crested head. It has been identified by different ornithologists with the Purple Heron *Ardea purpurea*, the Bateleur Eagle *Terathopius ecaudatus*, the Golden Pheasant *Chrysolophus pictus*, or one or other of the various species of parrots (Psittacidae) or birds-of-paradise (Paradisaeidae), but like other fabulous birds it is probably a composite symbol derived from many sources. There was said to be only one Phoenix in the world at a time, and it dwelt in paradise, a land of infinite beauty lying beyond the eastern horizon. Every 1,000 years (some versions of the legend say 350, 500, or 1,461 years) the Phoenix left paradise and flew westwards to die. It collected aromatic plants on the way from the spice groves of Arabia, and built itself a nest in the top of a tall palm tree. Here, on the first dawn after its journey, it sang a song of such surpassing beauty that the sun-god stopped his chariot to listen. When he whipped up his horses again sparks from their hooves set fire to the nest of the Phoenix, and it died on a blazing aromatic funeral pyre. The new Phoenix grew from a worm which was found in the ashes of the nest, and flew back to paradise for its own allotted life span of 1,000 years.

The fabulous birds of the west were in general less benevolent than their eastern counterparts. In Greek times the hideous harpies, with their birds' faces and claws, were universally regarded as evil and destructive beings; even the glamorous sirens, variously depicted as birds with womens' heads or women with birds' legs, used their charms to lure mariners to destruction rather than to succour them in their dangerous calling. More lethal still were the Stymphalian birds, which were dealt with so effectively by Hercules in the sixth of his labours. These were man-eating birds, a mixture of stork, crane, and eagle, armed with arrow-like feathers that wounded all who came within their range.

In conclusion a few less publicised fabulous birds must be briefly mentioned. One of the most magnificent was the Fung-whang, or Feng Huang, the Chinese Phoenix. This was known by the Taoists as the scarlet bird, and was one of the four fabulous creatures symbolizing the four quarters of the heavens. Representations of the Fung-whang on Chinese screens and elsewhere suggest that its ancestry owes a good deal to the Peacock *Pavo cristatus*.

In Japan there is still a belief in a race of fabulous birds known as Tengus. The king of the Tengus is said to have the wings and claws of a giant eagle, a long red beak, and exceptionally piercing eyes. The Tengus are nature spirits, not positively evil but decidedly mischievous. They are very skilled in dancing and the use of arms, and sometimes take possession of human victims who, although half-demented, acquire their prowess in these activities while under their influence.

In ancient Sumer a huge divine eagle named Imgig was the royal symbol of Ur. The bird-god Horus of ancient Egypt, almost certainly derived from the Egyptian form of the Black Kite *Milvus migrans aegyptius*, was perhaps the most ancient god of the Egyptian pantheon. In Russia violent winds are still said to be produced by the wings of the colossal eagle-demon Vikhar flying overhead. Similar associations between violent winds and fabulous birds are found in the folklore of many primitive peoples and peasant communities, especially in northern Europe and among the North American Indians. R.C. (2)

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FACIAL DISC: a well defined, relatively flat, forward-facing part of the head as seen in some owls. It probably helps the bird in locating prey by sound, focusing the sounds made by the prey on the owl's ear openings (see OWL). See photo VISION.

FACIES: among other meanings in biology, the general appearance of a species without regard to details; comprises size, shape, posture, or movement, perhaps with general hue and any conspicuous features (see JIZZ; SIZE).

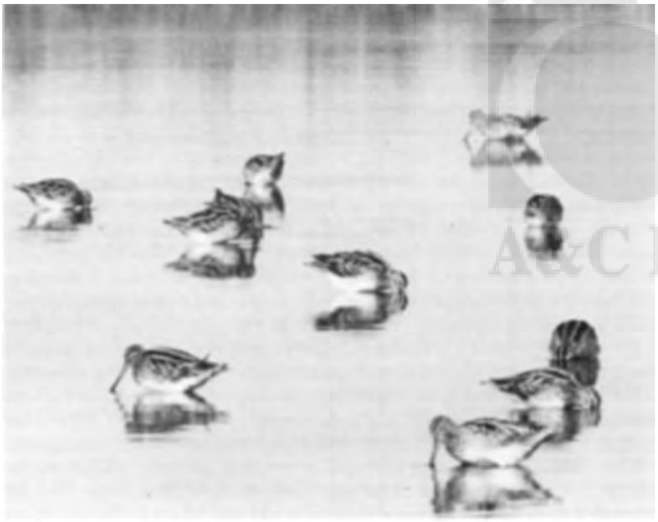
FACILITATION, POSTURAL: postural facilitation can best be defined by referring to an example. When a bird preens, it tends to work systematically from one region of the body to another. For example, preening the tail might be most often followed by preening the tail-coverts, rump or lower back. In other words transitions between successive preening acts occur in such a way that the bodily posture of the preceding act is similar to that of the following act.

The theory of postural facilitation predicts that changes between acts involving fewer body moves should occur more commonly than those involving many body movements. This is advantageous for the animal because it minimizes time and energy expenditure. J.R.K.

FACILITATION, SOCIAL: the term is not used very precisely, but a broad and a narrow sense can be distinguished. In its broad sense, social facilitation is the increase in frequency of a pre-existing activity caused by the presence or actions of another animal. In its narrow sense, it is an increase in the frequency of a particular activity caused by another animal's performing that very activity. The standard example from human behaviour is yawning: the sight of yawning causes other people to yawn.

Social influences on animal behaviour are multifarious, but not all such influences involve social facilitation. Social facilitation is an increase in the frequency of an activity; decreased frequency would be attributed to social interference. Social facilitation refers only to activities that are already established in the animal's behavioural repertoire. If an animal produces a novel act after seeing another animal do it, this would be a case of imitative learning, not of social facilitation.

Social facilitation has been documented for many kinds of behaviour. For example, in gulls, rates of visual and auditory displays, preening and copulation are all increased by the presence of other gulls doing the same. An example of social facilitation in the broad sense is the increase in male display rates that often occur in the presence of a female. M.R.



Snipe *Gallinago gallinago* feeding together. (*Photo: F. Pölking*).

FAECAL SAC: a white jelly-like 'envelope' in which the FAECES of the nestlings of nidicolous birds are enclosed. It is easily removed from the nest by the parents, thus promoting efficient nest sanitation. (See PARENTAL CARE).

FAECES: see ALIMENTARY SYSTEM; DROPPINGS; for nest sanitation see PARENTAL CARE.

FAILED BREEDER: a bird which nests but does not manage to fledge young.

FAIRY: substantive name of *Heliothryx* spp. (for family see HUMMINGBIRD).

Fairy-bluebird *Irena puella*. (*C.E.T.K.*).

FAIRY-BLUEBIRD: substantive name of the 2 species of the genus *Irena*, family Irenidae (Passeriformes, suborder Oscines).

Characteristics. Wholly arboreal passerines, 25–30 cm long, weighing approximately 60–80 g, with relatively small toes, short, thick tarsi, a moderately heavy beak with slightly curved culmen, finely notched tip and covered nostrils, and wings and tail of moderate length. The tail of some subspecies of *Irena puella* is overlaid almost to its tip by full upper and lower coverts. Fairy-bluebirds resemble leafbirds (Chloropseidae) and bulbuls (Pycnonotidae) in profusely shedding feathers when handled.

From the crown to the upper tail-coverts, exclusive of the back of *I. cyanogaster*, adult males are a brilliant, enamel-like ultramarine to turquoise or cobalt blue, this colour extending ventrally over the lower tail-coverts. Elsewhere they are velvety black or, in most forms of *cyanogaster*, deep blue. Females of this species differ only in being duller while those of *I. puella* are more or less uniform dull verditer blue. Immatures resemble females but lack the conspicuous carmine-red iris of adults.

Plumage and other external features have variously placed fairy-bluebirds near or with the bulbuls, leafbirds, drongos (Dicruridae) and cuckoo-shrikes (Campephagidae), and on osteological grounds they have been proposed as a subfamily of the Oriolidae. Their egg-white proteins support an affiliation with this general assemblage of passerine families but have provided no independent clue to a nearest relative. Ecologically, fairy-bluebirds most resemble leafbirds and the more frugivorous bulbuls.

Distribution. They comprise one of two bird families endemic to the Oriental biogeographical region, *I. puella* being distributed from the wetter parts of the Indian subcontinent, formerly also Sri Lanka, through South-east Asia to the Andamans, Nicobars and the larger islands of the Sunda Shelf, including Palawan. *I. cyanogaster* occurs allopatrically over most of the rest of the Philippines.

Habitat. Although occasionally tempted by a fruit supply into nearby disturbed habitats, fairy-bluebirds are normally found only in tall semi-deciduous or evergreen forest, ranging at times to an altitude of 2,000 m though they may not breed in montane biotopes.

Movements and food. *I. puella* is everywhere at least locally nomadic, dispersing over the forest canopy in search of suitable fruiting trees, although unlike some other Oriental forest frugivores it has not been recorded moving at night. Fruit, especially figs, forms the bulk of the diet and is taken mainly, but not exclusively, at canopy level. Certain tree flowers are regularly probed for nectar and fairy-bluebirds also take arthropods.

Behaviour. Typically, fairy-bluebirds disperse and forage in pairs or small, loose parties, which may show some temporary cohesion in their comings and goings at a fruit-source. In areas of extensive forest a mass fruiting may attract considerable numbers but such gatherings are short-lived only. No true flock movements or communal roosting behaviour have been recorded.

Voice. *I. puella* has various loud, liquid, incisive calls: *wait, wait-wait, wi-it, whi-tu*, uttered mainly while perched, and a sharp flight call *chichichichik*, repeated every few seconds.

Breeding. *I. puella* builds, usually several metres up, in the forks of saplings and subcanopy trees. The nest is a rough platform of long, often thick twigs capped by a layer of rootlets and green bryophytes in which is formed the open cup. The 2 eggs (occasionally 3 in India) are greenish white to olive-grey or buff to reddish grey, with irregular streaks of brown, grey and purplish coalescing into a cap over the broad end. Only the female has been recorded building, incubating and brooding. Both parents feed the young. D.R.W.

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FALCATED: sickle-shaped, as in some of the scapular feathers.

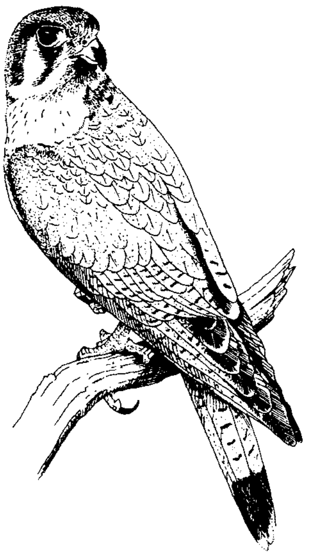
FALCON: substantive name of many species of the Falconidae (Falconiformes); in the plural, general term for *Falco* spp.—or, more loosely, for the whole family. Similar to the Accipitridae (see HAWK), with sharp curved talons and hooked bills, and remarkable powers of sight and flight; they differ, however, in details of skeletal structure, sequence of moult of primaries, and chemical composition of eggshells. As in other birds-of-prey, the females are larger than the males. The family contains about 60 species, divided among 4 subfamilies.

Forest Falcons. The Micrasturinae contains 5 species in the genus *Micrastur*, restricted to the New World tropics. Sometimes known as harrier-hawks, these birds are in general appearance between a harrier *Circus* sp. and a Goshawk *Accipiter gentilis* (see HAWK)—long-tailed, long-legged, and with a partial facial ruff. They were formerly placed close to the Circinae by some authors on that account, but are in fact primitive falcons which have become adapted for life in dense forests, where they prey largely on birds. Little is known of their habits. (The term 'harrier-hawk' is also applied to the subfamily Polyboroidinae of the Accipitridae—see HAWK).

Laughing Falcon. The Herpetotherinae contains one species, *Herpetotheres cachinnans*, which is falcon-like in appearance, dark above with white underparts and a striking white crown set off by a black mask. It inhabits forests in tropical America, where the birds sit on the tops of trees overlooking open ground and make their presence known by their loud calls. They nest in cavities in trees, but have been little studied.

Caracaras. The Daptriinae, comprising about 9 species in the genera *Milvago*, *Phalcobaenus*, *Daptrius*, and *Polyborus*, is a New World (mainly Neotropical) group of large (buzzard-sized) long-legged birds that look quite unlike falcons. They inhabit open country, forest or savanna, and are insectivorous or omnivorous, with a strong taste for carrion. Caracaras are very common in parts of Central and South America, and are in general rather sluggish birds, spending much of their time perched, or walking about on the ground; but they can run swiftly. They associate with vultures (Cathartidae) at carrion and sometimes force these and also other caracaras to disgorge in the same way as skuas will rob gulls. Unlike the true falcons, caracaras build their own nests; they lay 2–3 eggs, but otherwise little is known of their breeding habits. One species, the Guadeloupe Caracara *Polyborus lutosus*, has become extinct within historical times.

True Falcons. The subfamily Falconinae comprises the genera *Spiziapteryx* (one species, Argentina), *Polihierax* (2 species, Africa and south-east Asia), *Microhierax* (6 species, tropical Asia), and *Falco* (37 species, all continents). The first 3 genera are all very small falconets and pygmy falcons, the smallest of all the birds-of-prey and restricted to the tropics of Old and New Worlds. The Philippine Falconet *Microhierax erythrogonys* is only 15 cm long, black above and white below, and hunts insects from the tops of trees in the manner of a flycatcher (Muscicapinae); it breeds in old holes of woodpeckers (Picidae). The African Pygmy Falcon *Polihierax semitorquatus* is likewise very small, but within its limits it is a bold and dashing little predator, capable of killing small birds as well as the large insects which form the major part of its food. It breeds in the huge communal nests of Sociable Weavers *Philetairus socius* in South Africa, and in East Africa in the thorny nests of buffalo-weavers *Bubalornis* and *Dinemellia* spp. The Sociable Weavers do not object to the presence of the little falcon, which does not molest its hosts.



Red-headed Falcon *Falco chicquera*. (*K.J.W.*).

The genus *Falco*, containing the small to medium-sized typical falcons, is the largest genus in the Falconiformes. It can be conveniently divided into a number of adaptive types on physical characteristics and general habits. The falcons are found throughout the world, mainly in open or fairly open habitats.

The large true falcons are stocky, powerful birds of exceptionally swift flight, the wings being pointed and the tail relatively short. They are among the most accomplished fliers of all birds, and habitually kill their prey, principally birds, in full flight, either striking them dead by a blow or seizing them in the foot and coming to ground with them. Owing to the speed of their attack they rarely kill on the ground. Although they chiefly eat birds they will occasionally take mammals, and are fond of flying insects, such as termites or locusts, when available.

The largest of all falcons, the Gyrfalcon *Falco rusticolus* (length 50–60 cm), is a magnificent species inhabiting Arctic America and Eurasia and feeding largely on ptarmigan *Lagopus* sp. One of its colour forms is almost pure white, with a few black spots, but more commonly it is grey and white. The Peregrine Falcon *F. peregrinus* (length 36–48 cm), which typifies the larger falcons, is one of the world's most spectacular birds. Cosmopolitan in distribution, with 17 races, it is a perfect performer in the air, capable of feats of speed and precision flying scarcely to be equalled by any other bird. It is par excellence the falconer's choice, and has been used in all countries where the pursuit is followed (see FALCONRY). In most of its range it was much reduced in numbers during the 1950s and 1960s by DDT and other organochlorine pesticides (see EGG-SHELL THINNING; TOXIC CHEMICALS). Peregrines breed on tall buildings in towns in several countries, possibly attracted by the large numbers of domestic pigeons found there, but the habit has never become widespread. Other large falcons of the same general type are the Lanner *F. biarmicus* of Mediterranean countries and Africa, the Laggar *F. jugger* of India, the Saker *F. cherrug* of eastern Europe and central Asia, the Prairie Falcon *F. mexicanus* (closely related to the Lanner) of western North America. Most of these have been used for falconry to a greater or lesser extent. The Taita Falcon *F. fasciinucha*, a rare inhabitant of Africa, is probably close to the peregrine group although only half the size of a Peregrine. All these species nest solitarily, usually with 2 km or more between pairs.

The hobbies are a group of small (length 28–36 cm), long-winged, exceedingly swift falcons which live largely upon insects but can take some small birds, including swifts, in flight. They catch almost all their prey on the wing. They occur all over the world, and include *Falco subbuteo* of Europe, *F. severus* of India, *F. longipennis* of Australia, *F. cuvieri* of Africa, and *F. albigularis* and *F. femoralis* of South America. Eleonora's Falcon *F. eleonorae* (length 36–40 cm) and the Sooty Falcon *F. concolor* (length 33–36 cm) are conveniently placed close to hobbies. *F. eleonorae* is a very localized bird, breeding in loose colonies in late summer on certain Mediterranean and other islands, preying on the migrant streams of passerines on southward passage at that time, and thereafter migrating to Madagascar. *F. concolor* inhabits the North African deserts, and preys on birds and bats, as does *F. albigularis*.

The Merlin *F. columbarius* (length 25–30 cm) is a Holarctic species, inhabiting forest bogs, open moorland and grassland and preying on small birds caught on the wing; it is migratory throughout its range, moving mainly to temperate regions for the winter. With it may be placed *F. chicquera*, a dashing little falcon inhabiting Africa and India, also feeding on birds, and commonly associated (in Africa at any rate) with the Borassus Palm *Borassus flabellifer*. Both these falcons are solitary while breeding. They can be trained for falconry, but will not kill anything larger than a small dove.

The Grey Kestrel *F. ardosiaceus* and Dickinson's Kestrel *F. dickinsoni* of tropical Africa and *F. zoniventris* of Madagascar form another group. They are not true kestrels, having some of the habits of kestrels but being more like merlins in other respects. They kill a good deal of their prey on the ground, and eat small mammals, lizards, and insects as well as birds; they sometimes hover, but can fly very swiftly also. The Grey Kestrel has the strange habit of appropriating the huge domed nests of the Hamerkop *Scopus umbretta* in which to breed, ejecting the rightful owner. Dickinson's Kestrel breeds in the hollow tops of dead palm trees.

The Red-footed Falcons *F. vespertinus vespertinus* and *F.v. amurensis* are small (length 29–31 cm), migrant, insectivorous falcons of striking colouring, with red feet and (in the males) black and grey plumage set off with chestnut under-tail coverts. They are highly gregarious both on migration and when breeding, roosting in hundreds together in selected trees, and breeding in colonies in the nests of Rooks *Corvus frugilegus* after the Rooks have flown (*F. v. vespertinus*). In winter they migrate from central Europe and Asia to southern Africa. They are commonly to be found feeding on swarms of flying termites. The Lesser Kestrel *F. naumanni* (length 29–32 cm), although very like the Kestrel *F. tinnunculus* in plumage, is perhaps best placed with these two, being insectivorous and gregarious on migration and breeding in colonies on cliffs and buildings.

The kestrels are a large group of small falcons, cosmopolitan in distribution, and having the habit of hovering with gently fanning wings to assist in finding their prey, which is largely small mammals and insects taken on the ground or in long grass. They rarely take birds in flight and are typified by *F. tinnunculus* (length 32–35 cm), which has numerous races occurring all over Europe, Asia and Africa, and is closely related to *F. sparverius* (length 19–21 cm) of America. Other kestrels, *F. moluccensis*, *F. newtoni*, *F. araea*, and *F. punctatus*, inhabit islands in the Pacific and Indian Oceans; *F. punctatus*, inhabiting Mauritius but reduced to less than 5 pairs, is the rarest of all falcons. *F. cenchroides* is the Australasian representative, and to complete the group there are 2 rather larger species in Africa—the Fox Kestrel *F. alopex* and the Greater Kestrel *F. rupicoloides*, which are like other kestrels in many of their habits but seldom if ever hover; they eat small mammals, reptiles, and insects caught on the ground. Many of the kestrels are strongly gregarious when on migration, but breed apart and well separated. In all kestrels the plumage is mainly chestnut and grey in the male, with black spots, and in the female pale reddish-brown with black streaks and bars.

Falco berigora of Australia, known as the Brown Hawk and formerly placed in a separate genus '*Ieracidia*', is one of the commonest birds-of-prey on that continent, having many of the habits of kestrels but being much larger and generally darker in colour. It does not hover, but catches most of its prey on the ground (insects, lizards, and small mammals), and is both gregarious and migratory.

In their breeding habits members of the genus *Falco* vary greatly, but none of them build their own nests, although they may improve an existing structure. They either breed in a scrape on a rock crag, which may be resorted to year after year, or they appropriate the old nest (and sometimes the occupied nest) of some other bird, such as a large eagle or a buzzard or one of the crows. Some species use tree cavities. Their eggs are all very handsome, being generally buffish in ground colour, thickly speckled with dark red-brown, sometimes so as to obscure the ground colour completely; they are fairly round. Clutches are usually 2–3 in hobbies, 3–6 in other small falcons and 3–5 in large species; eggs are laid at 2–3 day intervals. Incubation periods range from 25–32 days in small species to 32–35 days in large ones; nestling periods from 25–32 days in small species to 40–49 days in large ones; and post-fledging dependency periods from 2–3 weeks in small species to 2 months in large ones. In all falcons while breeding, the male provides most of the food and the female does most of the incubation and tending the young.

As expected in such spectacular fliers, most displays take place in the air, though others are centred on nest-sites. Vocalizations are heard mainly in the breeding season, and consist of screams or chattering notes. Many species protest loudly when the nest is visited. (L.H.B.) I.N.

See photos COMFORT BEHAVIOUR; FLIGHT.

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FALCONET: substantive name of some small species of Falconinae (see FALCON).

FALCONIDAE: see FALCONIFORMES; FALCON.

FALCONIFORMES: an order, comprising the sole family Falconidae (see FALCON; CARACARA). In Wetmore's system treated as one of 4 families in the suborder Falcones in the order Falconiformes *sensu lato* (see ACCIPITRIFORMES), but anatomical features and probably isolated, radiating development of South American members considered as primitive, have led to raising the family to ordinal rank.

FALCONRY: also known as hawking, the use of trained birds of prey for taking wild quarry. It originated in the Far East, possibly as long as 4,000 years ago although the first indisputable written evidence is from Japan in 244 AD, and spread to Europe with the Germanic tribes. Falconry was widely practised in Britain before the Norman Conquest, and the Bayeux Tapestry depiction of soldiers carrying hawks is thought to symbolize a readiness for recreation or peace. There is a long and continuing Islamic tradition of falconry, with an injection of eastern techniques to Europe being noticeable immediately following the Crusades. Falconry flourished during the Middle Ages, being practised by people in all walks of life, although painting and literature have often associated it with the aristocracy who sponsored these arts. With the development of firearms, the enactment of land reforms and the evolution of a town-based industrial society, falconry declined throughout Europe. It was maintained during the 19th century by a handful of enthusiasts, with a succession of small British clubs playing a vital role. Increased leisure time and interest in birds of prey since about 1950 have produced a renaissance in western falconry, including its establishment throughout North America. There are now several hundred active falconers in Britain alone, mostly members of either the British Falconers' Club or the Welsh Hawking Club. Falconry clubs throughout the world combine to form the International Association for Falconry and Conservation of Birds of Prey.

Birds used. The birds most commonly trained are hawks (*Accipiter*), known to falconers as 'short-wings', falcons (*Falco*) called 'long-wings', and buzzards (*Buteo*) or eagles (*Aquila*, *Hieraaetus* and *Spitzaetus*) which are sometimes grouped as 'broad-wings'. The word 'falcon' is often applied only to the female Peregrine *Falco peregrinus*, while Gyr Falcon *F. rusticolus*, Saker *F. cherrug*, Lanner *F. biarmicus*, Merlin *F. columbarius* and Sparrowhawk *Accipter nisus* are used for the females of those species, whose males are the jerkin, sakret, lanneret, jack-merlin and musket respectively. The word 'tiercel', originally meaning the male Peregrine, but now also used for the male of many other species, is thought to derive from the male being about a third smaller than the female, although it may also have been believed that males came from the third egg in a clutch. Falconers often prefer to fly females, which are better able than males to subdue the largest prey.

Until the 1970s, all falconers' birds were obtained from the wild, birds taken from the nest being known as 'eyasses' to distinguish them from birds trapped as 'passagers' or 'passage-hawks' in first year plumage or as adult 'haggards'. After a moult in falconers' hands the birds are 'intermewed'. An 'intermewed eyass goshawk tiercel' would be a male Goshawk *Accipiter gentilis* of more than one year old which had been obtained as a nestling. Eyasses are usually taken when about to fledge, and then kept loose in a large shed without sight of man until their feathers are 'hard penned'. Otherwise, some birds start to scream at their handler for food, an irritating type of 'imprinting' which may continue through the bird's life. Eyass falcons are sometimes flown 'at hack', to practise their flying skills by fledging, from an isolated 'hack house' at which food is provided and where they can later be trapped for training. Similarly, trained birds may later be 'hacked back' to the wild, and the technique is also used for re-introductions in areas where wild stocks have been eliminated by persecution or pollution.

In the 1960s, as severe population declines became apparent among Peregrines and small accipiters in Europe and North America, many falconers turned to importing falcons and hawks from Asia and Africa, where birds of prey had been less affected by organochlorine or heavy metal contamination. Because these supplies often became commercialized, and some dealers sought to profit by robbing protected populations, many countries eventually prohibited or severely restricted exports. Other falconers had responded to the disappearance of favoured species by starting projects to breed them in enclosures, and restrictions on supplies of non-threatened species later encouraged further effort in this direction. Peregrines had first been bred by a German falconer, Renz Waller, in 1941, but there was no successful postwar domestic breeding of this species until 1970. By the end of the 1970s, falconers working alone or in research institutes had bred at least 12 species of falcons, 6 of broadwings and 3 of accipiters. About 200 Peregrines were being produced annually, and in several western countries there were more of some falcon species being bred domestically than were being allocated under licence from the wild.

Basic equipment. Extending 10–20 cm from each leg of a falconer's bird is a strap-like 'jess', usually made of strong yet supple leather, with a slit in the free end for joining both jesses via a metal swivel to a leather or nylon leash. A jess may be one continuous piece of leather round the leg, or be threaded through an eyelet in a much shorter anklet. The anklet system is called 'Aylmeri', after a forestry officer who promoted its use in Britain, but is eastern in origin. Since a bird with Aylmeri can be flown free wearing slit-less 'field-jesses', or the anklets alone, instead of the longer 'one-piece' jesses whose slits may snag on vegetation, Aylmeri jesses are now replacing the others. Traditionally, the only other equipment on a bird in the field is a small but amazingly loud bell, of beaten brass or other resonant alloy, attached to each leg by a leather 'bewit' or mounted on the tail. Bells help to locate birds which are out of sight in the field, and by their sound alone a falconer can tell much about the wearer's behaviour at any time. A tiny radio transmitter fixed to a leg or to the tail is a more modern location aid.

When not being flown, birds are often put to 'weather' outside, with the 1–2 m leash linked to the jesses and fastened at its other end, with a one-handed 'falconers' knot', to a running line or suitable fixed perch. The outside perch for falcons is a 'block', typically 20–40 cm high and shaped like an inverted cone in the west, but more mushroom-like as used by eastern falconers. Shortwings and broadwings are most commonly given a 'bow-perch', like a stout and very convex bow with its ends embedded in the ground. A shallow bath is provided, and large birds kept permanently outside have a shelter against inclement weather.

Inside quarters are called a 'mews', in which the bird may be secured to a 'screen-perch'. This is a 1–1.5 m high long, horizontal perch, with material stretched vertically beneath to help the bird regain its position if it 'bates' off the perch. Blocks and bow perches are often used inside too, and many falconers leave their birds loose in the mews to choose between different perch types.

Right-handed western falconers have a leather gauntlet on their left hand for carrying a bird, thus keeping the more versatile hand free. Eastern falconers tend to carry on a padded sheath, known as 'dastri' or 'maukala', round the right wrist. Other falconry accessories are for IMPING to mend broken feathers, for 'coping' overlong beaks and talons, for medical treatment of parasitic or other infections, for vitamin or mineral supplementation of the diet, and for weighing the bird to determine its feeding regime. Those who fly falcons use a light leather hood to protect a bird from sights which might frighten it, or to discourage attempts to leave the fist too early in the field. A hooded falcon will settle quietly as if asleep. 'Austringers', who fly hawks, use hoods less often.

Training. In the first stage, known as 'manning', a falconer must initially gain the bird's trust and then get it used to other people, animals, machines and strange places. The bird is gradually exposed to each new phenomenon while feeding on the fist. The second stage, 'calling off', is of encouraging the bird to fly increasingly long distances to the falconer. A light line, the 'creance', is attached to the bird's swivel in the early stages. Training is done at feeding times, which may be arranged a little later each day to ensure that a bird is 'sharp set'. The trainee must not be brought into low condition by under-feeding, which could lower its resistance to disease.

Falcons are introduced to the 'lure', a leather bag decked with feathers of an intended quarry and with a reward of food attached. Once off the creance, falcons are taught to 'stoop' at the lure, which is swung on a short line, to provide exercise and to call them back from a distance when hunting. Hawks and broadwings may be called to a lure pulled along the ground, but are usually expected to return direct to the fist.

Flying at quarry. Perhaps the most spectacular flights are those of falcons at game. 'When game hawking, i.e. flying at grouse or partridges, a wide-ranging setter or pointer is put down. When game is found, the falconer, having removed her leash, swivel and hood, puts his falcon in the air. She flies in a spiral, ringing until she has gained her pitch over the dog. The higher she mounts the better. There she will wait on until the falconer serves her by putting up the game, down wind, under her. On sighting the rising game she will stoop at it and either bind to it in mid-air or put it in to covert, over which she will make her point and wait on once more until the falconer can put out the quarry to her again. Having taken the quarry she will be allowed to plume it quietly, that is to pluck or even break into it, before the falconer makes in to her and takes her gently on fist again. There, sitting on his glove, she will assuredly be rewarded with a titbit before being hooded up and replaced on the cadge, a light wooden framework used to take falcons into the field. Not all flights are successful however. She may fly at check at other quarry, i.e. rake away after, say, a distant pigeon. Then must the falconer, his best foot foremost, follow her and endeavour to take her down with his lure.' (A.G. O'Carroll Scott).

Thrilling flights are also to be seen when two falcons are flown together, as a 'cast', and stoop alternately at a particularly wily prey, or when a Rook *Corvus frugilegus*, for instance, tries to outfly a falcon by 'ringing' up into the sky. 'Waiting-on' flights are uncommon in the east, where falcons are flown at game straight from the fist, and this style is usual in the west too for some quarry. In the east, large falcons are flown mainly at bustard and hares, whereas western falconers concentrate on partridge, grouse, pheasant and duck, sometimes also pursuing Rooks and crows. In Britain Merlins have traditionally been flown at Skylarks *Alauda arvensis*.

Flying falcons requires wide open spaces, in which prey seek safety in flight rather than by diving into the nearest cover, and over which wide-ranging flights can be kept in view. Accipiters, on the other hand, have the high acceleration and agile turning suitable for flights off the fist in more wooded country, where prey may often seek to hide or out-manoeuvre the hawk in the vegetation. Such flights tend to be short, but well-trained birds may accept long 'slips' at distant prey. If unsuccessful, the hawk can be called back to the fist, but may also be encouraged to follow overhead from tree to tree. Using these techniques, Goshawks are flown at pheasant, partridge, duck, rabbits, hares and other natural prey. Sparrowhawks have traditionally been flown at sparrows *Passer* and Blackbirds *Turdus merula*, or quail in the east.

Broadwings (buzzards and eagles) may be flown at similar prey and can sometimes be trained to wait on. The tribesmen of Central Asia still fly Golden Eagles *Aquila chrysaetos* at wolves from horseback. Unlike the sister art of fishing with cormorants, trained birds of prey do not carry their quarry back to the falconer, but must be 'taken up' from the kill. The bird may then be flown again, but it is unusual for more than two or three kills to be made in a day.

Conservation aspects. Falconry has a long tradition of studying and protecting birds of prey. Emperor Frederick II, who wrote the 13th century falconry treatise *De Arte Venandi cum Avibus*, has been called the father of modern ornithology. There were medieval laws to protect birds of prey in the name of falconry, and for most of the last two centuries falconers were considered eccentric in their desire to preserve these predators. Falconers such as the American Craighead brothers and Dr Heinz Brüll of Germany provided the first modern books on raptor ecology, and falconer-vets have ensured that raptor diseases are better understood than for any other group of wild birds. By release and inadvertent loss of birds falconry has re-introduced the Goshawk to Britain, and the development of domestic breeding with release techniques provides an insurance against extinction for endangered birds of prey. On the negative side, illegal procurement of birds for falconry increased human pressure on some populations which had been reduced by pollution. Falconry is recognized by law in many modern states, including the United Kingdom. It is to be hoped that the recent tightening of controls on obtaining or possessing birds, through national legislation and the international Washington Convention on Trade in Endangered Species, will prevent further irresponsible activities and preserve the beneficial aspects of this ancient art.

(A.G.O'C.S.) R.E.K.

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FALCUNCULINAE: see PACHYCEPHALIDAE; THICKHEAD.

FALL: a sudden arrival of large numbers of birds at a certain point, usually coastal. Falls may occur when migration is interrupted by the rapid onset of adverse weather, such as gales or fog (see MIGRATION).

FALSE PREENING: see DISPLACEMENT ACTIVITY.

FAMILY: a primary taxonomic category (or a particular example thereof), being a subdivision of an order and a grouping of genera. Secondary categories may be interpolated between these levels when considered necessary—suborder and superfamily as higher divisions of the order, subfamily and tribe as subordinate groupings of genera (see TAXON). Although the category was not used by Linnaeus (whose genera were very wide), it has become one of the most important. It is a level at which the taxonomist demands a high degree of probability that the taxon is monophyletic; though less so and with a less amount of certainty than in that of the genus. It is also one at which he expects to find gaps between the taxon and its neighbours, sufficient in magnitude to make each of them plainly distinctive; the gaps may have originated through either the reaching of different ecological levels or the extermination of intermediate forms. The grouping of families in higher taxa tends to become progressively even more speculative; the subdivision of a family into subordinate taxa (above species level) comes more and more to depend on points of minute detail.

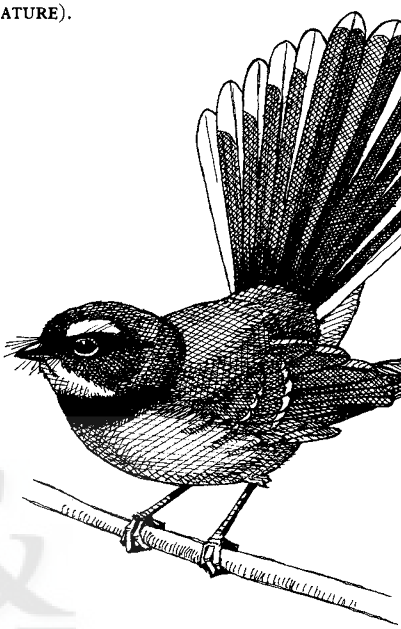
There are, of course, exceptions. On the one hand there are groups of rather similar families—so little different that some authors regard them as subfamilies of a single family, and that at least ordinal relationship is indisputable. On the other hand, there are families—as at the moment recognized—that include such diverse elements as to raise doubt about their monophyletic character; these groupings can be considered as no more than provisional, pending further evidence. And again, there are families that fail of distinctiveness because they are linked to others by species of apparently intermediate character; in this event, the present tendency is to reduce the families to subfamilial level, where a certain lack of distinctiveness can be more readily accepted. The whole question of familial status and interfamilial relationships is particularly difficult in respect of the passerine birds (see PASSERIFORMES), particularly the so-called Nine-primaried Oscines including the families of finches (Fringillidae), Hawaiian Honeycreepers (Drepanididae), American Warblers (Parulidae), Bananaquits (Coerebidae), Tanagers (Thraupidae), American Sparrows, Buntings and Cardinals (Emberizidae), American Orioles (Icteridae).

Subfamily and Tribe; Superfamily. Secondary categories that are sometimes interpolated between family and genus are subfamily and tribe. These may be useful where the genera within the family are sufficiently diverse and appear to fall into groups. The criteria of degrees of difference are necessarily subjective; so what one author may regard as a number of separate families, another may treat as subfamilies, or even tribes, of a single family. The tribal category is regarded as superfluous by some authors (e.g. Wetmore 1960), but it may help on occasion in breaking up a large family showing relatively little diversity. If the cladistic method of classification is strictly followed, however, a number of interpolated taxa may be obligatory (see CLADISTICS).

The names of superfamilies end in '-oidea', those of families in '-idae' (the 'i' is short), those of subfamilies in '-inae', and those of tribes in '-ini'. In all cases the stem of the name is taken from the name of the type genus. Each of the 3 higher taxa has a subordinate 'nominate' taxon at the next level below, with the same type genus and a name identical except for the termination. The names of nominate subfamilies and tribes are not used as separate entry words in this work, as they derive obviously from the name of the higher taxon.

A.L.T.

FAMILY GROUP: with reference to the ranks of taxa, term embracing those taxa that are based on, and are co-ordinate with, the family (see NOMENCLATURE).



Grey Fantail *Rhipidura fuliginosa*. (*N.W.C.*).

FANTAIL: substantive name for a passerine group (suborder Oscines) of unsettled limits and relationships, regarded by Beecher (1973) and Boles (1979) as no more than distinctive MONARCH FLYCATCHERS, but here given familial status as Rhipiduridae. Though yet to be rigorously investigated and defined anatomically, the fantails, like the monarchs, are already known to differ from the true flycatchers (see FLYCATCHER (1)) in lacking both the 'turdine thumb' on the syrinx (Ames 1975) and 'process D' of the carpometarcarpus (Harrison 1969).

The nucleus of the group is the Indo-Pacific genus *Rhipidura*, of some 39 spp. Associated with this have been *Chelidorhynx* (1 species, India and SE Asia, sometimes regarded as congeneric) and *Culicicapa* (2 species, India, SE Asia, Philippines, Sulawesi; Parker 1964). The African genera *Erythrocercus* and *Elminia*, currently listed in the Monarchidae appear similar to the fantails, as do 3 of the 5 species of the African '*Trochocercus*' (Hall and Moreau 1970).

Characteristics. *Rhipidura*: small to medium songbirds, 14–20 cm, with long, rounded, fan-shaped tails (more than half of total length) and moderately broad bills, the gape armed with rictal bristles; most species also have relatively short tarsi and small feet (not so in the atypical partly terrestrial Willie Wagtail *R. leucophrys*, see Harrison 1976). Plumage generally lacking in bright colours, predominant tones being greys, browns, white, rufous and black; a few species with strong bluish tones, e.g. Blue Fantail *R. superciliaris* (cf. the fan-tailed African monarchines *Elminia* and '*Trochocercus*' spp.); some species are strikingly patterned, e.g. the Black-and-Cinnamon Fantail *R. nigrocinnamomea*, and the black-and-white Willie Wagtail and Cockerell's Fantail *R. cockerelli*. *Chelidorhynx* is similar to *Rhipidura* but much smaller (8 cm) and bright yellow beneath, mainly greyish olive above. *Culicicapa* (9 cm) also has much yellow in the plumage, but the tail squared and of moderate length. There is little or no sexual dimorphism in the family. The young are unspotted but feathers of the upperparts, especially the wing-coverts, may be tipped cinnamon to buff.

Habitat. Forests, woods and thickets, including primary rain-forest, second-growth, mangroves, sclerophyll woodland, gardens; usually within or not far from the cover of canopy or dense shrubbery, though some species more frequently venture into the open than others, the

Willie Wagtail actually favouring open ground in the vicinity of trees and bushes.

Movements. As with many other groups, there is a tendency for populations breeding furthest from the Equator to be the least sedentary. For instance, at least some of the Tasmanian and south-eastern Australian populations of the Grey Fantail *R. fuliginosa*, and all the south-eastern Australian populations of the Rufous Fantail *R. rufifrons*, move north in autumn and winter. In addition, some high-altitude breeders may descend to lower altitudes in winter, e.g. Himalayan populations of the Grey-headed Flycatcher *Culicicapa ceylonensis*.

Food. Chiefly small insects, including termites, dragonflies, bugs (including lerps), beetles, flies, moths and their caterpillars, bees, wasps and ants; also spiders; emphasis on small winged insects. In addition, the Willie Wagtail has been recorded taking worms.

Behaviour. Fantails occur chiefly singly or in pairs, also in family groups; many species also form mixed feeding parties. The method of hunting, characteristic of many species, is to flit actively from branch to branch with tail fanned and wings drooped, fluttering against the foliage to dislodge insects (Harrison 1976) and sallying out to snap up prey in mid-air; in addition, the versatile Indian White-browed Fantail *R. aureola* has been recorded working up tree-trunks and boughs, flushing insects from crevices in the bark (cf. the monarch *Arses*), and attending and perching on grazing livestock, snapping up the tiny insects disturbed by the animals; the Willie Wagtail habitually indulges in this last practice. Some species are less active, perching more and fanning the tail less, e.g. the Dusky Fantail *R. tenebrosa* and Cockerell's Fantail, both of the Solomons, and the Northern Fantail *R. rufiventris* of Australia, New Guinea, Solomons and Indonesia. The African 'monarchines' *Erythrocercus*, *Elminia* and the 3 bluish '*Trochocercus*' spp. also hunt actively and fan the tail like the more typical *Rhipidura* spp. (Chapin 1953). *Culicicapa* hunts like a fantail, but tends to spread its shorter, squared tail less. As in the monarchs, some species of *Rhipidura* are reported to hold larger prey under the foot and eat it piecemeal.

Possible courtship display has been noted in *Culicicapa ceylonensis*, the presumed male flying continuously in a rough circle in front of a second, perched bird, which flew out to it once each circuit, there being at least 15–20 circuits in all (Lister *in* Ali and Ripley 1972). Agonistic display is common in the aggressive and strongly territorial Willie Wagtail, in which rival males expand their white eyebrows, submission being signalled by the defeated bird relaxing its feathers to hide the eyebrow completely.

Voice. Calls are simple chips, clucks and grating notes. The song is typically a weak, high-pitched but melodious phrase consisting of short clear whistles, and climbing and tumbling strophes of shorter notes. A few species have atypically loud forceful songs, e.g. Willie Wagtail.

Breeding. Fantail nests are deep cups compactly made of mosses, bark, fine grasses and lichens, the exterior plastered with spiderweb, some species of *Rhipidura* appending a 'tail' of nest-material to the bottom. The nest is placed in a fork (usually more or less horizontal) or on a horizontal branch; the Willie Wagtail will also build on man-made bases such as clothes-lines. The clutch-size is 2–4; in *Rhipidura* and *Culicicapa* the eggs have a pale or rich cream ground, with markings of brownish and greyish spots and blotches concentrated in a ring around the larger end or equator (eggs of the African *Elminia* and bluish '*Trochocercus*' spp. are similar to this); in *Chelidorhynx*, however, the eggs are cream or pinkish cream with pinkish-brown stippling that tends to form a solid cap at the larger end. In *Rhipidura* spp., the incubation period is 12–14 days, nestling period 13–15 days; the scanty information available indicates that both sexes build, incubate and care for the young. In *Culicicapa* nothing appears to be recorded save that the female alone builds the nest. S.A.P.

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FAP: see FIXED ACTION PATTERN.

FASCIA: a sheath of connective tissue.

FASTING: see FEEDING HABITS; PENGUIN; TORPIDITY.

FAT DEPOSITION: see METABOLISM; MIGRATION.

FAULT BAR: see PLUMAGE, ABNORMAL.

FAUNA: the total animal life of an area, the vegetable life being the 'flora' and the two together being sometimes known as the 'biota'; the 'avifauna' is the part of the fauna consisting of birds. Faunistic studies are those that deal with the occurrence, prevalence, and distribution of the different forms of birds or other animals in particular geographical areas (see DISTRIBUTION, GEOGRAPHICAL).

FAUNAL REGION: see DISTRIBUTION, GEOGRAPHICAL.

FAUNISTICS: the study of faunas, especially their composition, origin and history, and their relationships one with another.

FEAR: see BEHAVIOUR, DEVELOPMENT OF; PANIC; TAMENESS.

FEATHER: the component unit of the plumage and a structure outstandingly and uniquely characteristic of birds as a class (see also PLUMAGE; MOULT).

Development. The surface of the body of any vertebrate animal is covered by a skin, a highly organized structure consisting of two separate parts (see SKIN): a thick underlying dermis with muscles, blood vessels, and nerves in it, and an overlying epidermis. The epidermis consists, in the adult, of many layers of cells the deepest of which may be distinguished as a single layer of active cells lying upon a basement membrane which is firmly attached to the dermis. Each cell of this layer at intervals divides into two, and the products of these divisions lie, as a rule but not always, one outside the other. The cell remaining in the basal layer divides again, and so also may the one pushed outwards. In this way the products of these divisions generally find themselves progressively farther and farther from the underlying dermis and therefore from their only source of nourishment and of oxygen. Thus they die off. As the cells die they become filled with a horny substance called KERATIN. A feather is simply an astonishingly elaborate and specialized product of the epidermis of a bird, and it is made of practically nothing but keratin.

At about the fifth day of incubation the embryo of a fowl may be seen to have rows of pimples, in well-marked patterns, on its surface. Each pimple is a consequence of an increase in the rate at which epidermal cells are multiplying at that particular site. The dermis here also proliferates and there is thus a finger of dermis pushed out, covered by a thimble of epidermis, as is shown in Fig. 1. This is a feather germ. (See also DEVELOPMENT, EMBRYONIC).

Further localized growth now serves to push this feather germ down into a deepening depression. While this is happening, the feather germ continues to lengthen greatly, so that, instead of a pimple on the surface of the embryo, there is now a pit with a long cylinder projecting out of the mouth of a follicle (Fig. 2). The cylinder slopes backwards, so that obverse ('dorsal') and reverse ('ventral') sides can be distinguished.

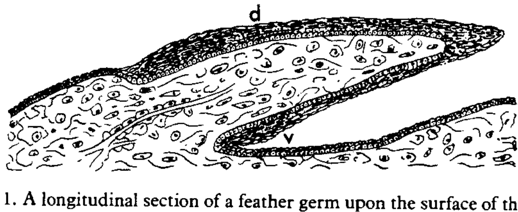

Fig. 1. A longitudinal section of a feather germ upon the surface of the skin of a developing chick (*Gallus*) at about 10 days incubation. A thimble of epidermis can be seen to enclose a finger of dermis. (*P.G. 'Espinasse*).
d. dorsal (obverse); v. ventral (reverse).

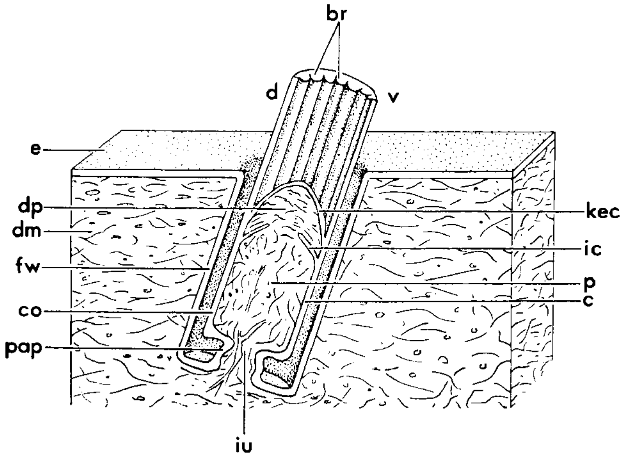

Fig. 2. A diagrammatic representation of a block cut from the skin of a bird during its development. The plane of the section nearest the observer cuts a developing feather in half longitudinally. The half of the feather remaining in the block is alone shown. The barb-ridges on the near aspect of the cylinder can be clearly distinguished. (*P.G. 'Espinasse*).
br. barb-ridges; **c.** calamus or quill; **co.** collar; **d.** dorsal; **dm.** dermis; **dp.** dead pulp; **e.** epidermis; **fw.** follicle wall; **ic.** incipient cap; **iu.** inferior umbilicus; **kec.** keratinised epidermal cap; **p.** pulp; **pap.** papilla; **v.** ventral.

A 'napkin-ring' of epidermis towards the lower end of the cylinder is distinguished and named the 'collar'. Beneath this again is the persistent papilla. It is within the collar that nearly all the growth leading to the production of a feather takes place. By this growth, which in an adult bird may continue at a high rate for weeks, the cylinder of epidermis is lengthened. Within the cylinder is the dermal pulp with nerves and blood vessels, which supply the nutrients.

The cells forming the outside of the cylinder, when they keratinize, are joined together to constitute a resistant sheath. This sheath is destined later to split and to be lost, so freeing everything it had been holding together.

The inner aspect of the lengthening cylinder becomes longitudinally pleated or ridged (Fig. 2). These ridges contain the developing barbs. Within the substance of the barb-ridges many cells fall away individually and take no part in the structure of the finished feather, but some become firmly joined to each other and form the rami of the barbs. Other cells become joined in columns, each column sloping downwards towards its barb, to which proximally it becomes firmly fixed. Two series of such columns are differentiated in each barb-ridge, and these columns of single cells will be the barbules when they have become fully keratinized.

In the developing contour feather the barb-ridges each take a half-spiral course. Each pair of barb-ridges is initiated ventrally, and one of them proceeds, as the cylinder lengthens, to be differentiated downwards and around the cylinder towards the dorsum on one side of the cylinder while its mate goes round the other side. The two fail to meet dorsally, and the strip down the cylinder dorsally thus left intact is the site of the developing rachis (Fig. 3).

Contour feathers. Different types of feathers can be recognized, of which the contour feather quantitatively is the most important and probably the fundamental type (see ARCHAEOPTERYX).

Contour feathers consist of a shaft on each side of which a long series of sidebranches (barbs) are attached (Fig. 4). A barb consists of a ramus which bears two rows of sidebranches, the barbules. The part of the shaft which bears the barbs is the rachis and it consists of an outer layer of solid cells (the cortex) and a core of air-filled cells (the medulla, pith). The lower part of the shaft, without attaching barbs, is known as the calamus. This is a hollow cylinder, the lower part of which sticks into the feather follicle. At both ends there is an opening, the inferior and superior umbilicus. The ramus also consists of cortex and medulla, while the barbules are solid.

A barbule is divided into a lamella-shaped base and a pennulum. The latter is usually as long as the base, tapers, and ends as the pointed tip of the barbule. In some cases the pennulum is thread-like and much longer than the base. Those barbules attaching to the side of the ramus closest to the feather tip are termed distal, those on the other side proximal. Two neighbouring barbs are locked together when the hooklets present on the distal barbules catch upon the obverse edges of the proximal barbules (Fig. 5). This interlocking system, together with the fact that rami and barbules all lie in the same plane, is what characterizes the pennaceous feather structure, of which the continuous-looking vanes (vexillum) of a typical contour feather, e.g. a flight feather, are constructed. The vanes are light, strong and almost air-tight and represent the basic structure enabling birds to fly.

In addition to this, the pennaceous part of a contour feather, a smaller or larger plumulaceous (downy) part is also present basally (Fig. 4).

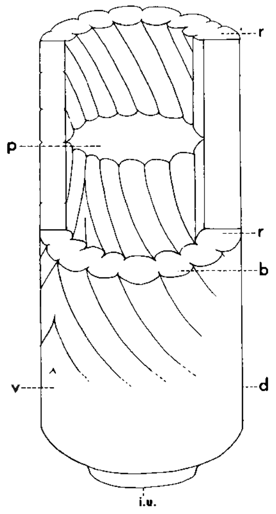

Fig. 3. A perspective view of a model of a developing feather. The barb-ridges instead of running straight up and down as in the first down feather can be seen in this to follow a half spiral course, so that each barb-ridge runs into a developing rachis dorsally, thus giving the form of a normal feather. (*P.G. 'Espinasse. Reproduced by permission of the Zoological Society of London*).
b. barb-ridge; **d.** dorsal; **iu.** inferior umbilicus; **p.** pulp; **r.** rachis; **v.** ventral.

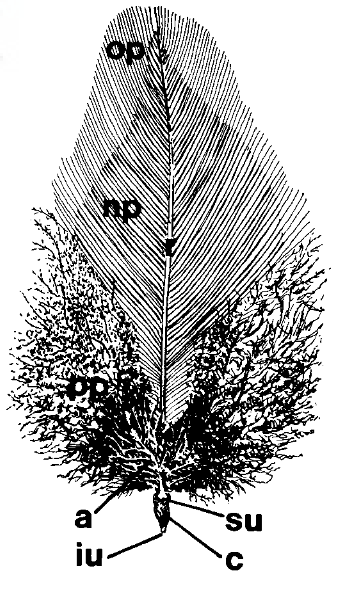

Fig. 4. Main parts of a typical contour feather, exemplified by a feather from the middle of the dorsal tract of a Single Comb White Leghorn Chicken. (*B. Beyerholm. Redrawn from Lucas & Stettenheim*).
a. afterfeather; **c.** calamus; **iu.** inferior umbilicus; **np.** normal pennaceous portion of feather vane; **op.** open pennaceous portion; **pp.** plumulaceous portion; **r.** rachis; **su.** superior umbilicus.

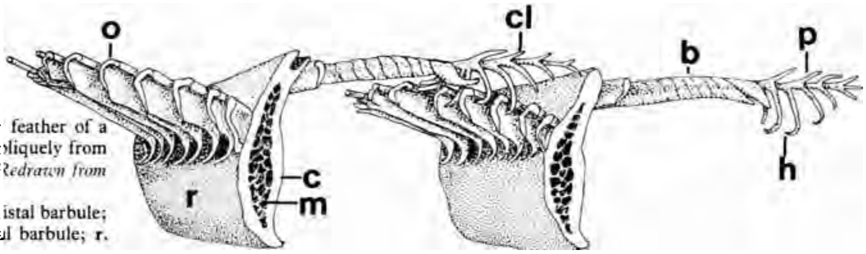

Fig. 5. Segments of two pennaceous barbs from a contour feather of a Single Comb White Leghorn Chicken. The barbs are seen obliquely from the distal end to show interlocking of parts. (*B. Beyerholm. Redrawn from Lucas & Stettenheim*).
b. base of distal barbule; **c.** cortex; **cl.** cilium; **h.** hooklet of distal barbule; **o.** obverse edge of proximal barbule; **p.** pennulum of distal barbule; **r.** ramus.

The variation in contour feathers is almost endless. The upper tail coverts of the Peacock *Pavo cristatus* are exceptional, not only because of the 'eyes' but also because of their shape and length (*c.* 1.5 m). The central tail feathers of the Great Argus Pheasant *Argusianus argus* measure *c.* 1.2 m and the longest primaries in larger vultures may measure 0.7–0.8 m.

The smallest contour feathers are found on the eyelids. In the smallest bird species, the hummingbird *Calypte helenae*, they measure *c.* 0.4 mm, but even in the domestic hen they are only *c.* 1 mm long.

Contour feathers of bizarre shape are e.g. the elongated primaries of some nightjars (Caprimulgidae) (Rutschke 1965) and the very long flag-bearing head feathers of the King of Saxony Bird-of-Paradise *Pteridophora alberti* (Lüdicke 1969).

Many modifications of feathers are related to colour. In most feathers the ramus is laterally compressed, usually pear-shaped in cross-section, and of the lamella-shaped barbules little more than the edges are visible. Where the feathers are structurally coloured, this normal situation may be markedly changed (see photos).

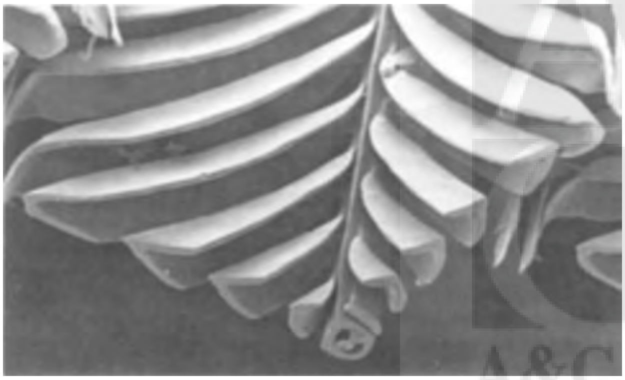

Photo (a). In iridescent feathers the barbules, which contain the colour-producing structure, are enlarged and their upper parts expanded. Together the barbule cells form an almost mirror-like surface which is responsible for the brilliancy of the structural colour. Scanning electron microscopical picture of a small part of a green feather of a hummingbird *Chlorestes notatus*.

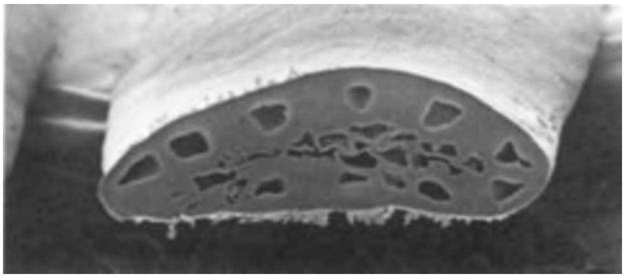

Photo (b). Where the colour-producing structure resides in the ramus, the barbules may be absent altogether, and the ramus is much expanded laterally. The ramus has been cut crosswise, so that the interior of the cells can be seen. The cells appear solid, but do in fact contain minute air-filled cavities which are of importance for the production of the turquoise colour. The large holes (one per cell) are formed when the cells dry up during feather formation. The irregular holes in the centre are medullary cells, which are empty except for some melanin granules. Scanning electron microscopical picture of a single ramus of a turquoise small wing covert of *Pitta sordida novaeguineae*. (*Photos: Jan Dyck & Bent Rasmussen*)

Down. Down feathers have a loose, fluffy texture, instead of the firm, closely-knit texture characteristic of contour feathers. This is in particular due to the structure of the barbules, which are more or less circular in cross-section, so that they may bend in all directions. Where two adjoining barbule cells meet there are usually some, e.g. 4, short projections (prongs). Some prongs of one barbule may become entangled with some spines on another nearby barbule. When this happens in several places a stabilized three-dimensional network is formed, which is the basic feature of the downy structure and the one which gives it its insulative properties.

The rami of down feathers are more flexible than those of contour feathers and they are sometimes branched; factors which also contribute to the down's fluffy structure. Natal down is mostly more simply built than the down of later plumages. A shaft is usually lacking so that the barbs are attached to the upper rim of the calamus (Fig. 6), the barb tips lack barbules and the barbules are shorter than in adult down.

The microscopic structure of down barbules varies considerably in different groups of birds, probably more so than that of pennaceous barbules. This variation may be used for the identification of feather remains.

Semiplumes. Down feathers, whether with a shaft or not, are usually short compared to contour feathers. But some feathers are long like contour feathers and have a downy structure throughout. They are termed semiplumes and are defined as downy feathers in which the longest barb is shorter than the shaft. There is a continuous intergradation between down, semiplumes and contour feathers, with a larger or smaller downy portion.

Powder down. These are feathers which produce a fine powder. In e.g. pigeons the powder grains are derived from cells that surround the future barbules in a growing feather. In other birds, e.g. herons (Ardeidae), parts of the feathers themselves also disintegrate to produce powder. At its most specialized, the powder feather consists of little more than barbules, attached by strips to the calamus, and clogged with powder. Possibly they grow continuously. The particles have an irregular shape, are colourless and *c.* 1 μm (1/1,000 mm) in diameter.

Bristles. These are best described as contour feathers which lack barbs in their distal portion, so that the shaft becomes the dominating feature. In an extreme case, e.g. the rictal bristles of the Band-winged Nightjar *Caprimulgus longirostris*, the bristle consists of nothing but shaft and calamus. The shaft tapers distally to a fine point, and this portion of the shaft in nearly all bristles is dark brown or black (Stettenheim 1974). It is probable that the melanin pigment responsible for the colour enhances the stiffness and hardness of the tip.

The bristles of passerines are mostly 2–8 mm long, with the longest ones on the rictus. A feather type intermediate between contour feather and bristle is the semibristle.

Filoplumes. These constitute the most aberrant feather type. If a domestic pigeon is plucked, the filoplumes will remain and can be observed as very thin and hair-like structures. Filoplumes are always situated beside other feathers, never by themselves. They may be as long as their host feather, but are much more simply built.

A filoplume consists of a calamus, a long, thin shaft and, at the tip, a short tuft of barbs (sometimes a few barbs are present also lower down on the shaft).

It has been suggested that filoplumes are degenerate structures without function, but it is now considered probable that their function is as sensors of the movements of the larger feathers. If the position of a primary is changed by the wind, the primary may displace the tips of some of its filoplumes, which in turn transmit the displacement to their

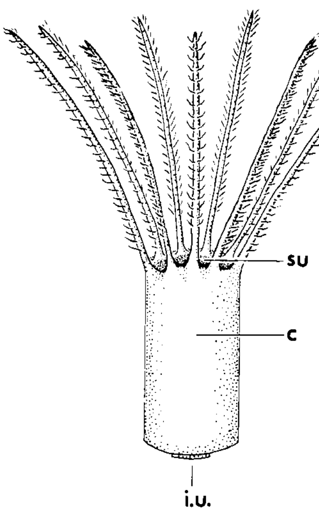

Fig. 6. The first product of a feather germ, a natal down. There is no rachis, and the barbs with small barbules stick up around the top edge of the calamus. (*P.G. 'Espinasse*)
c. calamus or quill; **iu.** inferior umbilicus; **su.** superior umbilicus.

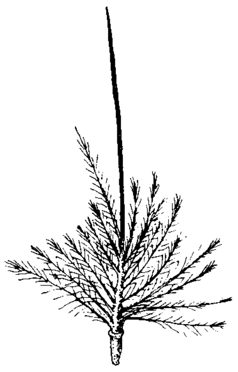

Fig. 7. (*left*) Bristle from the upper eyelid (eyelash) of European Starling *Sturnus vulgaris*. (*B. Beyerholm. Redrawn from Lucas & Stettenheim*).

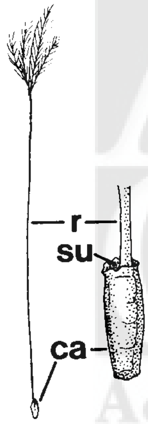

Fig. 8. (*right*) Filoplume. To the right the lower part of the shaft at higher magnification. (*B. Beyerholm. Redrawn from Lucas & Stettenheim*).
ca. calamus; **r.** rachis; **su.** superior umbilicus.

bases where nerve endings register it. Such a function is supported by the fact that the shaft of a filoplume is thicker at the tip than at the base and that remiges and rectrices usually have more filoplumes (8–12) than have body feathers, which make simpler movements.

Feather muscles. Feathers can be elevated, depressed or rotated by feather muscles (*musculi pennati*). These are unstriated (see MUSCULATURE) and are attached to the outer surface of the feather follicle wall by elastic tendons. In many regions feather muscles join together neighbouring follicles so that regular patterns of feather muscles arise.

See photos DISPLAY; LEK. (P.G.'E.) J.D.

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FEATHER-EATING: see under GREBE.

FEATHER LOUSE: see ECTOPARASITE.

FEATHER MAINTENANCE: see COMFORT BEHAVIOUR.

FEATHER MITE: see ECTOPARASITE.

FEATHERS, HUMAN USE OF: see ORNAMENTATION, BIRDS IN HUMAN; UTILIZATION BY MAN.

FEATHERS, NUMBER OF: although the numbers of typical contour feathers, plumulaceous TELEOPTILES and true down feathers on adult individuals of various bird species have been determined, virtually nothing is known about the number of filoplumes which are present. The total number of NEOSSOPTILES on newly-hatched passerine nestlings has also received attention. However, since passerine neossoptiles may (at least in some species) be degenerating structures without any embryonic or postnatal functions, this account is restricted to the plumage of adult birds. (See also FEATHER; PLUMAGE; PTERYLOSIS.)

Feather counts. In general, large birds have more feathers than small birds but this correlation with body size is by no means absolute. Feather counts published by different workers are not all directly comparable, since the totals given by some authors are for contour feathers only. The lowest number of contour feathers recorded to date is 940 for a Ruby-throated Hummingbird *Archilochus colubris*; and the highest is 25,216 for a Whistling Swan *Cygnus columbianus*. Eighty per cent of the feathers were found on the head and neck of the swan. Examples of feather counts for single specimens of other species are: Pied-billed Grebe *Podilymbus podiceps*—15,016; Green-winged Teal *Anas crecca*—11,450; Clapper Rail *Rallus longirostris*—7,224; American Coot *Fulica americana*—13,913; Least Sandpiper *Calidris minutilla*—4,480; Bald Eagle *Haliaetus leucocephalus*—7,182; Barred Owl *Strix varia*—9,206; Common Nighthawk *Chordeiles minor*—3,332; Red-bellied Woodpecker *Melanerpes carolinus*—3,665; Yellow-fronted Tinker Barbet *Pogoniulus chrysoconus*—2,210; Laughing Dove *Streptopelia senegalensis*—4,207; Brown-headed Cowbird *Molothrus ater*—4,297; Blue Jay *Cyanocitta cristata*—3,773; Eastern Meadowlark *Sturnella magna*—4,607; Green White-eye *Zosterops pallidus*—3,307. What limited information there is on distribution of feathers on the body suggests that in a land bird approximately one third are on the head. Future feather counts should record numbers of feathers by pterylae. This might contribute to better understanding of the function of feathers.

Individual variation. No marked differences in feather numbers occur between individuals of the same species and sex living in the same area at the same season; nor has significant sexual variation in numbers yet been recorded. However, in the species examined to date, there have not been marked differences in plumage complexity or body size between male and female, for which differing feather totals might be expected.

Seasonal variation. No thorough investigation of the total number of feathers comprising the plumage of individuals of a species at different seasons has yet been undertaken. Contour feather counts made on birds of the same species at different times of the year in the United States at Ann Arbor, Michigan and at Washington D.C., respectively, revealed a definite seasonal variation in the number of feathers present, more being found on a bird during the winter, when protection against cold would be required, than during the summer. For example, a loss from winter to summer of 11.5% of the total number of contour feathers was recorded for the House Sparrow *Passer domesticus* and the figures showed a progressive seasonal change. The gradual loss of feathers during the breeding season could be an adaptation for thinning of the bird's insulating layer in warm weather.

A small series of Laughing Doves from Pretoria, South Africa, was examined but no seasonal variation in feather number was detected. Further research is needed in order to determine whether the feathers of various species living in an equable climate remain relatively more constant in number all the year round than do the feathers of those birds inhabiting regions with marked seasonal changes in temperature.

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FEATHER TRACT: see PTERYLOSIS.

Herring Gulls *Larus argentatus* scavenging dogfish. (*Photo: J.B. & S. Bottomley*).

FEEDING HABITS: behaviour exhibited in obtaining or utilizing food (see also FOOD SELECTION). Few species of birds are so much specialists as to be limited to one prey or to show a distribution coincident with that of a single food item; the Everglade or Snail Kite *Rostrhamus sociabilis* lives entirely on gastropods of the genus *Pomacea*, and the distribution of the Limpkin *Aramus guarauna* in the south-eastern United States is coincident with that of the same molluscs. The breeding haunts of the Slender-billed Nutcracker *Nucifraga c. caryocatactes* are largely defined by the occurrence of the 'cedar' *Pinus cembra* (see FOOD STORING). Some species are, in parts of their range, so dependent upon one out of many possible foods that the lack of that prey may inhibit breeding or compel migration; this is the case with the Snowy Owl *Nyctea scandiaca* and the Long-tailed Skua *Stercorarius longicauda* in lemming (*Lemmus*) areas. But many groups—notably the crows and the gulls—can only be described as omnivorous, perhaps having preferences but able to subsist upon a remarkable variety of foods. In some species there is a marked change in diet with age—Partridges *Perdix perdix* and other seed-eaters are almost entirely insectivorous when young, though the adult birds are largely vegetarian. In the estrildid finch *Poephila guttata* the two sexes have been shown to have different food preferences; in the Sparrowhawk *Accipiter nisus* the females kill larger preys than do the more lightly built males; and in the extinct Huia *Heteralocha acutirostris* the marked difference in bill structure was correlated with a difference between the feeding habits of male and female (see BILL; WATTLEBIRDS (2)).

The feeding habits of any species may be divided into two components—the general dietary and hunting methods of the genus, family or order and the characteristic specific habits or preferences that give at all times a measure of ecological isolation by ethological means, and enable more than one closely related species to live within a single habitat (see ECOLOGY). The tits, with varied preferences for hunting at different heights, in different trees and in different parts of those trees, provide a notable example of specific distinctions within a genus. These ethological isolating mechanisms have not necessarily any anatomical basis; there is nothing structural to indicate that the Song Thrush *Turdus philomelos* has the innate capacity to crack open the shells of snails and that the Blackbird *Turdus merula* has not.

Methods of obtaining food. Birds have exploited all that grows or moves upon the surface of the earth or in the upper layers of its waters. The fossorial habit is the only feeding method not represented among birds, although the snow burrows of arctic grouse might be cited as an exception to this statement. Many short-billed species, notably among the Galliformes, will delve a little below the surface of the ground, with bill or feet or both, to obtain prey; longer-billed birds, notably among the Charadrii, probe in earth or sand or mud. The Starling *Sturnus vulgaris* thrusts the closed beak into the turf and then opens the mandibles, peering into the cavity so formed. Fallen leaves, moss and litter are tossed aside by many birds to reveal hidden morsels, and between tide-marks the Turnstone *Arenaria interpres* lives up to its name.

Common Sandpiper *Actitis hypoleucos* extracting ragworm *Nereis diversicolor*. (*Photo: J.B. & S. Bottomley*).

Growing herbage and the leaves of trees are cropped by some pigeons, gallinaceous birds (Galliformes) and geese (*Anser* etc.), and a parrot, the Kakapo *Strigops habroptilus*, is said to 'graze like a rabbit'; but in general birds depend more upon fruits, nuts and seeds—and in hummingbirds and sunbirds, so far as they may be regarded as vegetarian, upon nectar—than upon foliage. The kernels of armoured fruiting bodies are reached by bills adapted for crushing (Hawfinches *Coccothraustes coccothraustes*) or shearing (macaws Psittacinae) or by the crossed tips of the highly specialized bills of Crossbills *Loxia* spp., which first fray and then probe between the scales of fir-cones. The large, light bills of toucans enable these relatively heavy birds to pluck fruits without performing gymnastic feats or taking wing.

Just as stout or arched bills usually bespeak an herbivorous habit, long and light bills can generally be correlated with a diet wherein arthropods, annelids and other invertebrates predominate. The wide, lamellate bills of flamingos and of some surface-feeding ducks provide filter-feeding mechanisms for very minute food particles.

In the owls and the diurnal birds of prey (Falconiformes and Accipitriformes) the taloned feet are used to seize and often to kill the prey; if the formidable grip or lacerating impact be not sufficient to give the coup-de-grâce, the beak comes into action, usually attacking the base of the victim's skull. The long-winged falcons (Falconidae) rely upon speed

Broad-tailed Hummingbird *Selasphorus platycercus* male about to visit flower. Note protruding tongue. (*Photo: L. Rue Jr.*).

to secure their prey; the owls, harriers (Circinae) and round-winged hawks (Accipitrinae) depend more upon surprise. The eagles (also Accipitrinae) show a great variety of hunting methods, but usually capture their prey upon the ground. The falcons, which strike their prey in mid-air, will often kill birds larger than themselves; but in general the birds of prey, with their relatively fragile wing feathers, do not risk the rough and tumble with large victims that is so often undertaken by hunting mammals. The birds of prey, the tits (Paridae), the crows (Corvidae) and some 'minor raptors' hold their food with the feet while dismembering it; shrikes may hold prey with the feet or rend it after impalement upon a thorn. The parrots and—surprisingly, the Purple Gallinule *Porphyrio porphyrio* use one foot very much as a 'hand' to hold up morsels to be bitten.

The herons and all the fish-eaters with the exceptions of the Osprey *Pandion haliaetus* and the fishing eagles (*Haliaeetus* etc.) use the beak alone to secure their prey; but the Reef Heron *Egretta gularis* will extend a foot to stir a tuft of weed and then stab at the bolting fishes. The Black Heron *Egretta ardesiaca* when fishing converts itself into a 'peripatetic umbrella' by bringing the fully spread wings forward and downwards until the tips of the remiges touch the water; it is suggested that small fish take refuge in the shade, and so are caught.

Turnstone *Arenaria interpres* scavenging mussel *Mytilus*. (*Photo: J.B. & S. Bottomley*).

The shallows of the world's waters are worked by a great variety of methods—wading with beak or head submerged to skim or sieve or snatch, or walking wholly submerged along the bottom, aided by the pressure of the current (and sometimes by the action of the wings) as is the habit of the dippers. The phalaropes and the smaller petrels, swimming or flitting with paddling feet, feed largely upon organisms from the very surface of the sea. Swimming under water with wings or feet may follow a leap clear from the surface, a brisk downward tilt or a submersion so gradual that it can scarcely be described as a 'dive'. Birds that depend upon the impetus of a headlong plunge to carry them below the surface may dive from forward flight, after a hover or from a perch (see SWIMMING AND DIVING). The skimmers fish entirely upon the wing, ploughing the surface with the blade-like lower mandible and snapping down upon any fish that comes in contact with it; skimmers are said to work back over their tracks, seeking preys that have been attracted by the disturbance of the surface at the first passage.

In the air swallows, swifts and nightjars make many successive captures in the course of sustained flight, while the flycatchers (Muscicapinae) hawk from look-out posts for single victims. Both methods of aerial feeding are used by the bee-eaters. The hummingbirds are the outstanding exponents of stationary hovering while feeding, but many species of birds hover with more or less skill to obtain nectar, insects or fruit. Many small insectivores 'glean' their prey from leaves and twigs.

Among the woodpeckers there is a startling variety of diet and habit—sap-feeding of the sapsuckers *Sphyrapicus* spp., the ant-eating (with the aid of a long and mobile tongue) of the ground-feeding species, and the splitting of hard nuts or the demolition of fir-cones by the pied woodpeckers *Dendrocopos* spp. The kingfishers are remarkable for the inclusion of a number of tropical species which live far from water and feed entirely upon insects and other small terrestrial animals. Some food preferences and habits would never be suspected upon anatomical grounds—the aquatic hunting of the dippers, the fondness of the Palm-nut Vulture *Gypohierax angolensis* for the fruit of *Elaeis guineensis*, the berry eating of the Curlew *Numenius arquata* and the liking of the Turnstone *Arenaria interpres* for carrion.

Bewick's Swans *Cygnus columbianus* upending to feed, and Pochards *Aythya ferina*. (*Photo: A. Christiansen*).

Preparation of food. The preparation of prey ranges from bolting the victim whole to a careful plucking (often at some favourite stance) or rejection of some part—the heads of snakes by the Secretary-bird *Sagittarius serpentarius*, the bills of Starlings by Sparrowhawks, the albumen gland of the snail *Helix aspersa* by the Song Thrush and the stings of wasps by shrikes. Slugs are wiped to and fro in grass by thrushes or carried to dusty ground to be cleared of the slime which may be toxic; there is a record of a Mistle Thrush *Turdus viscivorus* treating a hairy caterpillar in the same manner.

Some of the straight-billed scavengers, such as the gulls and storks, depend upon a bird with a hooked beak or a mammalian carnivore to open up a carcass. Food invested in a hard shell is usually opened up by strength of beak, as is the habit of the Oystercatcher *Haematopus ostralegus*, which may also take limpets by surprise. The method of breaking open snails on anvil stones has been evolved at least twice—by the Song Thrush and by a bowerbird *Scenopoeetes dentirostris*. The

Squacco Heron *Ardeola ralloides* about to strike. (*Photo: J.F. Reynolds*).

Daurian Starling *Sturnus sturninus* male feeding on nectar. (*Photo: M.A. Omelko*).

Everglade or Snail Kite extracts the body of *Pomacea* by waiting until the gastropod is partially emerged and then crippling it with a stab of the sharp, slender beak—apparently into a nerve ganglion, showing an innate 'anatomical knowledge' more reminiscent of a hunting wasp than of a bird! That tortoises are dropped by the Lammergeier *Gypaetus barbatus* has been known since classical times, but it has been suggested that the victim may not be so much deliberately dropped as let fall during an effort to prize it open in the air. The dropping of bones (presumably for the marrow) has been confirmed in this species. Gulls and crows drop crustaceans, echinoderms and molluscs to break them open; often it seems a matter of chance whether the prey falls on hard or soft ground. The Pacific Gull *Larus ('Gabianus') pacificus* is credited, however, with carrying gastropods of the genus *Turbo* to selected dropping places.

Blue-cheeked Bee-eater *Merops superciliosus* with dragonfly. (*Photo: A.A. Karavaev*).

The employment of an anvil whereon prey is hammered or dropped may, perhaps, be regarded as the use of a 'tool' as may the wedging of nuts into crevices in bark by the Great Spotted Woodpecker *Dendrocopos major* and the impaling of victims by shrikes. A Grey Heron *Ardea cinerea* which has caught a large eel will quickly carry it some distance back from the water's edge to dispatch it in a place whence escape is difficult. There are two truly remarkable instances of the use of a tool in obtaining food. The Woodpecker Finch *Camarhynchus pallidus* of the Galapagos probes with a thorn into crevices in the bark of trees and thereby evicts insects which are beyond the reach of the somewhat short bill. Egyptian Vultures *Neophron percnopterus* break open the eggs of ostriches by throwing stones at them (see TOOLS, USE OF). Smaller eggs are picked up and dashed on the ground. In both Africa and America the Green-backed Heron *Butorides striatus* has been observed to use a white bait to attract small fishes.

Both corvids and ducks will carry hard food to water to soften it; and the Redshank *Tringa totanus* may carry large, muddy preys to the tide edge to wash them.

Frequency. The frequency of feeding activities range from the almost uninterrupted hunting of small passerines during daylight hours, through the one meal a day of the Red Grouse *Lagopus lagopus scoticus* and the one meal in 48 hours of Great Black-backed Gulls *Larus marinus* during the East Anglian herring fishery, to the fantastic fast two months long by the male Emperor Penguin *Aptenodytes forsteri*. The meal times of birds of prey that can obtain a day's supply in one or two kills often show a clock-like regularity.

American Robin *Turdus migratorius* swallowing mulberry. The seeds will later be dispersed. (*Photo: E.J. Hosking*).

Blackbirds in autumn and Starlings in spring seek earthworms early in the morning and other foods later in the day. Night and day dictate the major rhythm of hunting routine, but in some herons and ducks and many wading birds (Charadriiformes) the ebb and flow of the tide has an important influence on feeding routine. In feeding behaviour two components may be detected—the drive to forage and actual appetite. Hunger may be appeased before the drive to hunt is exhausted: when this happens a bird will capture and at once abandon prey. An unsatisfied foraging drive may be responsible for 'food storing' in many species—Jays *Garrulus glandarius*, woodpeckers, tits and shrikes. Very little is known of the frequency with which hidden food is recovered by many species, but in the Nutcracker the accumulation of stored food is of real biological importance. Nutcrackers rely upon hazel nuts gathered in the autumn for the bulk of their winter food and of supplies for the young in the following spring. The Acorn Woodpecker *Melanerpes formicivorus* drills long series of holes and stores them with acorns. 'Paper tearing. by tits in the autumn is probably an expression of frustrated or misdirected foraging activity as is the placing of a pebble by Acorn Woodpeckers in a hole for which no acorn is available.

Interrelations. The robbing of birds of other species of their prey

Fulmars *Fulmarus glacialis* and gulls *Larus* scavenging at sea. (*Photo: F. Pölking*).

(PIRACY or kleptoparasitism) is the regular custom of the skuas and frigatebirds. Black-headed Gulls *Larus ridibundus* frequently harry Lapwings *Vanellus vanellus* on pasture or plough-land, and on the coast may so persecute Sandwich Terns *Sterna sandvicensis* that the terns are able to fledge no young at all. Most species of birds will at times attempt to rob others of their food. There is an inter-specific order of dominance among the tits, though as between Great Tits *Parus major* and Blue Tits *P. caeruleus* much depends upon the élan of the displacing attack. In the thrushes the Song Thrush is always subordinate to the Blackbird: in one April in Suffolk a group of Song Thrushes lost 9% of their worm harvest to the heavier species.

It has been suggested that in a mixed feeding flock each bird acts unwittingly as a beater for the other members. Parties of members of a single species of pelican, or cormorant, will make concerted fishing movements, hunting strung out in line across a creek or shoal or (pelicans) dipping their heads in unison while swimming in compact formation.

Commensalism is most often practised by the use of some larger species as 'beaters' for the disturbance of insects or other small prey—horses, cattle, large game of many kinds and even railway trains are thus exploited. The Cattle Egret *Bubulcus ibis* is an outstanding example of this behaviour, but there are many other—Robins *Erithacus rubecula* are commensals of wild boars, moles and man. The use of foraging troops of monkeys as 'beaters' has been described for such different birds as hornbills in Africa, drongos in Asia, fairy-bluebirds in the Philippines and trogons in Panama. Off the south coasts of Arabia the driving of 'sardines' into dense shoals by tunny and sharks is the signal for the assembly of a company of screaming terns to swoop and plunge in the turmoil of spray and fish; and all over the world fishing boats are followed by gulls and other snappers-up of unconsidered trifles. Indeed, it has been advanced that the refuse of the fishing and whaling industries has been responsible for the great increase of the Fulmar *Fulmarus glacialis* within the last century. The strange relationship between honeyguides and ratels *Mellivora capensis* or man is symbiotic rather than commensal (see HONEYGUIDE). For the association between some birds and crocodiles, see CROCODILE-BIRD.

Commensalisms between birds are less common than these relations between birds and members of other classes. The most delightful avian example is that of Carmine Bee-eaters *Merops nubicus* riding on the backs of Abdim's Storks *Sphenorhynchus abdimii* and Kori Bustards *Ardeotis kori* and swooping in pursuit of the insects disturbed by their mounts. Chaffinches *Fringilla coelebs* will eat the seeds of crab-apples hacked open by Fieldfares *Turdus pilaris*, and House Sparrows *Passer domesticus* collect the legs deliberately knocked off cockchafers by thrushes.

The only birds to show parasitic feeding habits in the true sense of the words are one of DARWIN'S FINCHES, *Geospiza difficilis*, which, on two Galapagos islands only, take blood from the developing feathers of moulting boobies, and the OXPECKERS *Buphagus* spp., which take blood and perhaps tissue from wounds on large mammals (but feed primarily on the ticks which initially cause some of these sores).

Methods of study. Until comparatively recently the usual and, indeed, almost the only method of studying bird foods was the examination of gut contents. The value of the technique remains as great as ever, but it has been supplemented by other methods that are especially necessary when the rarity of a species forbids the collection of adequate samples; in the Hawaiian Goose or Nene *Branta sandvicensis* for example, much has been learned from the examination of droppings. The examination of pellets has long been of use in the study of hawks and owls, but is of very limited value in the investigation of such birds as herons which have very great powers of digestion (see PELLET). Feathers, fur and bones at plucking places have yielded much data. Of recent years photography has provided valuable results, both qualitative and quantitative. Much can be learned from the direct observation of such easily identified foods as wild fruits, seeds and carrion.

The food of nestling birds has been studied by direct observation from hides; by retrieving samples from the gullets of young birds fitted with collars tight enough to prevent the swallowing of meals; by inducing young herons, cormorants and hawks to disgorge by fright or massage; and by persuading parent birds of hole-nesting species to feed an 'artificial nestling' (see also BEHAVIOUR, DEVELOPMENT OF).

See photo LOCOMOTION, TERRESTRIAL. P.H.T.H.

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FEEDING NICHE: see ECOLOGY; NICHE.

FEEDING OF YOUNG: see GROWTH; PARENTAL CARE.

FEMUR: the 'thigh-bone' (see LEG; SKELETEON, POST-CRANIAL).

FERAL: literally 'wild', but applied only to populations of domesticated species that have reverted to a free existence.

FERAL PIGEON: a bird descended from domestic stock of *Columba livia* but living in a wild state. These birds are common both in towns and in the countryside and may be called 'domestic', 'London' or 'town' pigeons as well as 'feral' pigeons.

FERNBIRD: *Bowdleria punctata* (see WARBLER (1)).

FERN-WREN: the Australian warbler *Oreoscopus gutturalis* (see WARBLER, AUSTRALIAN).

FERTILITY: see HYBRID; ISOLATING MECHANISM.

FERTILIZATION: the union of the male gamete (spermatozoon, or spermatozoid) with the female gamete (ovum), taking place in the upper part of the oviduct following copulation (see COPULATION; DEVELOPMENT, EMBRYONIC; EGG; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

FIBULA: a bone of the leg (see LEG; SKELETON, POST-CRANIAL).

FIELD CHARACTER: a distinctive feature which enables a particular species to be identified in the field.

FIELDFARE: *Turdus pilaris* (see THRUSH).

FIELD GUIDE: see Regional articles.

FIELD-TYRANT: substantive name of the ground-living tyrant-flycatcher *Muscigralla brevicauda* of the arid west coast of South America (see FLYCATCHER (2)).

FIGBIRD: substantive name of *Sphecotheres* spp. (see ORIOLE (1)). See also BECCAFICO.

FIGHTING: see under AGGRESSION; DOMINANCE (2); TERRITORY; also COCK-FIGHTING. See photo AGGRESSION.

FILOPLUME: a type of feather resembling a fine, thin hair (see FEATHER; PLUMAGE).

FILTRATION FEEDING; see FLAMINGO.

FINCH: term used for the family Fringillidae (Passeriformes, suborder Oscines), or more generally for any small seed-eating song-bird, with a stout bill. Thus the word has been applied to at least 11 different groups of birds of varying degrees of affinity, namely the subfamilies Fringillinae (chaffinches and allies), Carduelinae (goldfinches and allies), Emberizinae (buntings), Thraupinae (tanagers), Geospizinae (Galapagos finches), Cardinalinae (cardinal-grosbeaks), Bubalornithinae (buffalo-weavers), Estrildinae (estrildid or weaver-finches), Viduinae (whydahs), Ploceinae (weavers) and Passerinae (sparrows). All these birds have the same specializations for dealing with hard seeds: stout conical bills, strong skulls, large jaw muscles and powerful gizzards. Yet they differ so much in the other details of their anatomy and their behaviour that they are without doubt derived from several ancestral stocks, providing an example of convergent evolution. Many of these groups are now given the rank of family, and are described elsewhere in this book. This article is concerned with only 2 of these subfamilies, the Fringillinae and the Carduelinae, which are usually grouped to form a single family, the Fringillidae. From now on the word finch will be used only for members of this family. They are distinguished from the various other seed-eating birds by certain details of skull structure, the presence of 9 (instead of 10) large primary feathers in each wing, 12 large tail feathers, and the fact that the hen is responsible for building the cup-shaped nest and for incubating the eggs. Some of these features are shared with other groups; it is the combination of characters that distinguishes the Fringillidae. The family contains a variety of species, ranging between 10 and 100 g in weight, some of them richly coloured and, within the limits imposed by a seed diet, showing great variation in the shape of their beaks, according to the types of seed they eat.

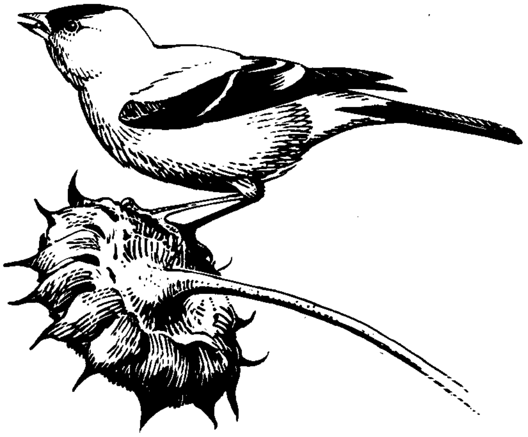
Characteristics. The Fringillinae contains only 3 species, the Chaffinch *Fringilla coelebs* and Brambling *F. montifringilla* of Eurasia, and the Blue Chaffinch *F. teydea* of the Canary Islands. All 3 are of similar shape, about 15 cm long, with fairly long tails, peaked heads, and prominent shoulder patches and wing markings. The Carduelinae contains around 122 species, of which 16 are found in Europe. The smallest ones are about 11 cm long, and the largest about 19 cm; they vary greatly in colour, but generally have prominent wing and tail markings; many species are streaked, especially in juvenile plumage.

Habitat and distribution. Among the Fringillinae, Chaffinches breed in all kinds of woodland, and over much of Europe are one of the most numerous birds, usually comprising between one-fifth and two-fifths of the total woodland bird population. The Brambling replaces the Chaffinch as a breeding bird in the sub-Arctic birchwoods of northern Europe, and also extends across Asia to Kamchatka, migrating south for the winter, and concentrating in areas with beechmast. The Blue Chaffinch is found only on the Canary Islands, and is a rare inhabitant of high altitude pine forests. The Carduelinae are widespread, represented naturally in North and South America, Europe and Africa (except Madagascar) and by introductions in Australasia. These finches occupy a range of habitats from closed forest, through scrubland and savanna, to open tundra, steppe and desert, though no one species is so widespread. In some regions, certain species have successfully colonized man-modified environments, and breed commonly in town parks and gardens, and in farmland. They are thus some of the most familiar birds in western Europe and in eastern North America. Populations of arctic and temperate regions tend to be migratory, and others resident.

Food. The beak of all finches is modified internally for holding and shelling seeds. Each seed is wedged in a special groove at the side of the palate and crushed by raising the lower jaw on to it. The husk is then peeled off with the aid of the tongue and discarded, thus releasing the kernel, which is swallowed. In cardueline finches the bill is also used for extracting seeds from the seed-heads of plants. Species differ in the size of seeds they prefer, and in the types of seed-head they can best exploit, corresponding with differences in the size and shape of their bills, and in the way the bill is used. Hawfinches *Coccothraustes coccothraustes* have big powerful bills for crushing large hard tree-fruits; Goldfinches *Carduelis carduelis* and Siskins *C. spinus* have long tweezer-like bills for probing into thistles and other seed-heads; Bullfinches *Pyrrhula pyrrhula* and Pine Grosbeaks *Pinicola enucleator* have rounded bills adapted for bud eating; while crossbills *Loxia* have crossed mandibles which help them extract seeds from hard closed cones. Moreover, the 4 species of crossbills in

Differences in breeding behaviour between the fringilline and cardueline finches. From Newton 1972.

	Fringillinae	*Carduelinae*
	Chaffinch and Brambling *(Fringilla)*	Goldfinches, siskins, linnets, redpolls, serins, rosefinches and crossbills *(Carduelis, Serinus, Carpodacus, Loxia)*
Food of young	Insects, fed frequently from parent's bill.	Mainly seeds, fed infrequently by regurgitation.
Nesting dispersion	Large territories. Elaborate fighting involving special postures.	Small territories, grouped into colonies.
Food obtained	Within territories, solitarily.	Outside territories, in flocks.
Sequence of behaviour	(1) establishment of territory. (2) pair-formation. (3) selection of nest site.	(1) pair-formation. (2) selection of nest site. (3) establishment of territory.
Type of song	Stereotyped, short, loud and clear.	Less stereotyped, prolonged and less loud.
Sexual behaviour	Inside territory.	Inside and outside territory.
Pair-formation	Sudden, hen attracted by song of cock in territory.	Prolonged, cock approaches hen in flock; courtship involves 'bill-scissoring'.
Courtship feeding	Absent.	Present.
Display flights over breeding area	Absent.	Present.
Incubation	By hen, feeds herself.	By hen, mainly fed by cock.



American Goldfinch *Carduelis tristis*. (*D.A.T.*).

Europe have different sized bills and feed primarily from different cones: the slender-billed Two-barred Crossbill *Loxia leucoptera* eats mainly the small soft cones of larch, the medium-billed Common Crossbill *L. curvirostra* feeds mainly from the medium cones of spruce, and the large heavy-billed Parrot Crossbill *L. pytyopsittacus* and Scottish Crossbill *L. scotica* mainly from large hard cones of pine. The various finches also differ in the proportion of food they obtain directly from vegetation, as opposed to the ground, and in the extent to which they use their feet in feeding, both being connected with differences in body weight and leg structure (Newton 1972). The feet are used mainly to clamp seed-heads to a firm perch, while they are worked with the bill.

Although the main food of all finches is seeds, the Fringillinae feed their young entirely on insects (especially caterpillars), while the Carduelinae feed their young either on a mixture of seeds and insects or on seeds alone. The raising of young entirely on a seed diet is comparatively rare among birds, but has been recorded for crossbills, Siskins, Redpolls *Carduelis flammea* and Linnets *C. cannabina*. Also, while the Fringillinae carry insects to their young one or a few at a time in the bill, the Carduelinae carry large quantities of seeds in their gullets and regurgitate them to the young. Some species have special throat pouches for this purpose.

Behaviour and voice. It is in their dispersion and social behaviour that the fringilline and cardueline finches differ most markedly (Table 1). The fringilline finches defend large territories while breeding, and pairs spread themselves fairly evenly through the habitat. The food is obtained from the territory itself, and the young are fed at frequent intervals (say every 5–10 minutes). The carduelines nest solitarily or in loose colonies, within which each pair defends only a small area around its nest; they forage away from the colonies in flocks, wherever food happens to be abundant at the time. They pack large amounts of seeds into their crop, and feed their young at infrequent intervals (say 20–60 minutes).

Chaffinches are noted for their strong melodious songs, which differ slightly from bird to bird, and form local dialects (Thorpe 1961). These arise because young male Chaffinches, taking a territory in their first spring, learn certain elements in their song from their neighbours. Individuals tend to return to the same territories year after year, so that dialects are perpetuated. Each cock, moreover, may have several slightly different songs in his repertoire, usually 2–3, but occasionally up to 6. This singing serves to attract hens and to repel cocks, and is loud, clear and easy to locate. An unmated cock Chaffinch on territory will sing every 7–15 s for most of the day—or 6 times a minute, 360 times an hour and more than 3,300 times in a 12-h day, feeding between times. Once he has found a mate, a cock sings less often, partly because one of the functions of the song has been fulfilled. Among cardueline finches, the song is generally quieter, but in some extremely melodious; it seems to be used as a form of advertisement, but is not restricted to the nesting territory. Many species have special song flights over the breeding areas.

Breeding. Like other birds, finches breed when their food is most plentiful, but this occurs at a different time in different species, according to what they eat. The Chaffinch, which needs caterpillars, has a short breeding season in late spring; while the cardueline finches, which need seeds, have long and varied seasons, in which individual pairs often raise more than one brood. Thus the Greenfinch *Carduelis chloris*, Linnet and Bullfinch, which in Britain eat a variety of seeds, breed for almost the whole growing season, continually changing their diet as different plants come into seed. The European Goldfinch, which likes the seeds of thistles and related plants, breeds later in summer, while the American Goldfinch *C. tristis*, which depends even more on thistles, breeds later still. The crossbills nest in any month, whenever conifer seeds are most available: in larch forests this is mainly in late summer or early autumn, in spruce forests in autumn to winter, and in pine forests in spring. If spruce and pine are available in the same area, breeding can occur continuously for 10 months.

The female is responsible for building the nest, incubating and brooding the young, and during this period is fed on the nest by the male. When the young are feathered and can keep warm, both parents collect food. All species build open, cup-shaped nests, mostly in trees or shrubs, and lay 3–6 eggs, which in most species are whitish with brown spots. Incubation takes up to 2 weeks, and the young then stay in the nest for another 2 weeks or so (longer in crossbills). Predation on eggs and young is often heavy but, in most areas, more than one brood is raised in a season. The young are born naked, but can fly within a few days after leaving the nest.

Moult. After breeding, adult finches undergo a complete moult, and at the same season the juveniles have a partial moult, replacing only the soft body feathers and retaining the large flight and tail feathers for another year.

Captivity. Because of their song, bright colours, engaging habits and simple seed diet, finches have for centuries been kept in cages as pets. Some species breed readily in captivity, and from the wild Serin *Serinus canarias* of the Canary Islands all the various strains of domestic Canary were derived. Certain finches are also important as pests, especially the Bullfinch which eats buds of fruit trees, sometimes devastating orchards and causing a major problem to the industry.

See CAGE BIRD and photos COURTSHIP FEEDING; NEST BUILDING.

I.N.

Newton, I. 1972. Finches. London.
Thorpe, W.H. 1961. Bird-song. Cambridge.

FINCH-LARK: substantive name of *Eremopterix* spp. (see LARK).

FINCH, PLUSH-CAPPED: *Catamblyrhynchus diadema*, a species that some authors place in a family of its own, the Catamblyrhynchidae (Passeriformes, suborder Oscines), and others treat as belonging to the Thraupinae (see TANAGER). The allocation is in either event provisional, as not enough is known about the relationships of this peculiar bird. It is found in the Andes of South America, from Venezuela to Bolivia, where it is apparently resident in the humid upper subtropical and temperate zones. It is a finch-like bird *c.* 15 cm long, mostly dark grey above, with black markings on the head, and reddish below. The forepart of the crown carries golden-brown feathers that are erect and stiff to the touch, like plush. The Plush-capped Finch is rarely found far from bamboos, and is apparently specialized for foraging on bamboos; it clings to and works along the stalks actively, adopting tit-like positions, foraging by probing into the axils of leaf whorls. Both insects and vegetable matter are taken. It is possible that the plush-like feathers of the fore-crown are adapted to this method of foraging, being less subject to abrasion, and perhaps also to soaking, than ordinary plumage. The species is usually seen accompanying mixed feeding parties, and its nesting biology is undescribed.

D.W.S. (1)

Hilty, S.L., Parker, T.A. & Silliman, J. 1979. Observations on Plush-capped Finches in the Andes with a description of the juvenal and immature plumages. Wilson Bull. 91: 145–148.

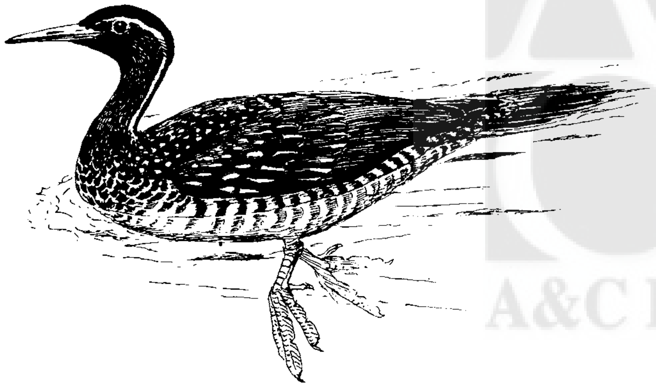
FINCH, SNOW-: substantive name of *Montifringilla* spp. (see SPARROW (1)).

FINCH, WEAVER: see ESTRILDID FINCH.

FINFOOT: (plural ‘finfoots’): name of the 3 species of Heliornithidae (Gruiformes); in the Americas still often called ‘sungrebes’. Confined to the tropics and subtropics, they recall in certain features of their structure, appearance and habits a number of other families of waterfowl, notably the grebes, cormorants, darters, ducks (especially torrent ducks *Merganetta* spp.) and rails (especially coots *Fulica* spp.). Egg-white protein analysis has, however, confirmed the balance of other evidence suggesting they are most nearly allied to the rails.

Among the distinctive anatomical characters of the finfoots are the elongated head and neck, very broadly lobed and brightly coloured toes, and strongly graduated long stiff tail. Of special interest is the possession by all 3 species, though its function has only been observed in the African bird, of a claw on the first digit of each wing. Resembling a fairly large thorn, it is doubtless used to assist the bird to scramble through vegetation in the manner of the HOATZIN. Unlike that species however, finfoots often seem to retain and use the claw when adult, which can perhaps be construed as another sign of their archaic origin.

Characteristics and distribution. The differences between the 3 widely separated species of finfoots are less remarkable than the similarities, indicating that the family is of great antiquity and once had a far wider and more continuous distribution. Smallest and least specialized of the survivors is the American Finfoot *Heliornis fulica*, only about 30 cm in length, and certainly the least known until 1969, when its nest was first found and a breeding population came under study for the next two years. It ranges from southern Mexico to north-eastern Argentina but is probably most common on Guianan rivers. Its predominantly pale olive brown colour is exactly matched in the intermediate-sized Masked Finfoot *Heliopais personata*, *c.* 53 cm in length, which ranges from north-eastern India to Cambodia, peninsular Malaysia and Sumatra. The third and largest species, some 60 cm in length, is the African Finfoot *Podica senegalensis*, which ranges from Senegal to Ethiopia and south to the Cape Province. The brown of its plumage lacks the olive tinge of the other two but in the adult is more or less noticeably washed with peacock green or blue. Suitable habitats within its range are often far apart and climatically distinct, so not surprisingly some 4 races are recognized (mainly on size criteria). All 3 species are sexually dimorphic, the smaller females tending in peak breeding plumage to be more conspicuously marked and brightly coloured.



African Finfoot *Podica senegalensis*. (*C.J.F.C.*).

Due to the difficulties of observation, the function and survival value of several morphological peculiarities of finfoots remain obscure. Thus the stiffer shafts of the tail feathers and a knob on the carpal joint in *Podica* may or may not indicate that it is more prone than the others to scramble through or over thick vegetation. A knife-edged erectile ridge or wattle at the base of the culmen in the male of *Heliopais* presumably has some unknown role in courtship since it disappears at the end of the breeding season. The significance of the 'zebra-striped' toes of *Heliornis*, the pea-green yellow-lobed ones of *Heliopais* and the scarlet of *Podica*'s is quite uncertain, but in the muddy waters which are perhaps most typical in finfoot habitats, display or recognition factors rather than aid to flushing or attracting prey seem likely to be involved.

The finfoot's mastery of its aquatic habitat is shown by its ability to float high in the water or so low that only the head and part of the neck are visible (a feat possibly aided by the absence of the water-repellent flexules at the tip of the breast feathers typical of many waterfowl). But it is also agile on land, preferring when alarmed to bolt into a thicket, body at a 40° angle to the ground, after scuttering coot-like round a bend in the river, rather than take wing, though it can fly swiftly. However, the principal factor in its inconspicuousness is undoubtedly its chosen habitat.

Habitat and food. The habitat is remarkably uniform for all 3 species, despite the great distances separating them. It consists essentially of the margins of perennial waters, large or small, fresh or brackish, placid or, more rarely, fast flowing, provided they are overhung by forest or thick vegetation. In such secluded and inaccessible surroundings single birds, pairs or family parties occupy and defend a length of the relevant bank and adjacent water as their territory, swimming, scuttering or clambering in pursuit of the insects that form the bulk of their food. Well adapted for diving, they have seldom been observed doing so, though fish, unreliably, and more often frogs, crustaceans and molluscs have been noted in stomach contents. Some vegetable matter (leaves and seed), mud and grit are also swallowed.

Movements. Although finfoots generally avoid taking wing, circumstantial evidence suggests that *Heliopais* is at least partly migratory.

Voice. There appear to be some differences in the voices of the 3 species. Although a variety of barking, growling or even booming notes have been recorded, and a soft clucking by birds engaged in nesting activities, *Heliopais* is said to produce a rather high-pitched bubbling, like air being blown through a tube into water. To judge from the recent study of *Heliornis*, it is likely that finfoot calls are mainly associated with agonistic behaviour on the part of males seeking to establish and defend their territories, and with subsequent courtship activities. At other times of year they seem generally very silent, another reason why an unusually interesting family of birds is so often overlooked and still poorly known.

Breeding. The nest, a shallowly indented platform of twigs, 30–40 cm in diameter and lined with leaves, is placed a metre or so above water on a horizontal branch or fallen tree, sometimes on refuse left by floods. Breeding, however, seems more often to coincide with the early part of the rainy season. The eggs, which are remarkably spherical but generally ralline in appearance, are cream-coloured with reddish-brown or purple markings. So far as is known *Heliornis* lays only 2 eggs, *Podica* also lays 2, very rarely 3, but *Heliopais* differs from both by laying 5 eggs, and sometimes as many as 6 or even 7. The incubation periods for *Heliopais* and *Podica* are unknown, except that a nest of *Podica* on the Athi river in Kenya contained 2 eggs which were thought to be on the point of hatching, or even already hatched, 14 days after their discovery. They or the chicks were, however, then taken by a Nile Monitor *Varanus niloticus*. The incubation period for *Heliornis* is only 10–11 days, an exceptionally short period for so large a bird. The naked young chicks are somehow deposited by the male in pockets of skin under his wings. The adjacent flank feathers are fanned to help hold the chick in place though its beak and head can be spotted as the finfoot flies past. This astonishing habit was first reported as long ago as 1830, and was confirmed in the early 1970s. The clutch of only 2 eggs is in keeping with its unique arrangements for transporting the young to safety. H.F.I.E.

Ali, S. & Ripley, S.D. 1969. Handbook of the Birds of India and Pakistan, vol. 2: 28 & 183–185. London.

Alvarez de Toro, M. 1971. On the breeding biology of the American Finfoot in southern Mexico. Living Bird 10: 79–88.

Percy, Lord William, with a note by Pitman, C.R.S. 1963. Further notes on the African Finfoot *Podica senegalensis* (Vieillot). Bull. Brit. Orn. Cl. 83: 127–132.

FIREBACK: substantive name of some *Lophura* spp. (see PHEASANT).

FIRECREST: *Regulus ignicapillus* (see WARBLER (1)).

FIRECROWN: substantive name of *Sephanoides* spp. (for family see HUMMINGBIRD).

FIRE-EYE: substantive name of *Pyriglena* spp. (see ANTBIRD).

FIREFINCH: substantive name of some waxbills *Estrilda* spp. (see ESTRILDID FINCH).

FIRETAIL: name popularly applied to various red-tailed species in different parts of the world; in Australia one of the recognized names for *Zonaeginthus* spp. (for family see ESTRILDID FINCH).

FIREWOOD-GATHERER: *Anumbius annumbi* (see OVENBIRD (1)).

FISCAL: substantive name, alternatively 'fiscal shrike', of some African *Lanius* spp.; used without qualification for *L. collaris* (see SHRIKE).

FISH-HAWK: American name for the Osprey *Pandion haliaetus* (see HAWK).

FISHING: see FEEDING HABITS.

FISSIPALMATE: term applied to a foot that is discontinuously webbed, with lobes or fringes on the separate toes.

FITNESS: a term used in evolutionary contexts, with a range of meanings from general to more specific. It may simply denote how well designed an organism is for its way of life. This is the meaning of 'fitness' in Spencer's phrase 'the survival of the fittest'. More precisely, in recent evolutionary theory fitness of a specified kind of organism (or genotype) is the ratio of the proportion in one generation to the proportion in the previous generation. This is loosely equivalent to the number of offspring left by an individual of the specified kind. Finally, an individual's *inclusive fitness* is its effect on the reproduction of all of its genetic relatives, including its own production of offspring as only one class among many classes of relatives. To calculate the inclusive fitness of an act, the appropriate coefficient of relatedness is needed. This is, for example, half between parents and offspring and between siblings, and a quarter between an organism and its grandchildren. The effect of an act on each class of relatives is multiplied by the individual's coefficient of relatedness to that class, and then the resulting weighted effects are added up to give the inclusive fitness. See also NATURAL SELECTION. M.R.

FIXATION (1): in the nomenclatural sense, a general term for all methods of determining the type species of a genus or subgenus (see TYPE SPECIES).

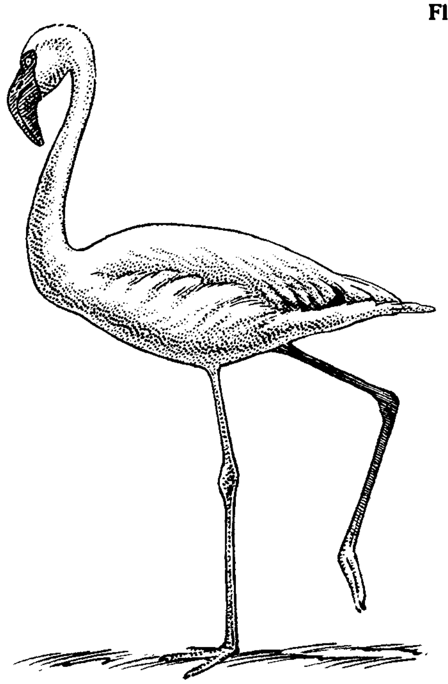
FIXATION (2): in behaviour studies, a term sometimes used to describe an abnormal attachment of one individual to another of a different species, usually caused by conditioning in early life.

FIXED ACTION PATTERN: translation, abbreviated to 'FAP', of the term 'Erbkoordination'; a behaviour pattern which, as defined by Lorenz, (i) is invariant; (ii) is relatively independent of external stimuli once started; (iii) has its own specific motivation revealed in vacuum performances; and (iv) shows specific exhaustion, in that one performance makes an immediately subsequent performance less likely. See BEHAVIOUR, HISTORY OF.

FLAMINGO: substantive name of the species of Phoenicopteridae (Phoenicopteriformes); in the plural (-gos). Here the order is assigned between Ciconiiformes and Anseriformes, but evidence of relationship is contradictory. Flamingos have usually been considered as a suborder of Ciconiiformes. On anatomical evidence they have been supposed to have affinities with the storks (Ciconiidae) and ibises (Threskiornithidae), while work with egg-white proteins appears to place them close to the herons (Ardeidae). On the basis of behaviour and Mallophaga, they have seemed most like the waterfowl (Anseriformes). Recently, affinity with the waders (Charadriiformes) has been stressed, and familial status in the suborder Charadrii next to Recurvirostridae proposed (Olson and Feduccia 1980). This suggestion is based on similarities between flamingos and the Australian Banded Stilt *Cladorhynchus leucocephalus*. A comparative ethological study in the field is required, and new evidence can be expected.

All flamingos are very similar and, although 3 genera are usually recognized, this is not based on widely accepted taxonomic evidence. The 5 species are placed in 2 groups on bill morphology: *Phoenicopterus*, which has a relatively primitive feeding apparatus, and *Phoenicoparrus* (Andean and James') and *Phoeniconaias* (Lesser) which are more specialized. The last 2 genera are separated only by the presence or absence of the hind toe. Possibly a single genus *Phoenicopterus* would suffice; however, the older nomenclature has been retained here. *Phoenicopterus r. ruber* (also called the Caribbean) and *P. r. roseus* (*'antiquorum'*) are usually regarded as races of the Greater Flamingo, while *P. chilensis*, the Chilean Flamingo, is felt to be sufficiently different to have specific status.

Characteristics. Flamingos form a remarkable and ancient group, and are easily recognized. They are large birds (90–180 cm long) with a long sinuous neck, long legs ending in webbed feet, an 'upside-down' bill and rosy pink plumage. Because they may occur in huge numbers they have been called 'the most impressive and colourful of all bird spectacles' (Brown 1973). Flamingos swim and upend with ease and extend the neck and legs in flight. Males are larger than females, but they are almost indistinguishable.



Lesser Flamingo *Phoeniconaias minor*. (*R.G.*).

Habitat. Being specialized ecologically, they are often superabundant in certain habitats and entirely absent from others. They are confined to shallow soda lakes and salt lagoons with a high pH (up to 10.5), usually barren of vegetation and surrounded by almost desert-like wastes.

Distribution. From fossils it is known that flamingos were once widespread in Europe, North America and Australia as well as in areas where they are found today. They are now a relict group occurring in isolated pockets, mainly in the tropics and sometimes at high altitudes.

The very bright pink Caribbean Flamingo *Phoenicopterus r. ruber* numbers about 60,000 and occurs in the West Indies with a small outlying population in the Galapagos Islands. The paler, Old World form of the Greater Flamingo *P.r. roseus* is the largest, weighing on average 3.0 kg; it is more common, at an estimated 790,000, and is the most widespread species, ranging from West Africa to south-east India, and from southern France and Kasakhstan to the Cape Province of South Africa. The Chilean Flamingo *P. chilensis* numbers about 500,000 and is found from central Peru southwards along the Andes to Tierra del Fuego and from sea level to 4,500 m. *Phoenicoparrus andinus*, the Andean Flamingo, differs from the others in having yellow legs. It is restricted to the high Andes, mainly above 2,500 m, from southern Peru to central Chile and northwest Argentina. Its population is estimated at 150,000. James' Flamingo *P. jamesi* has the most restricted range of all, from 15°–26°S in the Andes and mainly above 3,500 m; it is the rarest species, numbering only about 50,000 individuals. The smallest species, at 1.9 kg, is the Lesser Flamingo *Phoeniconaias minor*. It is also the most numerous, with about 2.5 million birds in Africa in the rift valley, Namibia, Botswana, and in Mauretania, and an unknown number breeding in north-west India, probably numbering some tens of thousands.

Movements. Birds breeding at high latitudes or altitudes move to warmer climates in the winter, the young travelling separately from their parents. Other irregular movements, often at night, are thought to be in relation to changes in food supply.

Food. The feeding methods of flamingos are characteristic and peculiar. The bill, which is held upside-down in the water, has 'the lower jaw large and trough-like and the upper small and lid-like' (Jenkin 1951). Jenkin has described the bills of flamingos in detail, and has pointed out that their filter feeding is comparable with that of whale-bone whales (Mysticeti) and otherwise unique among adult vertebrates. *Phoenicopterus* has the upper mandible 'shallow keeled' with only parts of the mouth equipped with filtering lamellae, while in the 'deep keeled' bills of *Phoenicoparrus* and *Phoeniconaias* the lower jaw is deep and swollen and the upper mandible is narrow. In both, the tongue is enlarged and acts as a piston. Water and mud are taken in along the whole gape and expelled, 3 or 4 times a second, past the filtering devices. In the more specialized forms, coarse particles are kept out by stiff excluder lamellae and finer particles, such as algae, are caught. The Caribbean, Greater and Chilean Flamingos feed mainly on invertebrates (brine fly *Ephydra*, shrimps *Antemia*, and molluscs *Cerithium*) from the bottom mud, normally wading in shallow water, more rarely swimming or upending like ducks. They are thus usually found feeding at a shoreline or on mud banks. The smaller Lesser Flamingo feeds on the erratic but occasionally dense blooms of the planktonic blue-green alga *Spirulina* which is rich in protein, and on benthic diatoms. It is a primary user of the lake and spends 60% of the daylight hours extracting its food from the top 6 cm or so, often while swimming. It can therefore coexist with the Greater Flamingos, and does so in large numbers, without competition. The feeding habits of *Phoenicoparrus* are less well-known, but both species are algivorous, and James' has a bill designed for taking smaller food items than the Andean Flamingo. The brilliant red colour of flamingo plumage reflects rich sources of carotenoids in their diets, and great efficiency in the metabolism of these labile compounds. All 5 species have been found to carry canthaxanthin as the predominant pigment in blood and feathers.

Voice. The flamingo's voice is rather goose-like and loud and may be important in keeping the flock together.

Behaviour. Flamingos are among the most social of birds, and display in large groups with sometimes hundreds of birds taking part. Both sexes participate, although displays are usually initiated by the males whose performances may be more intense and protracted. Many of the ritualized displays are similar to the preening and stretching movements that the birds adopt in everyday activity. The displays are only more stiffly performed, more contagious amongst members of the group, and given in typical, predictable sequences. Head-flagging followed by wing saluting is common: a bird in or near the displaying group suddenly stops headflagging, spreads its wings and folds them again. The effect is a flash of black in a pink field. A twist-preen may then follow: the bird twists its neck back, flashing a wing downward to expose the black primaries, and appears to preen behind the wing with its bill. In the inverted wing salute, the bird bends forwards and the wings are flashed partly open and held above the back. Marching is a display in which flamingos gather in a tight mass, and walk backwards and forwards in synchronized quickstep, sometimes making feeding movements with the bill in the water. Displaying occurs months before, as well as after, actual nesting.

Breeding. In areas with seasonal climates, nesting usually occurs at the beginning of the rains, such as in late November or early December in the Andean altiplano of South America. Flamingos nest in huge colonies: indeed, they seldom breed in flocks smaller than 10 pairs. Nesting is synchronized, presumably in relation to food abundance for the laying females and the chicks. Only the nest site is defended vigorously with various threat postures and the nest mounds themselves are usually two neck-lengths apart. Nests are built with movements similar to those of waterfowl and waders; both sexes pick up mud and stones within reach and place them beneath their bodies to form a circular pile with a shallow depression at the top. Nest mounds may be 30 cm high and presumably give protection from flooding and from the excessive heat often experienced in the mud at ground level. A single white egg, the yolk of which is blood-red, is laid and both male and female incubate it for 28–30 days. After hatching, the chick, unlike young waterfowl and most waders, remains in the nest until 5–8 days of age. It has grey down and a straight, pink bill and swollen pink legs both of which turn black within a week. While in the nest, the chick is fed by both parents on a secretion formed by glands in the upper digestive tract. Initially, this crop-milk is dark red in colour due to a high canthaxanthin content; after a while this fades and the secretion appears to be a pale straw colour. The length of time for which the chick is dependent for food varies: the Caribbean Flamingo can feed itself from 4–6 weeks but in the Greater and Lesser Flamingos parental feeding continues until fledging, by which time the bill is hooked, as in the adult. After they leave the nest, the young form into large crèches up to 30,000 strong, and the parents apparently find their own chick in the group and feed it alone. The young of most species are fledged within 3 months. The first plumage is grey, with brown and pink markings, and the legs and bill are black. Most are fully pink at 2 years of age, the richest red being on the wing-coverts. Individuals may breed when 3, but presumably many do not nest for several years. Flamingos are long-lived and have been estimated to reach an average of 25–60 years in the rift-valley of East Africa. Predation levels are normally low, and there is little response to terrestrial predators. (L.H.B.) J.K. (1)

Brown, L. 1973. The Mystery of the Flamingos (2nd edn.). Nairobi.
Jenkin, P.M. 1951. The filter-feeding and food of flamingos. (Phoenicopteri). Phil. Trans. Roy. Soc. 240B: 401–493.
Kear, J. & Duplaix-Hall, J. (eds.). 1975. Flamingos. Berkhamsted.
Olson, S.L. & Feduccia, A. 1980. Relationships and evolution of flamingos (Aves: Phoenicopteridae). Smithsonian contributions to zoology; no. 316.

FLANGES: enlarged light coloured margins of the gape found in some nidicolous species (see PARENTAL CARE).

FLANK: see TOPOGRAPHY.

FLATBILL: substantive name of *Rhynchocyclus* spp., sometimes applied also to other genera (see FLYCATCHER (2)).

FLAVOUR: see PALATABILITY OF BIRDS AND EGGS.

FLEAS: see ECTOPARASITE.

FLEDGING: term usually applied to the acquisition by a young bird of its first true feathers; when the process is complete the bird is 'fledged', and may for a short time be described as a 'fledgling' (see PLUMAGE; YOUNG BIRD).

FLEDGLING: a young bird which has just left the nest (fledged). The term is used of nidicolous young, which leave their nests only when they are fully feathered and ready to fly.

FLICKER: substantive name of *Colaptes* spp. (see WOODPECKER).

FLIGHT: the form of locomotion especially characteristic of birds as a class; even flightless species show unmistakable signs that their ancestors once flew. Birds are not the only flying animals, but their wings are constructed on an entirely different mechanical principle from those of bats and pterosaurs, the only other vertebrate groups to achieve powered flight. In birds the lifting surface is formed by the flight feathers, which are stiff, and need to be supported at one point only, the base of the shaft. The entire force from the wing is transmitted to the body through the shoulder joint, whereas the flexible membrane forming a bat or pterosaur wing has to be supported between the wing skeleton, the side of the body, and the hind leg. See WING.

The performance of bird and bat wings in flight is not very different, and indeed bats are generally more manoeuvrable than birds of similar size. The importance of the bird arrangement is indirect. Because the legs are not involved in the wing structure, they have continued to evolve as completely separate locomotor organs. Birds have two locomotor systems, which usually serve different types of locomotion. Typical birds fly with their wings, keeping the legs tucked up under the flank feathers. On the ground, the wings are folded up, and the legs are used for walking or perching. There are many variations on this. Water birds use their wings or feet, or both, for swimming. Birds of prey use the feet for catching and manipulating food, and so on. In all cases the legs and feet remain clearly recognizable as the bipedal walking legs of the birds' close relatives, the dinosaurs. The vast range of adaptations seen in birds has been achieved with only minor modifications of the original dinosaur-like body plan. The development of FEATHERS has enabled birds to fly without the drastic modification of the legs seen in bats and pterosaurs.

Power required to fly. Any flying animal (or machine) has to support its own weight in a thin medium, and overcome the drag caused by its own forward motion. The weight is supported by constantly pushing air downwards. To be exact, the rate at which downward momentum is imparted to the air has to equal the weight. This means that if the bird is flying slowly, or hovering, it has to accelerate a stream of air to a high downward speed. If it is flying fast, a more copious supply of air is streaming past, and less downward velocity has to be imparted to it. This is reflected in the rate of energy expenditure (power) required. Supporting the weight is most expensive in terms of rate of energy expenditure in hovering, and gets progressively cheaper as speed is increased, roughly as shown in Fig. 1.

The opposite is true of the power required to overcome the drag of the body. The faster the body moves forwards through the air, the larger is the drag force tending to hold it back. The power required to overcome this is zero when the speed is zero and builds up with approximately the cube of the speed, as in Fig. 1.

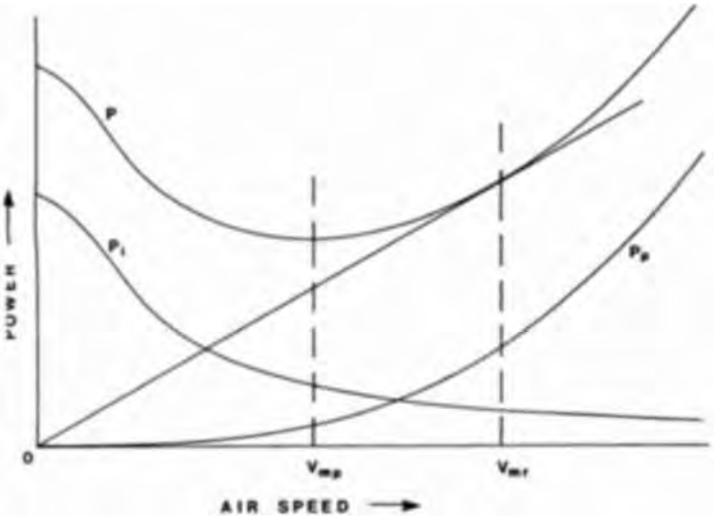


Fig. 1. The induced power P_i is that needed to support the weight in air. It declines with increasing speed. The parasite power P_p is that needed to overcome the drag of the body. It starts at zero, and increases with speed. The total power P has a pronounced minimum resulting from adding these two components together, even though various other components also have to be added. The two speeds marked are for minimum power and maximum range.

The horizontally flying bird has to supply both components of power at the same time. Consequently, hovering flight is strenuous, because of the high cost of supporting the weight, and so is high-speed flight, because of the cost of overcoming the drag. There are also other components of power which have to be supplied, but there is always some moderate speed at which the power required to fly is less than at either slower or faster speeds (Fig. 1). If the bird chooses to fly at this 'minimum power speed', the rate at which it consumes fuel and oxygen will be a minimum.

In most circumstances, and especially when migrating, birds normally fly faster than the minimum power speed. This is because a migrating bird needs to minimize the energy consumed per unit distance, rather than that consumed per unit time. This is achieved at the speed at which the ratio of power to speed is a minimum, which can be found from the power curve by drawing a tangent from the origin as in Fig. 1.

Speed in different birds. In general the speeds at which birds fly are faster in larger than in smaller birds. This is because each unit of wing area has to carry more weight in a large bird, since the ratio of surface area to volume is less. Therefore the air has to flow faster over the wing, and the bird achieves this by flying at a higher forward speed. As a rough guide, the speeds at which birds of different sizes fly vary with the square root of the body length, but there are wide variations about this general trend. At any particular size, birds with thick bodies and small wings (like auks), fly faster than those with slender bodies and large wings (like terns).

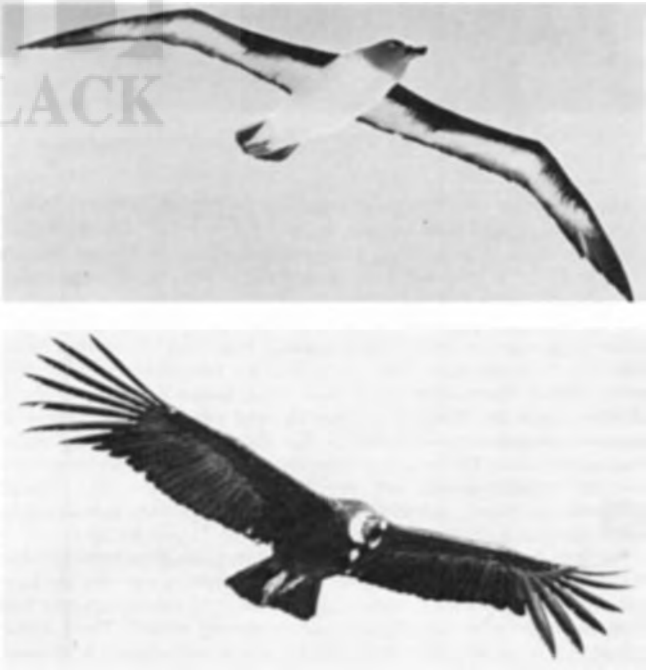
Many methods have been tried for measuring the speeds of free-flying birds, including radar, various optical methods and following with a car or aircraft. The results are usually assumed to be representative of the maximum range speed. Accuracy is difficult to achieve, besides which there is much variation between different species, and indeed in the same species depending on the weather and on what the bird is doing. As a general guide, small passerines cruise at 6–8 m/s (22–29 km/h), small gulls at 9–10 m/s (32–36 km/h), large gulls and small waders at 10–12 m/s (36–43 km/h), and the faster ducks and waders at up to 20 m/s (72 km/h) (see FLIGHT, SPEEDS OF).

The power source. The mechanical power required for flight comes from the flight muscles, of which the most important is the pectoralis, the large breast muscle which pulls the wing down (see MUSCULATURE). In birds other than hummingbirds most of the work in flapping flight is done during the downstroke, in which the fully spread wing is swept downwards and forwards. The wing is normally flexed at the elbow and wrist joints during the upstroke. At high forward speeds the lift developed by the wing is sufficient to carry it up without a great deal of help from the muscles. In slow flight the humerus is raised by the supracoracoideus muscle, and the manus flicks up somewhat later, in a complicated motion which usually causes the flight feathers to separate from each other. It is generally agreed that the function of this type of upstroke is just to get the wing into position for the next downstroke, and that not much aerodynamic work is done by the supracoracoideus muscle.

Limits of body mass. The pectoralis muscle more easily satisfies the demands made on it in small birds than in large ones, for two reasons. First, the power required to fly would be directly proportional to the weight if all birds flew at the same speed, but since the larger ones have to fly faster, it follows that the power required from each gram of muscle is greater in a large bird than in a small one. The second effect aggravates the first. The power available from each gram of muscle is less in a large bird than in a small one. The work done per unit mass of muscle is roughly constant, and the power is this work times the flapping frequency. Vultures are obliged to flap their wings at a lower frequency than hummingbirds, and consequently get less power out of each gram of muscle.

These two effects acting together mean that the power requirements for flight become more difficult to satisfy as birds become larger, and there is therefore a definite upper limit to the mass of flying birds. This limit seems in practice to be in the region of 10–15 kg. Birds of around this mass are found in several unrelated groups, notably the American vultures (Cathartidae), storks (Ciconiidae), swans (*Cygnus*), cranes (Gruidae), bustards (Otididae) and albatrosses (Diomedeidae). The largest members of all these groups show obvious signs of lack of power in flight. In particular condors (*Gymnogyps*, *Vultur*), flap horizontally only with the greatest reluctance and difficulty.

At the opposite end of the scale, the tiny hummingbirds are the only birds capable of continuous hovering (the most strenuous form of flight) over periods of many minutes. Their wing beat frequencies are in the region of 30 Hz in normal flight, giving the characteristic audible hum when they fly, and go over 50 Hz in maximal exertion. Hummingbirds do not suffer from lack of power, but are prevented from reducing their size still further by the still higher wing beat frequencies that would be required. The muscles would not be able to react quickly enough. Hummingbirds overlap in mass with the larger insects, whilst smaller insects have a special type of muscle, which is able to operate at frequencies far higher than any vertebrate muscle can attain.



Grey-headed Albatross *Diomedea chrysostoma* (upper); Andean Condor *Vultur gryphus* (lower). Contrasting wing shapes in large soaring birds. The albatross showing streamlined body, and narrow wings with pointed tips; the Condor showing broad wings, with slotted tips characteristic of birds which soar in thermals over land. (*Photo: C.J. Pennycuick*).

Sand Martin *Riparia riparia* about to enter nest hole. (*Photo E.J. Hosking*).

Galapagos Hawk *Buteo galapagoensis* about to land on tortoise. (*Photo: F. Pölking*).

Puffin *Fratercula arctica* about to land. (*Photo: H.E. Grenfell*).

Great White Pelican *Pelecanus onocrotalus* landing on water. (*Photo: E.J. Hosking*).

The difficulties resulting from large size are partially offset by differences in body proportions between birds of different size. Although there is great variation of wing shape at any particular size, the general trend is for large birds to have relatively longer wings than small ones, which helps to reduce the power required by large birds to fly.

Long distance flight. Powered flight has provided birds with the means of prodigious feats of long-distance migration. Some land birds make very long passages over water, the best known being the Pacific Golden Plover *Pluvialis dominica fulva* which makes a crossing of about 2,600 km from the Aleutians to Hawaii, and the Greenland Wheatear *Oenanthe oenanthe leucorrhoa* which flies about 4,100 km on the trans-atlantic route from Greenland to Morocco. Many small passerine species cross the Mediterranean and the Sahara in a single 'hop' (about 3,000 km), and there is another route of similar length from north-eastern North America over the western Atlantic to the Lesser Antilles.

The long-distance migrants are mainly small to medium-sized species. The distance a bird can fly without landing to feed is not very strongly dependent on body size. It is determined mainly by two factors, the first being the fraction of the take-off mass consisting of fuel. The fuel for migration is invariably fat, and migratory species are adapted to increase their food intake just before departure, so as to lay down massive deposits of fat, up to half the total body mass. A 'fat fraction' of this order is typical of small and medium-sized birds, but large birds cannot carry so much, because of the limitations on muscle power, mentioned above. Therefore the range attainable in flapping flight begins to decline as body mass increases above about 1 kg.

The second factor affecting migration range is the 'effective lift-to-drag ratio', a quantity which expresses the energy needed to propel unit mass of bird unit distance. This lift-to-drag ratio has mechanical and metabolic components. The mechanical part is simple. If the wings are long in relation to the width of the body, the effective lift-to-drag ratio is high, and so is the attainable range. Furthermore, for a given fat fraction, birds of the same shape should go the same distance, irrespective of absolute size. This simple rule has to be modified when the energy expended on basal metabolism is taken into account. Basal metabolism is a larger fraction of the whole in small than in large birds. Also small birds fly more slowly, spend longer in the air when flying a given distance, and use more energy for basal metabolism while they do so. Small birds therefore go less far than larger ones on the same fat fraction, because a bigger fraction of the energy is expended on basal metabolism. This effect might give a medium-sized wader, say, twice the range of a small passerine, on the same fat fraction.

The result of these effects is that the longest-distance fliers are medium-sized birds such as waders and plovers (Charadrii). Smaller birds are at a moderate disadvantage because of their higher metabolic rates and lower speeds, whilst large birds are unable to lift large amounts of fat.

Changes during long flights. On the longer migratory routes, small birds spend 2–3 days and nights in continuous flight. At the end of such a flight, the bird has consumed half its take-off mass, but still has the same wings. Speed and power therefore have to be progressively reduced in the course of the flight. Migrants also climb gradually in the course of long flights. As the cruising speed and power decline, the bird can maintain them in progressively thinner air. Flying higher increases the cruising speed, and to some extent offsets the loss of speed caused by using up fuel. Passerine migrants typically climb to heights of 1,000–2,000 m soon after take off, and then climb gradually, reaching 6,000 m or so towards the end of a long flight. The cross-current arrangement of the avian lung allows birds to extract an adequate supply of oxygen from thinner air than would be usable by equivalent mammals. Keeping warm at high altitudes is not a problem, as the exertion of flight causes excess heat to be generated. (See RESPIRATORY SYSTEM.)

Take-off and landing. Small birds jump straight into the air when they take off, whereas large ones need a take-off run. The reason lies in the relationship of power required to power available (Fig. 2). Small birds can generally muster enough muscle power to fly at zero speed (hover), at least for a short time, whereas large ones can only fly over a limited range of speeds, between some minimum and maximum. They have to run over the ground or water until the minimum speed is attained. The speed in question is the air speed, not the speed relative to the ground. Therefore birds always face into wind when taking off and landing, so that the wind speed contributes to the air speed. Large land birds perch on a tree or slope whenever possible, as they can then acquire the minimum flying speed by dropping from the perch. Seabirds achieve a similar result by accelerating down the windward slope of a wave.

When taking off from level ground, large land birds run with steps synchronized with the wing beats. Both the Old World vultures (Aegypiinae) and their New World equivalents (Cathartidae) run with a curious asymmetrical, sidling gait, for reasons unknown. Most water birds use their webbed feet in a running motion to push themselves forward through the water, but those of the order Pelecaniformes use a rowing motion with both feet together, synchronized with the wing beat.

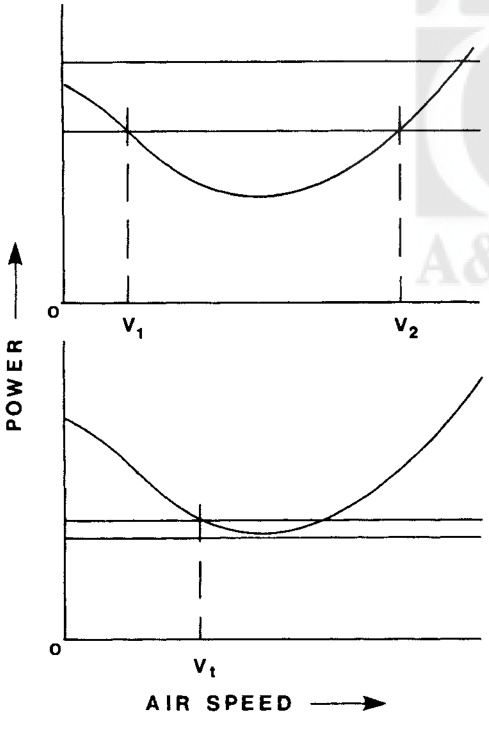


Fig. 2. The curves show total power required to fly, as in Fig. 1. The upper horizontal line represents the maximum power available from the muscles in a brief sprint, whilst the lower line is the maximum power which can be continuously supplied, without incurring an oxygen debt. A small or medium-sized bird (upper) can fly briefly at zero speed, and can therefore take off from a standing jump. It has sufficient power available to fly continuously only in the speed range between V_1 and V_2. Some very large birds (lower), such as condors, have insufficient power to fly continuously at any speed, and have to accelerate by running or diving to a take-off speed V_t before they can fly at all.

Large birds also have to contend with high landing speeds. One method of dealing with this is to use a 'ballistic approach', in which the bird dives to a high speed a little below the intended landing spot, then pulls up into a steep climb. If correctly judged, this results in the speed dropping to zero just above the perch. Large birds use this method to land on trees or cliffs, as do some smaller ones with heavy bodies and small wings, such as auks (Alcidae). A high landing speed is less of a problem for water birds. Most of them hydroplane to a halt on their large webbed feet, whilst a few such as gannets (*Sula*), always dive into the water, however slow their ground speed. Some water birds such as divers (Gaviiformes) land only on water, and can therefore accept a high landing speed and posteriorly placed legs. In most water birds these adaptations are not carried to such extremes as in divers, to allow acceptable landing performance on land. Albatrosses are able to alight on land, but are notably clumsy when doing so, as indeed are many of the smaller Procellariiformes.

Uses of the tail and feet. Birds do not have the long, jointed tails seen in other vertebrates, including their own reptilian ancestors. The tail consists of a fan of stiff feathers, which can either be furled, or spread out sideways, so varying its area by a factor of 3 or more. A bird's tail does not have the same function as that of an aircraft, in which loss of the tail renders the aircraft uncontrollable. Birds can still fly without their tails, but have difficulty in manoeuvring at low speeds, and particularly in landing. The tail is spread in low-speed flight, and helps to deflect air downwards over the wings. The effect is to augment the lift developed by the wings, and to keep the air flowing smoothly over them at lower speeds than would otherwise be possible.

Birds with small wings and tails, and large webbed feet, such as auks, augment their tail area when flying slowly, by spreading the feet on either side of the tail. A more common use for webbed feet in flight is as airbrakes. When extended below the body, the feet generate a large amount of drag, enabling the bird to descend at a steep angle without excessive speed. Cliff-nesting birds such as fulmars *Fulmarus* use the feet in this way to soar level with the cliff-top, and avoid being carried above it by the wind. Gulls depress the furled tail for the same purpose, but it is unusual for birds to use the tail as an airbrake in this way. The spread tail, seen in birds about to land, is usually not acting as an airbrake, as often stated, but in a manner more akin to an aircraft's flaps.

Birds' feet do not have to be webbed to make effective airbrakes. The long legs of storks and cranes are extremely effective as drag generators. The legs of vultures and even pigeons are sufficiently effective to be of major importance as airbrakes.

Adaptations for powered flight. Scale effects impose general trends which make birds of different size fly in different ways. At any particular size, there is a wide range of adaptations in which one feature is developed at the expense of others. For example birds with very long wings are adapted to minimize the power required to fly at low speeds, or to hover, as in terns and frigatebirds. Swifts are commonly thought of as fast-flying birds, and indeed they can attain quite high speeds in a dive. The primary function of their long wings, however, is to enable them to fly and manoeuvre slowly in pursuit of flying insects, and also to remain airborne day and night, flying slowly and expending energy at a low rate.

Hummingbirds are the only birds able to hover continuously without incurring an oxygen debt. When they hover, their wings beat to and fro almost horizontally. The wings are nearly symmetrical in cross section, and are inverted on the backward stroke, so producing about the same amount of lift on both the forward and backward strokes. This mode of hovering is more characteristic of insects than of birds, other kinds producing lift mainly on the downstroke when hovering. The hummingbird method produces a smoother downward flow of air, which is less wasteful of energy than the more intermittent flow produced by other birds.

Those water birds which use their wings under water tend to develop small wings in relation to their body size, because the denser medium requires this. Some, such as the auks and diving petrels (Pelecanoididae) continue to fly in air, with wings which also perform much the same motion under water. Such birds fly fast and with high wing beat frequencies. When they come ashore to breed, they rely heavily on ballistic landing and take-off techniques. The fact that such an awkward compromise is retained in so many living water birds testifies to the selective value of retaining the power of flight. Penguins, by breeding in places inaccessible to terrestrial predators, were able to dispense with flight long ago, and so to specialize entirely on aquatic locomotion

Kestrel *Falco tinnunculus* female wind-hovering. (*J.B. & S. Bottomley*).

(incidentally removing the restriction on maximum body mass). More recently individual species of other groups have embarked on the same course, sometimes successfully as in the Flightless Cormorant *Nannopterum harrisi* and sometimes, as in the Great Auk *Pinguinus impennis*, with disastrous results.

Short wings allow high wing beat frequencies to be attained, and are found in birds which need bursts of high power output from their muscles. Game birds, with their short, rounded wings, are adapted for good take-off performance rather than for sustained cruising flight. The smaller ducks have well streamlined bodies and relatively small, pointed wings, giving fast and efficient cruising at the expense of rather high speed landings and take-offs. Swans are of special interest as the largest birds which undertake substantial migratory flights without soaring. Unlike other large birds (except albatrosses—see below), their bodies are well streamlined, and their wings are of an efficient, pointed shape.

Soaring. A bird's own muscles are not necessarily the only source of energy for flight. Energy can often be extracted from the air in which the bird flies. Flight based on this principle is called soaring. For various reasons it is more advantageous to large birds than to small ones.

Soaring depends on exploiting motions in the atmosphere which are non-random, and therefore predictable. The simplest method is slope soaring, which depends on the fact that the wind is deflected upwards when it blows against a vertical obstruction such as a hillside or a line of trees. By flying back and forth along the windward side of the obstruction, the bird can remain continuously in rising air. If the vertical speed of the air exceeds the sinking speed of the bird when gliding, the bird can maintain height, or climb, without flapping its wings. Gulls and other seabirds make extensive use of slope lift along sea cliffs. In Britain Kestrels *Falco tinnunculus* can often be seen using motorway embankments to slope soar in a fixed position over the ground, looking for food below, while the American Turkey Vulture *Cathartes aura* is adept at using trees for slope soaring. Slope lift is easy to find because it is always over the slope, but for that very reason is limited in its usefulness. It is also usually limited vertically, seldom extending far above the top of the slope, even on a high mountain ridge.

Lee waves, which form on the downwind side of an obstruction, and remain stationary relative to the ground, provide the basis of another method of soaring. Lee waves extend to much greater heights than slope lift, but are more difficult to use because their location is less obviously related to the landscape. The European Gannet *Sula bassana* and Andean Condor *Vultur gryphus* have been reported using lee waves on a small scale, and this method may be important for the latter.

Most bird soaring is done in thermals, which are vortex structures in the atmosphere, usually triggered off by solar heating of the ground. Cumulus clouds are caused by thermals, and serve as indicators of their presence, although thermals can also occur in a clear blue sky. Thermals normally have a zone of rising air in the middle, surrounded by a zone of rotating or sinking air. To exploit the thermal, the bird flies in circles of small radius, so that it remains inside the central zone of lift, or 'core'.

Thermals are used extensively by birds of prey, simply to keep them airborne for long periods, while they patrol in search of food. Migratory species also use thermals for cross-country travel, by alternatively climbing in a thermal, then gliding off, losing height, in the required direction. Because of the time taken for the climbs, during which no progress is made, this method of travel is slower than continuous powered flight. On the other hand the energy consumption is less, especially in large birds, whose basal metabolism is relatively low. In small birds the time lost climbing in thermals would lead to an undue increase in the energy consumed in basal metabolism. As the basal metabolic rate is large compared to the power required to flap the wings, it is metabolically cheaper for small birds to migrate by flapping, and they soar only incidentally. The smallest soaring birds are the swifts, but they soar to remain airborne in pursuit of their insect prey, rather than for migration as such.

Thermals occur where relatively cool air is heated from below by a hot land surface, and are consequently most reliable as a source of lift in the drier parts of the tropics and sub-tropics, and in inland continental areas at higher latitudes in summer. The seasonal occurrence of good soaring conditions is exploited in both the Old and New Worlds for the annual migrations of birds of prey and storks. These birds make a detour around the Mediterranean Sea, in order to take advantage of better thermals over the land. During the autumn migration they converge in spectacular concentrations to cross isthmuses and narrow straits, as at the Bosphorus and Suez. Similar concentrations of migrating birds of prey and Turkey Vultures are seen on the isthmus of Panama. The European Crane *Grus grus* also migrates by using thermals, but is less dependent on them. It crosses the Mediterranean in flapping flight, and reverts to thermal soaring further north.

Thermals, accompanied by characteristic cumulus clouds, also occur over the sea in the trade wind zones, in which the air converges continuously towards the Equator from both north and south, and is therefore heated from below by the progressively warmer sea surface. Unlike thermals over land, which generally cease as the surface cools at night, these trade wind thermals continue with little variation during the night. Frigatebirds are adapted for soaring in these weak but consistent thermals. Although primarily coastal in their distribution, they are regularly seen several hundred km from land, and are apparently able to soar by day and night, as they never alight on the water.

A variety of coastal and freshwater birds, including gulls and pelicans soar in thermals over land, but rely mostly on flapping flight over the sea. The Procellariiformes are a truly pelagic group using various methods of soaring over the open sea. Being most abundant in the windy middle latitudes of the southern hemisphere, petrels and albatrosses rely to a large extent on slope soaring along waves. The larger members of the group, from albatrosses down to medium-sized petrels and shearwaters, also make use of the variation in the horizontal wind speed in the bottom 15 m or so of air, caused by friction with the sea surface. It is possible to extract energy from this wind gradient by pulling up against the wind. The wind speed progressively increases as the bird climbs, so offsetting the decline in its airspeed. A further gain can be made by gliding downwind through the wind gradient, which has the effect of flattening the angle of glide.

Storm petrels have a special method of soaring, which they use for feeding at the surface. The bird points into wind with its wings extended, but with its feet in the water acting as a sea anchor.

Adaptations for soaring. Gaining height in thermals or slope lift calls for gliding at a low air speed, and a low rate of sink. This is achieved by a low wing loading (large wing area relative to body weight), long narrow wings, and a well streamlined body. Frigatebirds are specialized in this way, being adapted to remain airborne in weak thermals for long periods, without any requirement for fast cross-country progress. Those birds which migrate by thermal soaring, or make long daily forays in search of food, as some vultures, need to glide fast between thermals, in addition to flying slowly when climbing. These needs are difficult to reconcile, as fast gliding calls for a high wing loading. Wing loadings are higher in migratory species than in those which use thermals purely for patrolling a small foraging range.

Birds which use thermals over land do not, in general, show the long narrow wings which would be most efficient for this. They have characteristically broad, rectangular wings, in which the primaries are emarginated to form a series of slots at the tip. The gliding performance resulting from this shape is not impressive by comparison with that of sailplanes. The broad, slotted wing characteristic of eagles and hawks (Accipitridae), American vultures (Cathartidae), storks, cranes and pelicans is most probably adapted primarily to the requirements of take-off on land, rather than to those of soaring as such. Water birds seem to have less difficulty with take-off, and the long, narrow, glider-like wing is seen most highly developed in the albatrosses. Their wing loading is relatively high, and they skim fast along waves, following the zone of slope lift.

Many marine and freshwater birds habitually fly as close to the surface at they can, with their wing tips almost touching the water. The close proximity of the surface results in a significant increase in the efficiency of the wing, a phenomenon known as 'ground effect'. Some birds such as skimmers *Rynchops* use ground effect as the basis of their foraging technique.

Body measurements. Reliable predictions about birds' capabilities in flight depend on accurate body measurements, but these are less easy to come by than might be supposed. The wing measurements traditionally made by ornithologists are of little value for flight calculations. It is not difficult to collect more useful measurements, and much could be learned if those who regularly trap and handle birds would do so. The following three measurements supply a foundation for the more basic flight calculations.

Body mass. This can be measured in the usual way, but not forgetting to note whether the bird is fat or thin, and whether its crop is full or empty.

Wing span. The wings should be extended to their fullest extent, without actually straining the structure, and the extreme distance measured, from tip to tip. 'Wing length' as usually recorded is not a useful measurement (see WING SPAN).

Wing area. This is a more time-consuming measurement, in which the bird's body is held by the edge of a table, one wing is spread out to its fullest extent over a sheet of paper, and the outline is carefully traced. The area required is the projected area of both wings, including the section of the body in between them, as in Fig. 3a. To achieve this, the tracing of one wing must be extended to the midline, by measuring a distance equal to half the span, inwards from the tip (Fig. 3b). The area can then most easily be measured by counting squares on a grid overlay, made by ruling a grid on a sheet of transparent plastic.

A collection of masses, areas, and wing spans is always worth publishing, provided explicit details of the methods of measurement are given.

See photo CARRYING. C.J.P.

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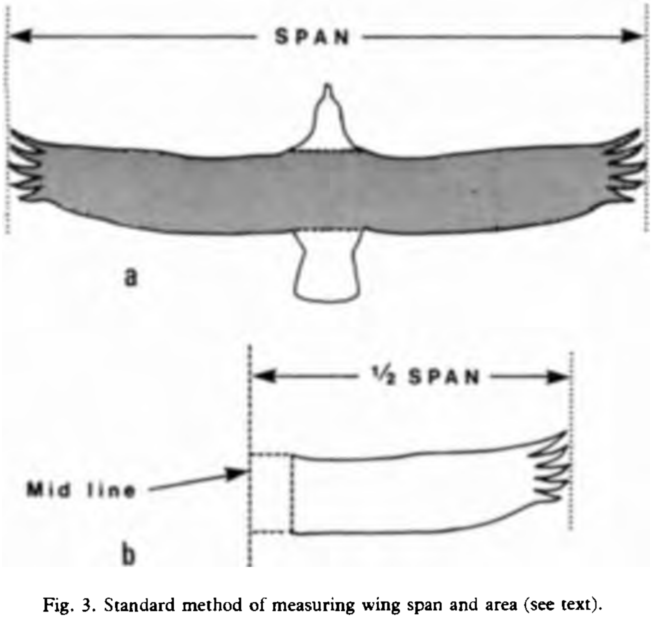

Fig. 3. Standard method of measuring wing span and area (see text).

FLIGHT FEATHERS: general term for the primary and secondary feathers of the wing (see REMEX; WING).

FLIGHTLESSNESS: a condition whereby the flight apparatus is reduced or absent, rendering the adult form totally unable to fly. This phenomenon, widespread among various orders within the Class Aves, occurs in two totally different adaptive zones, the aquatic and terrestrial environments. In both, however, all flightless forms have been derived from flying ancestors (see EARLY EVOLUTION OF BIRDS).

In the water two very different types of swimmers and divers have become flightless. These are foot-propelled and wing-propelled divers. Flightless foot-propelled divers are ancient, with one form, *Enaliornis*, from the early Cretaceous, going back nearly to the time of the first known bird, *Archaeopteryx*. *Enaliornis* is the earliest of the toothed, foot-propelled hesperornithiform birds (order called Hesperornithiformes: genera *Enaliornis*, *Hesperornis*, *Baptornis*, *Neogaeornis* and *Coniornis*). These flightless divers ranged in size from that of a moderate sized grebe to over 1½ m in length (*Hesperornis regalis*), and although not related to the living divers or loons, resembled them through convergent evolution. Modern foot-propelled divers that are flightless occur in a variety of orders. Among the ducks (Anatidae) 2 of the 3 steamer ducks *Tachyeres* spp. are flightless or nearly so. They are more heavily built than their flying congener: when speed is necessary, the wings are flapped to aid progress over the surface of the water (see DUCK). A recently extinct flightless goose *Chendytes* from the Pacific coast of America is another example of anatid flightlessness. Among the grebes (Podicipedidae) we also see a tendency to become flightless or nearly so, with examples such as the nearly flightless *Podiceps gigas* of Lake Atitlan, or the flightless *Centropelma micropterum* of Lake Titicaca. Finally, among the cormorants (Phalacrocoracidae), the foot-propelled diver *Nannopterum* (*Phalacrocorax*) *harrisi* of the Galapagos Islands is completely flightless.

Flightless Cormorant *Nannopterum harrisi* with small chicks on Galapagos. (*Photo: F. Pölking*).

The case of wing-propelled flightless divers is quite different. Here evolution has led to adaptation for a largely marine existence, with modification of the wings as flippers for swimming (see PENGUIN; SWIMMING AND DIVING). This use of the wings requires strong pectoral muscles and a carinate sternum, as in the case of flying birds, since these birds literally fly through the water, and may be considered among the 'best' flyers. Penguins, thought to be derived from procellariiform ancestors, are the only totally flightless wing-propelled divers known from the Southern Hemisphere, but from the Northern Hemisphere the recently extinct Great Auk *Pinguinus impennis* evolved from alcid stock. Its ancestor *Pinguinus alfrednewtoni*, known from the lower Pliocene of North Carolina, was slightly less specialized for wing-propelled locomotion. The Lucas auks, intermediate in structural specialization for wing-propelled diving, are also flightless forms from the upper Miocene to Pleistocene deposits of California. Finally, there are the recently discovered plotopterids (Plotopteridae), Northern Hemisphere pelecaniform derivatives that converged on the extinct giant penguins of the Southern Hemisphere. These, the largest swimming birds known, with one species over 2 m in length, occur in the late Oligocene and early Miocene of Japan, Washington and California. Their extinction occurred at the same time, the early Miocene, as that of the giant penguins of the Southern Hemisphere. They are thought to have occupied the pelagic niches for endotherms the size of seals and porpoises, both of which were undergoing adaptive radiation at that time.

Equally, or perhaps more diverse are the myriad of terrestrial birds that have lost their flying powers. In almost all of these cases we see the evolution of flightlessness as a case of arrested development or neoteny, though the reasons for the evolution of flightlessness may be quite different.

The earliest flightless terrestrial forms are the diatrymas from the Paleocene and Eocene of North America and Europe. These were giant forms, 2 m or more tall, with a head the size of a modern horse's. *Diatryma* and its allies (*Gastornis*, etc.) apparently took over the niche for a bipedal carnivore left vacant by the extinction of the flesh-eating dinosaurs. Another group of birds evolved in South America from the Oligocene to the close of the Pliocene, a period during which South America was totally isolated from the rest of the world and therefore isolated from the invasion of advanced mammalian carnivores. These were the phorusrhacids (*Phorusrhacos*, *Brontornis*, *Andalgalornis*, and allies) which were more lightly built than the diatrymas. They ranged in size from 1½–2½ m, with the speed to run down their prey, unlike the diatrymas which probably were not capable of great speed. One giant phorusrhacid, *Titanus walleri*, which was larger than the African ostrich, is known from the Pleistocene of Florida.

Another flightless flesh-eater was the giant owl *Ornimegalonyx oteroi* from the Pleistocene of Cuba which, standing over 1 m tall, had a tarsometatarsus twice as long as that of the modern *Bubo virginianus*.

Another avian order to have given rise to flightless forms is the order Columbiformes, the pigeons and doves. Flightless derivatives include the now extinct DODO *Raphus cucullatus* of the island of Mauritius; it weighed about 23 kg. A flightless cousin of the Dodo, and presumably derived from the same stock, was the Solitaire *Pezophaps solitarius* on the neighbouring Mascarene island of Rodriguez. They became extinct in the 17th and 18th centuries.

Among the Psittaciformes, the Owl Parrot (or Kakapo) *Strigops habroptilus* of New Zealand is flightless, although it sometimes opens its wings when pressed or while climbing in trees and may glide to the ground from heights. Several other parrots, although not flightless, are primarily terrestrial; these include the Ground Parrot *Pezoporus wallicus* and the Night Parrot *Geopsittacus occidentalis* of Australia (see PARROT).

Within the heterogeneous order Ciconiiformes two flightless ibises are now known: from the Quaternary of Jamaica *Xenicibis xympithecus*, and from the Pleistocene of Hawaii *Apteribis glenos*. *Apteribis* coexisted with a large flightless Hawaiian goose, *Thambethochen chauliodus*, characterized by possessing blunt, bony, toothlike projections on both jaws. A larger extinct flightless goose *Cnemiornis calcitrans* is known as a subfossil from New Zealand, and was no doubt contemporaneous with man and the moas.

Among the Passeriformes there are also a few flightless members, including the now extinct Stephen Island Wren *Xenicus lyalli* of New Zealand. The Central American Wren-thrush *Zeledonia cornonata* is also flightless or nearly so, as are a number of species of the Neotropical family Rhinocryptidae, in which the sternal keel is nearly wanting. Within the coraciiforms, a recently extinct flightless hoopoe *Upupa antarios* is known from the island of St Helena in the South Atlantic Ocean.

However, it is within the rails of the order Gruiformes that we see the greatest proclivity to become flightless; nearly one fourth of all island rails, living or recently extinct, having lost their powers of flight. Some of the more notable are the wekas *Gallirallus* spp. of New Zealand, the Takahe *Notornis mantelli* (at one time thought to be extinct) of the same country, *Porzanula palmeri* of Laysan Island, *Gallinula nesiotis* of Tristan da Cunha (subspecies extinct) and Gough Island, and the very small *Atlantisia rogersi* of Inaccessible Island. Rails prove that: (1) flightlessness may evolve in a very short period of time (e.g. generations), and (2) their flightlessness in all cases is a result of arrested development or neoteny. Even after hatching, the flight apparatus of flying rails is only poorly developed. Neotenic features of flightless rails (which also characterize other flightless birds and the RATITES) include a keelless sternum, an obtuse angle between the scapula and coracoid, and a large opening of the ilioschiatic fenestra. Flight is an energetically expensive ability to maintain, and in island rails, as well as other flightless birds, it appears that, if there is no strong and continual selection to maintain the flight apparatus, it will tend to disappear, along with the extensive pectoralis muscles and the entire flight architecture.

Other gruiforms to become flightless include the KAGU *Rhynochetos jubatus* of New Caledonia, the sole member of the family Rhynochetidae. There are a number of extinct flightless gruiforms known, including the highly cursorial ergilornithids from the mid-Tertiary of Mongolia, and the large Pleistocene gruiform *Aptornis* from New Zealand.

None of the 3 species of Mesitornithidae (see MESITE), a gruiform family of ground-dwelling birds peculiar to Madagascar, is known to fly; although they have fair-sized wings the clavicles are much reduced.

Perhaps the most notable of the living flightless birds are the so-called 'ratites'. Whatever the relationships of the various ratite groups (e.g. monophyletic or polyphyletic) they show similar neotenic features to those found in other flightless birds, and most have evolved in the direction of large size, very strong legs, and a wholly terrestrial mode of life (see CASSOWARY; ELEPHANT-BIRD; EMU; MOA; OSTRICH; RHEA). The KIWIS of New Zealand are exceptional in having attained only moderate size and in having developed nocturnal habits instead of relying on fleetness of foot for safety. The ratites are thought by some to be allied by their common possession of a peculiar conformation of the palatal bones known as the palaeognathous PALATE, but this feature may be either primitive within birds or neotenic, or both.

The large living ratites include the South American rheas (2 species), the African Ostrich *Struthio camelus*, the Australian Emu *Dromaius novaehollandiae*, the Australian and New Guinea cassowaries, and the smaller New Zealand kiwis. Extinct forms include the large ELEPHANT-BIRDS of Madagascar, a great variety of Australian dromornithids (Dromornithidae: Miocene to late Pleistocene), one of which may have equalled or exceeded in size the largest elephant-bird, and the 13 or so species of greater and lesser moas of the Quaternary of New Zealand.

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FLIGHT LINE: see MIGRATION.

FLIGHT, PRECOCIOUS: flying by young birds well before they have attained full size. The general rule is that a bird does not fly until it is practically full grown, which is usually at a very early age; and it is clear that the flight feathers appropriate to an adult would, in the partly grown bird, be out of proportion to the other factors involved in flying (see FLIGHT). It is, however, characteristic of the Galliformes that a miniature set of remiges is grown by the chicks so that they can fly when quite small. This is no doubt a useful safety-device for ground-living birds; on the other hand, it may on occasion lead to undue scattering of the brood while its members are still of an age to need parental protection. Precocious flight reaches its extreme in the Megapodiidae (where the question of scattering does not arise); for instance, the chick of the Mallee-fowl *Leipoa ocellata* can fly almost as soon as it leaves the egg (see MEGAPODE). More often, in other families of the Galliformes, flying does not begin until later, e.g. 3–4 days in curassows (Cracidae) and 12–14 days in the Pheasant *Phasianus colchicus*. Precocious flight is also found in the gruiform family Turnicidae (see BUTTONQUAIL).

FLIGHT, SPEEDS OF: dictated by many factors in different situations. Since flight ability is closely related to ecological success the selection of speed is of crucial importance. Flight is used by birds predominantly to gather food, to search for mates (and to display for them) and to move to more favourable habitats (including migration). Optimal flight performance is that which gives the best contribution to evolutionary fitness in return for the effort expended. However, the measure of 'best return' must be defined in relation to the particular circumstances of an individual and its behaviour, and there is no general definition of optimum flight strategy or speed. Powered flight is demanding in the quantity of energy required, and generally the flight pattern is selected so that the energy consumed is minimized, or that (while foraging) the nett energy gain is maximized. The rate of energy consumption in flight (power) depends strongly on speed, and there is strong pressure on any bird to choose an optimum speed; it is in flight speed measurements that we can expect to see the response of an animal to varying ecological and environmental conditions. An individual will not always fly at the same air speed, regardless of what it is trying to achieve or of environmental conditions, and flight speeds are not dictated by wing size and proportions alone; on the other hand as a result of evolutionary specialization the wing morphology of any species is best adapted for the predominant flight conditions encountered.

Flight performance. Power consumption in level flapping flight can be depicted as a U-shaped graph (see FLIGHT); curves of this kind have been obtained from aerodynamic theory and from measurements of gas exchange for birds flying in wind tunnels. The detailed shape of the curve depends on the aerodynamic characteristics of the bird and on wing morphology, and has important consequences for the speed of flight.

Hovering—flight at zero air speed—is demanding in energy as there is no forward air velocity contributing to support of the animal's weight and therefore all air currents must be generated by the wings; it is only used continuously by birds which can exploit a rich or high-energy food reserve guaranteeing sufficient return for the energy expended. As speed is increased the energy needed for lift (weight support) decreases, and power consumption falls; at higher speeds still the frictional drag of body and wings becomes important, and power must rise (Fig. 1). Since there are physiological limitations on the rate of steady oxygen supply to the muscles and on the rate at which muscles can develop force there must be a fixed upper limit to the metabolic power available, and hence to the speed range. The same constraint can also set a lower limit: indeed, few birds are capable of sustained hovering for this reason, although many can 'hover' very briefly for a few wing strokes while landing or manoeuvring. Although frequently described as 'hovering', birds such as the Kestrel *Falco tinnunculus* and Rough-legged Buzzard *Buteo lagopus* cannot sustain the high power output this would entail, and they remain stationary relative to the ground while hunting by flying into moderate winds. In larger birds slow flight speeds can also be difficult or impossible to achieve because a minimum speed is required for lift generation; this can be particularly important in take-off, and can frequently demand a long run to build up sufficient air speed.

The most common criterion by which speed is determined is the reduction of energy for a given flight. Assuming that any flight speed (within the range set by metabolism) can be obtained by variation of the wing-beat geometry, then presumably the bird selects a speed primarily according to this rule. The shape of the power-velocity curve shows that two important characteristic speeds can be defined: V_{mp} at which power (energy/time) is least, and V_{mr} at which cost of transport (energy/distance) is least, or equivalently at which flight range is greatest for given fuel. (In the largest birds physiological factors may limit the maximum available speed to less than V_{mr}.) If the intention is to remain in the air for the longest possible time (roosting of swifts, some forms of hunting) a bird will fly at about V_{mp}, while if pressure is to maximize distance flown (migration, flying to feeding site) it will fly at V_{mr}. In some situations reducing time becomes important (escape from predation, foraging to feed young), and the bird will then fly as fast as possible. Typical flight speeds relative to the power curve for different flight conditions are summarized in Fig. 1.

Migration. Perhaps the most important situation demanding best possible flight performance is migration. As a contribution to the animal's annual energy budget the extra flight energy consumed must be more than balanced by improved energy intake in the more favourable habitat, and by the associated increase in reproductive fitness. The large distances involved place strong pressure for a strategy that minimizes total energy for the distance covered, and migrants can be expected to fly (in still air) at speed V_{mr}. If the bird is influenced by wind, as is often the case in migration, ground speed and air speed will not correspond, and air speed must be adjusted so that ground distance is as large as possible. Theory suggests that in head winds air speed should be increased by about 30% of wind speed (up to the maximum set by metabolism, beyond which forward progress is impossible), while in tail winds the bird should reduce air speed by the same amount. Several migrants (e.g. Chaffinch *Fringilla coelebs*) have been observed to respond in this way when the wind is parallel to the flight path and does not drift the bird to the side of its goal. In crosswinds the situation is more complex, but one possible response is for the bird to fly at high altitude in a strong wind without compensation for drift or wind speed until abreast of its goal, then to descend to lower altitudes where the winds are weaker and to fly direct to its destination: in this way the total energy needed can be minimized. The large fuel reserves stored as fat at the start of migration by many small birds also affect flight strategy: as the flight proceeds, fuel is consumed and mass decreases, and speed should be reduced: at all times, however, the bird should fly at V_{mr} (with appropriate compensation for wind etc.), and the change in mass alone dictates the change in speed.

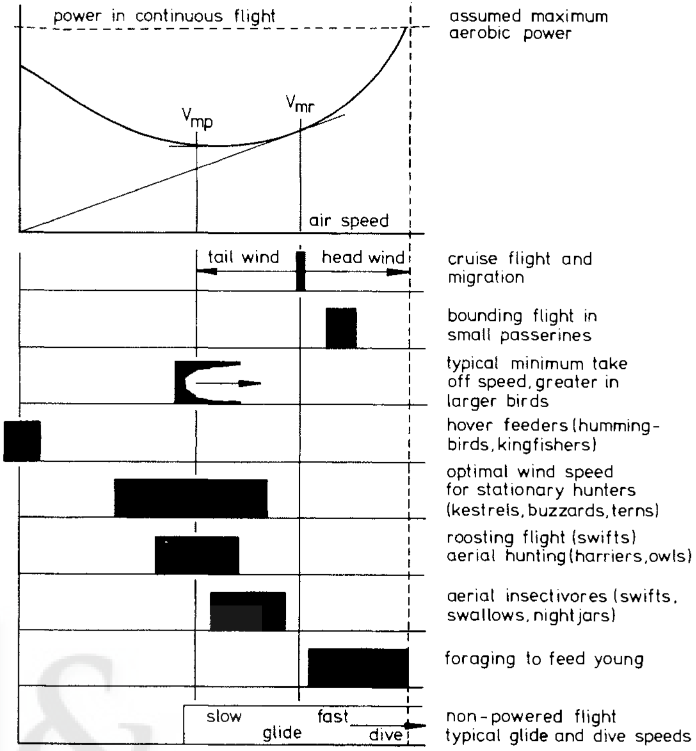

Fig. 1. Typical graph of power against speed for level flapping flight in birds, showing characteristic speeds V_{mp} and V_{mr}, together with the likely ranges of flight speed in different flight conditions, as they are related to the characteristic speeds and to the shape of the curve. Morphology adapts so that power is minimum at the appropriate speed range.

Morphology. The active selection of flight speed according to the demands of performance allows a bird to optimize flight behaviour, but the speeds available to it are dictated by the aerodynamic features of the animal and by the size and shape of the wings. Selection favours the development of wings specialized for the type of flight pattern associated with the animal's behaviour and ecology, and as the design of wings becomes more extreme, allowing less flexibility in flight behaviour, so the animal becomes more specialized not only in its flight but also in ecology and ethology. Wing size is described by wing loading (weight supported by unit wing area), and wing shape by aspect ratio (wing span squared, divided by area), and the major trends of flight adaptations may be distinguished with these parameters. Measurements of air speed in level flapping flight for a number of species are shown in Table 1, together with body mass, wing loading and aspect ratio. The considerable variation in speed even between birds of the same mass is the effect of wing morphology: speed rises with both mass and wing loading since higher speeds become necessary if lift is to be sufficient to support weight, while speed shows a slight decrease as aspect ratio rises since longer wings are more efficient. Birds which fly slowly or hover while foraging (e.g. Kestrel, terns, kingfishers, hummingbirds), and aerial insectivores (swifts, swallows), have long, high-aspect-ratio wings so that V_{mp} (and also V_{mr}) is low and power at that speed is as small as possible, even though the penalty of low maximum speed is unavoidable. On the other hand divers, ducks, geese and some waders have short, high-aspect-ratio wings allowing high speeds without unduly high power, because their feeding behaviour is dramatically influenced by weather and tide, and high speeds are of great importance to their success, as many of these species breed in arctic latitudes where the season is short and weather can be unfavourable. Many small passerines have short, rounded wings of large area and low aspect ratio. The low wing loading permits the large increases in weight prior to migration without flight becoming impossible, and these birds compensate for the high wing drag

Table of speeds of flight for a sample of birds, with average mass and wing morphology for each species. Speeds, obtained from radar measurements from a variety of sources, are cruise speed (V_{mr}) in light winds or still air.

		Mass	*Aspect ratio*	*Wing loading*	*Speed*	
		(kg)		(N/m^2)	(m/s)	(km/h)
Red-throated Diver	*Gavia stellata*	0.96	12.2	106	17	61
Wandering Albatross	*Diomedea exulans*	8.7	15	140	15	54
Wilson's Petrel	*Oceanites oceanicus*	0.038	8	19.4	11	40
Grey Heron	*Ardea cinerea*	1.32	7.8	39.8	12	43
Bewick's Swan	*Cygnus columbianus bewickii*	6.2	9.2	147	20	72
Barnacle Goose	*Branta leucopsis*	1.15	10.1	98	19	68
Whitefronted Goose	*Anser albifrons*	1.72	10.8	92	15	54
Mallard	*Anas platyrhynchos*	1.01	9.1	113	18	65
Eider Duck	*Somateria mollissima*	2.18	8.4	194	21	76
Sparrowhawk	*Accipiter nisus*	0.188	6.5	28.1	12	43
Osprey	*Pandion haliaetus*	1.1	8.9	38.5	13	47
Kestrel	*Falco tinnunculus*	0.200	7.9	30.7	9	32
Pheasant	*Phasianus colchicus*	1.2	5.5	123	15	54
Crane	*Grus grus*	4.8	7.3	85	19	68
Oystercatcher	*Haematopus ostralegus*	0.42	9.7	64	14–16	50–58
Dunlin	*Calidris alpina*	0.045	8.6	29.8	13	47
Herring Gull	*Larus argentatus*	1.0	10	49.9	10–11	36–40
Common Tern	*Sterna hirundo*	0.121	13.2	24.5	9–12	32–43
Woodpigeon	*Columba palumbus*	0.461	6.6	57.5	17	61
Swift (roosting)	*Apus apus*	0.042	10.5	29.1	6.5	23
Swift (migrating)					11	40
Swallow	*Hirundo rustica*	0.022	8	16.1	9	32
Blue Tit	*Parus caeruleus*	0.010	6.8	16.8	8	29
Chaffinch	*Fringilla coelebs*	0.022	5.9	20.2	10–14	36–50
House Sparrow	*Passer domesticus*	0.028	5.5	26.4	8–11	29–40
Starling	*Sturnus vulgaris*	0.076	7.2	36.6	9–10	32–36
Crow	*Corvus corone*	0.46	6.8	36.7	14	50

by adopting bounding flight, in which the wings are closed for about half the time they are airborne, and speed is rather higher than V_{mr}. In every flying bird morphology is best adapted to suit performance largely so that speed and energy are optimized: flight is so demanding on energy consumption that selection will ensure that no resources are wasted and that food is gathered in the optimum way.

Speed measurement. In view of the numerous factors involved in the selection of flight speed and the great difficulties inherent in measuring it, it is hardly surprising that published bird speed records show little coherence. Many methods have been used with remarkably little success; techniques such as triangulation or pacing from cars, trains or aircraft are particularly unlikely to produce meaningful data. The best method is probably low-range Doppler radar tracking of a known individual; with tracking radars the bird may not be accurately identified, and exact wind strength and direction are rarely known. High-speed cinematography can be valuable if the camera used and distances are accurately calibrated, but with every technique it is vital to record wind velocity and to take note of what the bird is trying to achieve. Because many observers have been prevented from doing this, published speed records, such as those tabulated by Meinertzhagen, are often misleading and inaccurate. Table 1 lists recent radar measurements of cruise (usually migration) flight speeds in still air or light winds. These are believed to be reliable, and in most cases represent flight at or near V_{mr}.

Considerable popular interest is devoted to records such as the 'fastest' bird, and to this end many fanciful estimates of speed have been published. Comparisons of this kind between species are invidious, but from the table it can be seen that speeds rarely exceed 20 m/s (72 km/h), and doubt must be expressed over air speeds for steady powered flight much in excess of this. The fastest speed for any type of flight probably occurs during the stoop of the Peregrine *Falco peregrinus*, but no accurate determination of speed has been made, and it is probably no more than about 50 m/s (180 km/h). In steady flight the fastest bird reliably clocked as yet is the Eider *Somateria mollissima* at 21 m/s (76 km/h); this bird has the highest recorded wing loading. Contrary to popular opinion, swifts are among the slowest of birds, as is consistent with their long, thin wings; speeds for the Common Swift *Apus apus* in foraging (6.5 m/s, 23 km/h) are slightly higher than V_{mp}, at the expected optimum for an aerial insectivore; in migration they fly at about 11 m/s (40 km/h), that is at V_{mr}. J.M.V.R.

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FLIPPER: term applied to the modified wing in the Spheniscidae (see PENGUIN; SWIMMING AND DIVING).

FLOCK: see ASSEMBLY, NOUN OF.

FLOCKING: term for the positive social behaviour of individual birds that results in their joining into groups (flocks), as distinguished from aggregations of animals resulting from the influence of ecological factors alone.

Characteristics of flocks. Flocks may consist of one to several species, the latter usually referred to as mixed-species flocks. Dominance hierarchies may exist in both single and mixed-species flocks, and an individual's ranking may affect its access to food. In the tropics flocks exist year-round, while at higher latitudes they are confined to the non-breeding season and to non-breeding birds. Flocks range in size from a few birds to thousands of individuals, as seen in some icterid or finch flocks. Many flocks are constantly on the move, showing a loosely coordinated, unidirectional movement that distinguishes them from chance aggregations. They may cover as much as several hundred metres within an hour, even when their individuals are successful in finding food. Members of compact open-country flocks frequently exhibit conspicuous 'leap-frog' movements, in which birds at the rear fly over and land in front of the other members. In this way they minimize the probability of encountering just-exploited areas.

Although flocks result in a large-scale clumped distribution of birds, at a smaller scale these birds are evenly spaced. Members of open-country flocks are usually spaced much more closely than those of forest-dwelling flocks, sometimes not over a body-length apart. Birds in forest-dwelling flocks usually remain at least several metres apart, but their minimal tolerated distances (individual distances) vary among species or at different times. Half of the advances by Black-capped Chickadees *Parus atricapillus* to within 3 m of a conspecific resulted in a supplanting action or retreat; in Blue Tits *Parus caeruleus*, the corresponding distance was one metre.

Flock members may either roost communally or apart. Icterid and starling flocks sometimes remain as units within large roosts. Members of forest-dwelling flocks, however, usually roost in holes or other sites independently of each other and join shortly after becoming active in the following morning.

Flock members obtain one or more general advantages: feeding, predator-avoidance, and reproductive. In most cases, reproductive advantages (*sensu stricto*) may be separated from the others and they will not be further discussed here (see NATURAL SELECTION). Bird flocks bear many functional similarities to fish schools and mammal herds or troops.

Feeding advantages. Foraging flocks are a common phenomenon among birds. Hypothetically, birds may obtain several food-related advantages while in them.

Facilitation of food-finding. Probably the most frequently suggested feeding advantage is that participating in a group facilitates food-finding. One bird may observe another foraging and join it if the original forager is successful. For this to be advantageous, food must be so abundant that one individual can not consume it all quickly. Alternatively, an individual may simply forage at a site similar to one where another individual is foraging successfully. The only experimental evidence supporting either alternative is from the laboratory studies using Great Tits *Parus major*. Several field studies have also produced evidence consistent with this advantage. Rather than increasing the amount of food that an individual will find, flocking may lessen the danger of an individual going without food for long periods. Given the severe conditions often experienced by birds at high latitudes during the winter, and the tendency for flocking to increase as climatic conditions grow more severe, this hypothesis has merit.

Minimizing duplication of effort. If flock members deplete an area other birds must avoid that site. They may obtain this advantage by watching the movements of others, although little direct evidence exists that they do this. This pattern would be advantageous if food were evenly distributed in parcels too small for more than one individual to exploit.

Success from numbers. Individuals may have access to certain resources by sole virtue of their numbers. If Cedar Waxwings *Bombycilla cedrorum* enter a Mockingbird *Mimus polyglottos* territory, the Mockingbird will attempt to drive them out, but if their flock consists of several score individuals, the Mockingbird may be able to evict only a small minority of them. In this way the Waxwings can exploit the rich berry sources often defended by a Mockingbird during the winter.

Beating. It is often suggested, particularly in the older literature, that a major advantage of flocking lies in the insects that are flushed (and subsequently captured) by the participants. Some individuals may so benefit when insects are active; however, the advantage cannot occur in all cases, since flocks of small insectivorous birds are most prominent at high latitudes during winter, when insects are inactive. Further, unless birds can capture flying insects, they are unlikely to benefit. For beating to be a direct advantage of flocking, rather than an advantage only to certain members, more flushed prey must be captured by birds when in groups than when alone, and this advantage must hold for all members. Such conditions are not met in most flocks of small insectivorous birds, and certainly not in flocks that feed on non-motile prey. However, Cattle Egrets *Bubulcus ibis* feeding in groups may obtain this advantage, although their foraging success is lower than when they follow cattle. Flocks of pelicans, cormorants and mergansers may also drive schooled fishes into shallow water where these birds can capture their prey more readily than in deep water.

Predator-avoidance advantages. Flock members may enhance their ability to escape predators in several ways.

Increased awareness of predators. Individuals should be apprised of predators more rapidly in groups, because many eyes are present. Predation is less severe on members of wader and Woodpigeon *Columba palumbus* flocks than on single individuals. Vulnerability decreases as flocks become larger up to a certain point. In the case of waders and corvids, detailed observations have shown that more birds were taken from larger flocks than from smaller ones. If flocks become too large, an individual on one side of the flock may not see a predator approaching from the other. Alternatively, individuals might get in each other's way during an escape. Evidence on these points is not available for most bird flocks, and some workers have argued that the increased conspicuousness of flock members may negate any advantages. Members of many flocks call nearly continuously, including notes that may not be given at other times. Thus, although the percentage of successful attacks might decline, the number of attacks might increase.

Confusion effect. A mass response, whether a sudden flight or calling, may confuse a predator, at least temporarily, giving flock members the opportunity to escape. When confronted with many simultaneous stimuli, a predator may find it impossible to separate out a single individual. When attacking a flock, a predator's typical strategy is to separate an

Oystercatchers *Haematopus ostralegus* flocking. (*Photo: H.E. Grenfell*).

individual if possible. Many, although not all, flocking species give characteristic calls upon detecting a predator. These calls have been considered difficult to localize because of their acoustical properties. However, at least some avian predators can localize them; but in any case the fact that it is calling means that the flock member is aware of the predator. As a consequence, the predator may not attempt to capture it.

Discouraging predators. Some animals may repel predators as a consequence of their numbers, by posing a threat. Flocks in flight tighten their formation, thereby providing a target that may be dangerous to any predator that attempts to fly into the middle of it. Starling *Sturnus vulgaris* and Red-winged Blackbird *Agelaius phoeniceus* flocks may even turn on their attackers, forcing them on to the ground or into the water. Alternatively, if being in a flock makes individuals more difficult to capture, it may not be worth the predator's efforts to attack, though no data known to the writer support the existence of this effect in bird flocks.

Cover-seeking. A given flock member might obtain protection from predators by hiding behind other members, or at least by positioning itself so that one or more flock members lie between it and the predator. This behaviour would favour central individuals over peripheral ones and would tend to result in a compact group. Little direct evidence exists for this in birds. In flocks with widely-spaced individuals, such as mixed-species insectivorous flocks, such a hypothetical advantage would seem confined to maintaining a core position, thus keeping other individuals between the actor and the periphery, from which an attack would normally come. However, even if these effects were demonstrated, they could not be considered a primary advantage of flocking, unless all members benefited from it. Thus, if peripheral individuals suffered increased predation as a consequence, they would be continually peeled off the outside. More likely, peripheral individuals would stop flocking before severe predation ever took place.

Decreasing the probability of discovery. Several workers have suggested from mathematical formulations that animals in groups should be discovered less frequently than if they were solitary. However, it is questionable whether such advantages exist in the real world. These models assume random movement on the part of the flocks and predators and do not account for possible behavioural changes of members between solitary and social situations. Flock members and their predators, at least when in heterogeneous habitats, concentrate their activities in certain places. Further, they perform various behavioural patterns that are not typically given by solitary individuals. For instance, tits in flocks regularly produce calls that are not given elsewhere. If a flock member becomes temporarily separated from other individuals, it often calls loudly from a conspicuous perch. Both these behaviours make flocks conspicuous to human observers, and probably to flock predators as well.

Single-species and mixed-species flocks. Both single-species and mixed-species flocks may share the non-reproductive advantages discussed above. However, differences should exist in the magnitude of advantages obtained. Although members of mixed-species flocks overlap with each other in foraging, this overlap is lower than that among members of the same species. Thus, if food is scarce, individuals of different species would not be disadvantaged as greatly as members of the same species. However, any food-related advantages should not be as great as those obtained in a single-species flock.

If the energetic stakes are lower in mixed-species flocks than in single-species flocks, some other factor should account for the existence of mixed-species, as opposed to single-species, flocks. Anti-predator advantages should be relatively greater in mixed-species flocks, by virtue of the greater variety of eyes brought to bear, the wider range of locations often exploited at a given time, and the larger size often possible in mixed-species groups, a probable consequence of lowered competition.

Certain species often sound anti-predator warnings first. Carolina Chickadees *Parus carolinensis* usually sound the warning in mixed-species forest flocks in eastern USA. It is not clear whether they are thus being parasitized by other species, or whether the sentinels obtain special advantages in return. However, species sharing relatively little foraging similarity to other members of flocks sometimes move with them for considerable distances. For instance, Eastern Bluebirds *Sialia sialis*, Dark-eyed Juncos *Junco hyemalis*, and Chipping Sparrows *Spizella passerina* often follow tit flocks through open woodlands, spending much of their time foraging on the ground. If individuals in the trees sound warnings, these 3 species fly rapidly to cover. They probably take advantage of the others' elevated locations to lessen the danger of being captured unaware. If so, this relationship is a commensal one; that is, one in which they benefit and the other members are unaffected.

Migrants in flocks. Flock function has been little studied during migration, although migrants often move in groups or join other flocks between their flights. Migrants might find rich food sites or protection from predators by following resident groups. Since migrants are unfamiliar with their surroundings, their potential reward from joining residents should be large.

Evolution of flocking. Many workers have argued that either foraging or anti-predator advantages are responsible for the evolution of flocking. These arguments are fraught with danger, because it is unlikely that either advantage will exist in the absence of adaptations associated with the other. Thus, if individuals commenced to form flocks that enhanced foraging, they would quickly become vulnerable to predation, unless they simultaneously developed anti-predator adaptations lowering predation at least to a point where feeding advantages outweighed the increased risk of predation.

Alternatively, if individuals formed flocks that enhanced avoidance of predators, they would be likely to incur feeding disadvantages as a consequence. Strong pressure would consequently develop to minimize foraging disadvantages. In either case, if one capability develops, the other should quickly follow.

Flock size. A close relationship may exist between energetic conditions, aggression levels, predation pressure, and consequent flock size. When energetic demands are stringent, foraging occupies so much of flock members' time that they have little time left to fight. This might happen at a time of deteriorating food supply, or when cold weather makes high energetic demands. Flocks increase in size and cohesion at such times, and individuals simultaneously decrease their frequency of scanning for predators, permitting an increased proportion of time to be spent searching for food, presumably with no added danger of predation. If conditions become less stringent, more time is available for fighting. Flock size declines at such times, probably because subordinate birds are harassed so frequently that it no longer benefits them to participate in the flock. However, certain reports are not consistent with these observations. For instance, increased fighting for food accompanies extremely severe conditions in corvid and tit flocks. Whether or not flock sizes in extremely large groups follow this pattern remains to be explored. The flocks discussed here are of modest size, within the range in which individual recognition remains possible.

Other groupings. In practice it may be difficult to distinguish between flocks and other groupings (see ROOSTING; COLONIALITY). Some of the flocks discussed above have clearly-defined commensals attached to them, such as the bluebirds *Sialia* and sparrows (Emberizidae) that follow tit flocks. It is not a great jump from these associations to two-species feeding associations, such as those between grebes and ducks or coots, in which the former obtain food dislodged by the latter. Similar associations may even form between birds and other animals, such as squirrels that follow bird flocks, or monkeys that follow hornbills.

See photos FACILITATION, SOCIAL; ROOSTING.

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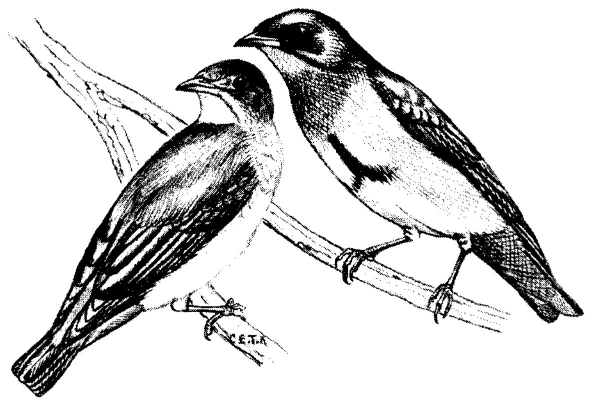
FLORA: the total plant life of an area (contrasted with FAUNA); see HABITAT.

FLORICAN: substantive name (also spelt 'floriken') of 2 Indian species of Otididae (see BUSTARD).

FLOWERPECKER: substantive name of some species of Dicaeidae (Passeriformes, suborder Oscines); in the plural, general term for the family. This is a group of small or (rarely) medium sized arboreal birds (7.5–19 cm long) of Oriental and Australasian distribution.



Mistletoebird *Dicaeum hirundinaceum*, female (left) and male. (*C.E.T.K.*).

Characteristics. Most (40 out of 55 species) are grouped within the 2 widely distributed genera *Prionochilus* and *Dicaeum*. These typical flowerpeckers are small birds, with a wing length in adult individuals of 4.0–7.5 cm, and with short, stumpy tails. The bill, in which the edges of the distal third are serrated, is short, varying in structure between a stout and blunt type like that of tits (Paridae) and a thin, attenuated, more or less decurved type like that of warblers (Sylviinae) or short-billed sunbirds (Nectariniidae). The short tongue has, in its deeply cleft distal half, the edges curled to form two slender semitubular tips; this somewhat resembles the tongue structure in sunbirds and is probably an adaptation to nectar feeding. The plumage coloration in some species is plain, similar in both sexes; in other species the males are brightly coloured, often with contrasting patches of red and with glossy areas, the females as a rule being more dully coloured. The outermost (tenth) primary is well-developed in *Prionochilus*, but vestigial in *Dicaeum* except in *D. melanoxanthum*.

Habitat. Habitat selection is very varied. Some species frequent lowland rain-forest, others the montane mossy forests, and *Paramythia montium* ascends even to the stunted trees of the timberline. Many species prefer second growth, bamboo groves, and cultivated areas, and may, as in the case of the Scarlet-backed Flowerpecker *Dicaeum cruentatum* of Burma and Malaya, be common inhabitants of village and town gardens. The New Guinean endemic genera mainly frequent forest understory. The Mistletoebird *Dicaeum hirundinaceum* of Australia occurs in diverse habitats, ranging from rain-forest to arid *Acacia* woodland.

Distribution. The distribution of the family covers the whole Oriental Region westwards to the drier parts of India, and the Australasian Region (not New Zealand) eastwards to the Solomon Islands. Two species, *Dicaeum ignipectus* and *D. melanoxanthum*, range into the Palearctic parts of the Himalayan area and south-western China. Richest in species are the Philippines (13 species, of which 11 are endemic) and New Guinea (11 species, all endemic).

The New Guinean genera *Melanocharis* (with 5 species) and *Rhamphocharis* (monotypic) are more primitive and have a rather simple structure of the tongue, but in many ways show relationship to *Prionochilus*. The New Guinean monotypic genera *Oreocharis* and *Paramythia*, as well as the Australian genus *Pardalotus* (pardalotes or diamond-birds) with 7 species inhabiting the Australian continent and Tasmania, are more aberrant, and their relationship with the typical flowerpeckers is obviously remote. They share with *Dicaeum* the vestigial outer primary, but differ in having simple tongue structure and in lacking the serration of the bill. Even in habits they differ strikingly. The Tit Berrypecker *Oreocharis arfaki* resembles a large tit, while the Crested Berrypecker *Paramythia montium* is the size of a thrush *Turdus*. The pardalotes come nearest to the typical flowerpeckers in appearance. They are small birds with short tails, tit-like bills, and a variegated plumage in which a spotted pattern is very conspicuous and has given rise to the common names. Nevertheless, the pardalotes may probably belong to a separate family, the Pardalotidae, as protein analysis indicates they are closer to other Australian families than to the Dicaeidae.

Movements. All flowerpeckers are sedentary in high degree, except the Mistletoebird *Dicaeum hirundinaceum*, which has nomadic habits and is a powerful flyer with long swallow-like wings.

Food. The food of the typical flowerpeckers consists of berries (chiefly those of the family Loranthaceae), nectar, and insects. The pardalotes are almost entirely insectivorous, while the 4 New Guinean endemic genera are fruiteaters.

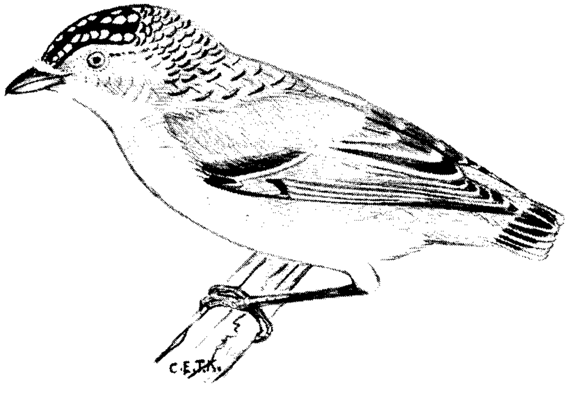
Behaviour and voice. The typical flowerpeckers resemble sunbirds in appearance and general habits. They usually frequent high trees, where they fly restlessly around in search of food, their favourite hunting grounds being flowering epiphytes, strangling figs, or, particularly, clumps of parasitic plants growing high up in the branches. They are energetic and noisy birds that turn and twist about in every kind of attitude and constantly twitter when feeding. During flight they utter rather sharp call notes that can be rendered as *chip*, *chip*. Some species have modest warbled songs. The flowerpeckers are not especially gregarious, but appear in pairs or family parties.

Breeding. The pendent, domed nests of the typical flowerpeckers are similar to those of sunbirds. They are pear-shaped structures, suspended by the stalk from a twig, with the entrance high on one side, built of vegetable fibres, rootlets, grass, and cobwebs, lined with silky down. The nest of the Thick-billed Flowerpecker *Dicaeum agile* (Indo-Malayan) differs in its peculiar felt-like fabric. The pardalotes place their nests in holes in trees or hollows or crevices in the ground, or in a tunnel excavated by the birds themselves, usually in the side of a bank. The nest itself is elaborately built of bark and grass, and is usually cup-shaped—but domed in some species. Nests of the endemic New Guinean *Paramythia* and *Melanocharis* are cup-shaped and placed in dense bushes.

Most flowerpeckers lay white eggs, only *Paramythia*, *Melanocharis* and a few species of *Dicaeum* have spotted eggs. The clutch size is 1–4 (usually 2) in *Dicaeum* and *Prionochilus*; 2 in *Melanocharis*, one only in *Paramythia* while *Pardalotus* lays 2–5, usually 4. In the species investigated the female alone builds the nest and incubates the eggs, while both sexes participate in the feeding of the young. In *Pardalotus* it is known that the excavating of the nesting tunnel is shared by both sexes.

Ecological relations. A close association exists between certain flowerpeckers and the mistletoes (chiefly Loranthaceae: *Amyema*, *Lysiana*, *Muellerina*, *Dendrophthoe*, *Viscum*). Many species among the typical flowerpeckers feed almost exclusively on the fruits of these plants (apart from insects), and at the same time they constitute by far the most effective disseminators of the mistletoe seeds. In this way a mutual dependency, highly specialized, has evolved between the plants and the birds. In spreading these harmful parasitic plants, which are a serious pest in many areas, the flowerpeckers become important birds from an economic point of view.

The method of eating the mistletoe berries differs according to the structure of the bill. The thick-billed species, such as *Dicaeum agile*, use the bill to separate the fleshy epicarp from the seed, swallowing the former and getting rid of the latter by scraping it off on a twig. The thin-billed species, such as Tickell's Flowerpecker *Dicaeum erythrorhynchos* of India, swallow the berries whole and void the viscous seeds after an astonishingly short time, usually a few minutes. The seeds are able to germinate in both cases, i.e. whether they have passed through the alimentary canal of the birds or not. The extraordinary rapidity with which the mistletoe fruits pass through the intestines is due partly to the laxative effect of the berries, but mainly to a special structure of the stomach. The muscular stomach has developed into a blind sac with a sphincter at its opening, which construction allows the easily digestible



Red-browed Pardalote *Pardalotus rubricatus*. (*C.E.T.K.*).

berries to pass directly from the oesophagus to the intestine without entering the stomach; on the other hand, insects and spiders, which need grinding and a more thorough treatment before the digestible parts can be assimilated, are not prevented from entering the muscular stomach. The alimentary canal of *Melanocharis* and *Paramythia* is not so specialized, but more closely resembles that in other fruit-eating passerines.

Owing to their nectar feeding, many flowerpeckers are of importance as pollinators of various flowers, but in this respect play a lesser role than honeyeaters (Meliphagidae), sunbirds (Nectariniidae), and some other groups (see POLLINATORS; SEED DISPERSAL.) F.S.

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FLOWER-PIERCER: substantive name of *Diglossa* spp., a group of specialized Neotropical passerine birds (suborder Oscines) formerly included in the family Coerebidae but now treated as members of the tanager subfamily, Thraupinae (see HONEYCREEPER (1); TANAGER). Relationships within this large passerine assemblage are still uncertain, and future research may well modify the arrangement adopted here. The most striking character of the flower-piercers is the form of the bill and associated feeding method. The upper mandible has a sharply hooked tip and is notched along the cutting edge, while the lower mandible, which is a little shorter, ends in a very sharp point. Flower-piercers extract nectar from flowers by hooking the upper mandible round the corolla tube, thus holding it in position while the lower mandible pierces the tube and the tongue, which is unusually long and U-shaped in cross-section, is inserted into the slit. By this means flower-piercers are able to visit and take the nectar from small flowers in very rapid succession, as well as extracting more slowly the more copious nectar from larger flowers. Since they do not come into contact with the reproductive parts of the flower they are 'nectar thieves' rather than pollinators, and where they coexist with hummingbirds they may be important ecological competitors. On occasion, however, they may also extract nectar in the 'legitimate' manner, by inserting the bill into the mouth of the corolla tube if the mouth is wide enough. Not all species of flower-piercers are equally specialized; in some the bill is less highly modified and fruit may be an important part of the diet. Probably all the species also take insects.

Distribution. The flower-piercers have their centre of abundance in the Andes, where they are a characteristic element in the avifauna of woodland and shrubby country at subtropical and temperate levels. One species extends to the highlands of Central America, and 2 endemic species occur in the isolated highlands of southern Venezuela. The total number of species of *Diglossa* is problematical, as there has evidently been much recent diversification of populations isolated in different parts of the Andes, and it is in several cases not clear whether the isolates have diverged sufficiently to qualify as separate species; 11 species are currently recognized.

Characteristics and breeding. Flower-piercers are mainly dull-plumaged birds, largely slaty grey or black in the male and paler grey and olive in the female; but dark shining blue plumage occurs in some species, and in another the black plumage is set off by a conspicuous tuft of white feathers on each flank. Their voices are generally weak and high-pitched. The nest of the only species that has been well studied, the Slaty Flower-piercer *D. baritula* in Central America, is a substantial cup placed in a shrub or sapling, and the 2 eggs are bright blue spotted with brown. The nestlings are fed by regurgitation, and receive the food into a large protuberant crop, in which respect they resemble the hummingbirds. D.W.S.(1)

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FLUKES: see ENDOPARASITE.

FLUSH: disturb bird, usually into flight.

FLUVICOLINAE: subfamily of Tyrannidae (see FLYCATCHER (2)).

FLYCATCHER (1): substantive name of the family Muscicapidae (Passeriformes, suborder Oscines), comprising about 150 species distributed throughout the Old World.

Characteristics. The species in this large group are very variable in plumage and behaviour but most are about 10–20 cm in length and are characterized by broad, flattened bills surrounded by rictal bristles and short, weak legs that are used mainly just for perching. Most of the larger species have long wings and are good fliers, feeding by hawking flying insects in mid-air or by diving from a perch on to insects on the ground. Some of the smaller species feed like warblers (Sylviidae), hopping amongst vegetation and picking insects from the foliage. In the New World the flycatcher ecological niche is occupied by the tyrant-flycatchers of the family Tyrannidae (see FLYCATCHER (2)).

Habitat and distribution. The family includes the *Ficedula* and *Muscicapa* flycatchers of Europe, Africa and Asia, the *Melaenornis* and *Bradornis* flycatchers from Africa, and the *Niltava* and *Eumyias* flycatchers from Asia.

The habitats occupied come under two broad categories related to foraging behaviour. Some species inhabit parks, orchards, gardens and woodland edges where they sally forth from prominent perches and capture flying insects or prey on the ground, often returning to the same perch again after a capture attempt (e.g. Spotted Flycatcher *Muscicapa striata* and Verditer Flycatcher *Eumyias thalassina*). Other species inhabit woodland where they capture insects on the wing amongst the branches or pick up prey from the foliage in the canopy (e.g. Pied Flycatcher *Ficedula hypoleuca*). Some species may join mixed-species flocks in the foliage of forest trees. In the Himalayas, for example, the Rufous-bellied Niltava *Niltava sundara*, is frequently seen with small parties of tits, warblers and babblers, snapping up small insects disturbed by the flock as it moves through the trees.

Populations and movements. As might be expected from their specialized insect diet, flycatchers are migratory. All the Palearctic species winter in the tropics. The Pied and the Collared Flycatcher *F. albicollis* winter in Africa south of the Sahara, probably mainly in evergreen forest in the canopy and along forest edges. The Spotted Flycatcher winters from Kenya south to the Cape in thorn country, forest edges and gardens. The Red-breasted Flycatcher *F. parva* winters in India and Sri Lanka. Species breeding in the Himalayas show altitudinal migration, moving down into the valleys in winter.

In the breeding season the Pied Flycatcher inhabits deciduous, and sometimes coniferous, woodland in western and northern Europe. In south-eastern Europe it is replaced by the very similar Collared Flycatcher and there is an area of overlap in central and eastern Europe and on the island of Gotland in the Baltic where the 2 species occasionally interbreed. On Gotland, the Collared Flycatcher is 10 times as abundant as the Pied Flycatcher and the 2 species hybridize (4% of all matings) at frequencies less than predicted for random mating (13%). Mixed pairs produce just as many offspring as same-species pairs but fewer hybrids breed than would be expected from the proportion of hybrid fledglings in the population, probably due to poorer survival after fledging and also, perhaps, to the inefficiency of hybrids at mate attraction.

Food. Pied and Collared Flycatchers feed their young on both adult and larval insects, particularly caterpillars collected from the tree canopy. The Spotted Flycatcher takes mainly large flying insects, especially Diptera (Muscidae, Calliphoridae, Scatophagidae, Syrphidae), Lepidoptera and Coleoptera. They also eat bees (*Bombus*) and wasps (*Vespula*) and beat these against a perch to remove the stings before swallowing them or giving them to their nestlings. Early in the morning or during cold, wet days, when large flying insects are scarce, they feed up in the tree canopy on swarms of small insects, especially Chironomidae and Aphididae. During the egg laying stage the female seeks out calcium-rich prey including snails (Mollusca) and woodlice (Isopoda) presumably to help her form the egg shells. These prey are also given to the nestlings, probably to help bone growth. Nestlings are given larger prey than the adults eat themselves because it is more economical to carry large prey back to the nest.

Spotted Flycatcher *Muscicapa striata*. (R.G.).

Behaviour. Most species are territorial in the breeding season. Pied Flycatchers defend their nest holes and Spotted Flycatchers defend their nest sites and favourite feeding perches presumably to avoid interference in prey capture from conspecifics. Male and female within a pair may also avoid interference by feeding in different parts of the territory. Other species, including the Pied Flycatcher, defend feeding territories even during the short stop-overs on migration when they spend a week or so fattening up prior to the Sahara crossing.

In the breeding season the nest defence behaviour of the Pied Flycatcher is beautifully adapted to the dangers presented by particular predators. Woodpeckers and squirrels, which are only a threat to the brood, are attacked with swooping dives accompanied by snarling calls. Owls and Red-backed Shrikes *Lanius collurio* on the other hand prey upon both the adults and the young and are merely mobbed from a safe distance. Experiments with hand-reared, naive birds showed that recognition of these predators is innate. The Spanish population of the Pied Flycatcher, *F. hypoleuca iberiae*, reacts to owls but not to Red-backed Shrikes, which are absent from Spain. Therefore geographical variation in enemy recognition matches the occurrence of the predators.

Voice. Some species have songs consisting of musical warbles but in others the song is very weak and is just a few thin, squeaky notes. Many species utter loud alarm calls, much heard when the young have fledged.

Breeding. Some species build neat, open cup-shaped nests in crevices in walls or against tree trunks (Spotted Flycatcher). Others breed in holes in trees (Pied and Collared Flycatchers) and will regularly occupy nest boxes. The Black and Orange Flycatcher, *Ochromela nigrorufa*, of southern India builds an enclosed nest of moss, with a side entrance, under tree roots on the forest floor. Sometimes the old nests of other species are used, for example old thrush and blackbird *Turdus* nests (Spotted Flycatcher), old weaver bird nests (Swamp Flycatcher *Alseonax aquaticus*) and old woodpecker holes (Pied Flycatcher).

The eggs of flycatchers are blue, brown, red, yellow or white in background with spots and mottling. In tropical or subtropical species the clutch is usually 2–3 eggs but in temperate regions it is larger (usually 5–7 but up to 10 in the Pied Flycatcher and usually 4–5 in the Spotted Flycatcher). In *Ficedula* spp. it is usually the female who incubates alone but in other species both sexes take part. Both parents feed the young. Incubation and nestling periods are both about 10–15 days.

In the Spotted Flycatcher the male may provide up to 30% of the female's food by courtship feeding during the egg-laying period and he also feeds her while she is incubating on the nest. In the Pied Flycatcher the male may provide the incubating female with half her food requirements. There have been several detailed population studies of the Pied Flycatcher with densities of up to 4 nests per hectare. Early broods are more successful than late broods, reflecting the decline in the abundance of the caterpillar food for the young. There is a seasonal decline in clutch size; for example in the Forest of Dean in England, mean clutch size is 7.5 at peak in May and 4.5 in the middle of June.

In both the Pied and the Collared Flycatcher, some males are successively bigamous and some first year males fail to breed. A male increases his reproductive success through polygamy but his second female suffers because only the first female gets the male's help with chick feeding. A male goes a long way from his first nest site (up to 3.5 km) in order to attract a second female, perhaps to deceive her into thinking that he is unmated.

In Britain, the Spotted Flycatcher is one of the last summer visitors to arrive and breed, usually laying at the end of May. This is probably because it is not until fairly late in the summer that there is a guaranteed supply of large flying insects on which this species feeds its young.

N.B.D.

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FLYCATCHER (2): substantive name of most species of Tyrannidae (Passeriformes, suborder Deutero-oscines, infraorder Tyranni); in the plural forms 'tyrant-flycatchers' or 'New World flycatchers', general name for the family; a diverse assemblage of 375 species in about 90 genera, entirely restricted to the New World, predominantly the Neotropical realm where it is numerically the dominant land-bird family. Other major substantive names for members of the family include 'tyrant', 'tyrannulet', 'kingbird', 'phoebe', 'pewee', 'flatbill', and 'elaenia'.

Systematics. Closely related to Cotingidae and Pipridae, with which its taxonomic boundaries have been enigmatic. Presently considered to contain at least 3 subfamilies, Elaeniinae, Fluvicolinae, and Tyranninae; by some authors, a fourth subfamily, Tityrinae, is provisionally moved to this family from Cotingidae. The family is defined primarily by cranial, syringeal, and tarsal characters.

Characteristics. In its great diversity of body forms and foraging styles, the family replaces numerous Old World families, principally the Muscicapidae (see FLYCATCHER (1)). The family includes ecological counterparts of warblers, wrens, vireos, jays, shrikes, pipits, thrushes, and certain icterids, as well as many sorts of aerial flycatching species of various families. Body sizes range from the smallest passerine species (Short-tailed Pygmy-Tyrant *Myiornis ecaudatus*; total length 5 cm, wing length (3.0–3.5 cm) up to medium-sized birds in the genera *Agriornis*, *Xolmis*, *Tyrannus* and their relatives (wing lengths 11–14 cm). Body weights span from 4.5–80 g. Sexual dimorphism in size is minor, males averaging slightly the larger.

Variation in body form is primarily associated with the diversity of foraging styles. Wings are short and rounded among the tody-tyrants (*Todirostrum*, *Hemitriccus*, and related genera), which glean prey with short hops in dense foliage. Wings are long and pointed in the many genera that forage with powerful aerial sallies in open places, such as the kingbirds *Tyrannus* spp. and pewees *Contopus* spp. Deeply forked and greatly elongated tails occur in many of these 'aerial hawkers', including the genus *Tyrannus* (contains Scissor-tailed *T. forficatus* and Fork-tailed *T. savana* Flycatchers, formerly genus *Muscivora*), in the Streamer-tailed Tyrant *Gubernetes yetapa*, Long-tailed Tyrant *Colonia colonus*, and others. Tarsi vary from extremely short in the Cliff Flycatcher *Hirundinea ferruginea*, to long and strong in several terrestrial genera such as *Muscisaxicola*, *Muscigralla* and *Machetornis*. Bills tend to be broad at the base, but great variation is evident in this character as well; the longest and broadest bill is that of the Boat-billed Flycatcher *Megarhynchus pitangua*; specialized, wide and spatulate bills occur in the spadebills *Playtrinchus* spp., flatbills *Rhynchocyclus* spp., and relatives; narrow, warbler-like bills occur in several genera (e.g. *Ornithion*, *Camptostoma*, *Inezia*) that probe and glean for insects without sallying from perches.

Rictal bristles are in general well developed, excessively so in *Onychorhynchus*, *Myiobius* spp. and relatives; in species that are either heavily frugivorous (e.g. *Elaenia* spp.) or do not sally while foraging (e.g. Southern Beardless Flycatcher *Camptostoma obsoletum*), rictal bristles are reduced or absent.

Overall coloration typically is drab; the most common pattern is olive-green above, bright or pale yellow to whitish below, with or without pale superciliary eye rings, stripes, or wingbars. Other colours include browns, greys, black and white. Bright colours besides yellow are rare, and blue is virtually absent. Eight tyrannine genera share a common colour pattern of bright yellow underparts, dull olive back, and contrasting black or grey and white stripes on the crown. Many species show slight to well developed crests. Semi-concealed red, orange, yellow, or white crown patches occur in 30 of the 90 genera. The most extreme crown ornamentation is a long, erectile crest of brilliant orange feathers tipped iridescent blue, in the Royal Flycatcher *Onychorhynchus coronatus*. Pronounced sexual dimorphism in plumage is rare except in one group of fluvicoline genera, in which males typically are black or black-and-white, and females are brownish (e.g. *Knipolegus*, *Fluvicola*, *Alectrurus*). The male Vermilion Flycatcher *Pyrocephalus rubinus* is predominantly brilliant scarlet, unique in the family. The Many-coloured Rush Tyrant *Tachuris rubigastra*, a marsh-dwelling species of Argentina and the high Andes, shows a harlequin pattern of reds, yellows, blue, green and black.

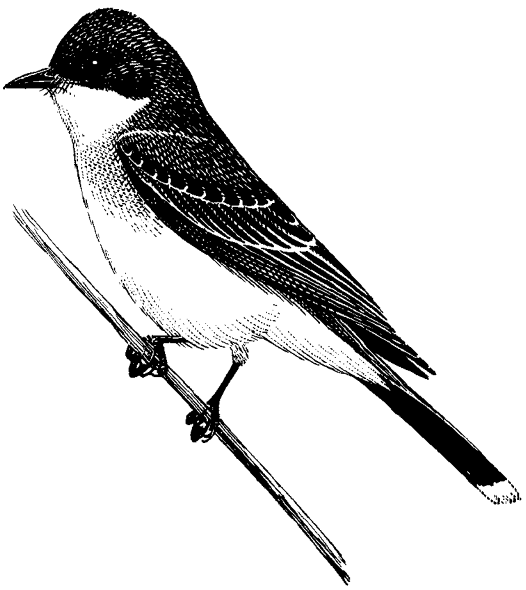
Habitat. Foliage-gleaning species, which predominate, occur in all vegetation types from temperate woodlands and tropical desert scrubs to dense deciduous and evergreen forests, from treeline to sea-level. Aerial hawking flycatchers occupy open, forest-edge habitats, water margins, and cliff faces. Terrestrial species, such as the Cattle Tyrant *Machetornis rixosus* and various ground-tyrants (genus *Muscisaxicola*), predominantly occupy savanna or bare, rocky alpine habitats. Many species dwell along stream, river, and lake margins, where they may take aerial prey (e.g. Black Phoebe *Sayornis nigricans*), aquatic prey from the surface (e.g. Lesser Kiskadee *Pitangus lictor*) or even from underwater (e.g. Greater Kiskadee *Pitangus sulphuratus*, a frequent fish-eater).

Distribution. Found virtually throughout the New World, tyrant-flycatchers occur from the taiga of Alaska and northern Canada (where all species are migratory) south through the Americas and West Indies to the southern tip of South America and adjacent islands, including the Galapagos Archipelago (2 species). Only about 30 species occur north of Mexico. Greatest diversity is reached in the Amazonian and eastern Andean forests. More than 70 species have been found together at several localities in western Amazonia.

Many lowland species occur throughout the forested Neotropics. Certain open-country species such as the Tropical Kingbird *Tyrannus melancholicus* and Vermilion Flycatcher occur from southern North America south to central Argentina. Others, especially those inhabiting cloud forests or oceanic islands, show greatly restricted distributions.

Movements. All species that breed in North America are at least partially migratory, wintering primarily in Central and northern South America. In some species only the northernmost populations migrate. The Eastern Kingbird *Tyrannus tyrannus* migrates in huge flocks from as far north as Alaska and northern Canada south as far as Bolivia and northern Argentina. Many long-distance migrants, such as the Eastern Wood Pewee *Contopus virens*, maintain exclusive territories on their wintering grounds. Many, perhaps most, of the temperate-zone species of Patagonia, southern Argentina, and even southern Brazil migrate northward to equatorial latitudes. The Piratic Flycatcher *Legatus leucophaius* migrates entirely within tropical latitudes, apparently in response to seasonal patterns of fruiting by tropical forest trees. Local movement patterns within tropical forest regions by Olive-striped and Ochre-bellied Flycatchers and relatives (*Mionectes* spp.) have been recently documented, but remain poorly understood.

Food. Feeding habits vary enormously within the family, but nearly all species are predominantly insectivorous. Insects of all kinds are eaten, most frequently snatched from the air or from leaf surfaces during a rapid, sudden flight (sally) from a stationary perch. Some species, like the shrike-tyrants *Agriornis* spp. and the monjitas *Xolmis* spp., drop to the ground from exposed perches in the manner of bluebirds (*Sialia*). Others, mentioned above, take various invertebrates while walking on the ground. The larger species, especially the Greater Kiskadee, frequently feed on fish, tadpoles, frogs and lizards as well as large moths, orthopterans and other arthropods. Many tropical species regularly eat fruit from vines, mistletoes, or trees. The Piratic Flycatcher and several species of *Elaenia* and relatives are almost entirely frugivorous during much of the year.



Eastern Kingbird *Tyrannus tyrannus*. (R.G.)

Behaviour. Most species live as monogamous pairs on territories, in a relatively simple social structure. Some migratory species, such as the Variegated Flycatcher *Empidonomus varius*, and the Fork-tailed Flycatcher *Tyrannus savana*, congregate in flocks of up to several hundred individuals during the non-breeding season, but no true coloniality is known to occur in any species. Intra- and interspecific communal roosting occurs among some tyrannine species. Helpers at the nest occur in a few species, especially the White-bearded Flycatcher *Conopias inornatus*, but this, too, is uncommon. The Piratic Flycatcher breeds within large colonies of caciques (Icteridae), whose nests it takes over through harassment. Members of the genus *Mionectes* (incl. '*Pipromorpha*' spp.) are known to exhibit loose LEK behaviour in their forested habitats, associated with their highly frugivorous diet. Some sexually dimorphic grassland species, especially the Cock-tailed Tyrant *Alectrurus tricolor*, may be polygynous. This and numerous related species have peculiar and highly stereotyped aerial displays. The Spectacled Tyrant *Hymenops perspicillata*, in which the all-black male has wide, fleshy yellow eyerings, performs spectacular aerial loops and somersaults over its marshy habitat during courtship. Tail flicking or pumping is common, particularly among terrestrial forms such as the Masked Water Tyrant *Fluvicola nengeta*. The tail is cocked and spread like a fan during active foraging by *Myiobius* spp. Wing-stretching, flicking, whirring or buzzing are featured in the territorial or courtship displays of almost all species. The Common Tody-Flycatcher *Todirostrum cinereum* cocks its tail vertically and hitches sideways along a perch during such a display.

Voice. Tyrant-flycatcher vocalizations are notably simple and weak, with only a few exceptions. Most species whistle uncomplicated single syllables, phrases, or short trills. These include some of the least conspicuous advertising songs of any species of Passeriformes. The most remarkable vocal feature of the family is the propensity of nearly all its members to utter repetitive 'dawn songs', at or before first light during breeding seasons. These typically include more extended and complicated versions of the simple, daytime advertising songs, but in some species certain vocal patterns are restricted to this period of active calling. Thus, in the Neotropics, flycatchers of many species are frequently the first birds to be heard vocalizing as dawn breaks. Aerial displays are accompanied by special flight songs in some fluvicoline species and in the kingbirds.

Breeding. Nest structure varies considerably. Most typical is a simple cup placed in a forked twig or stem, as in the genera *Empidonax* and and *Tyrannus*. Cups may be elaborately decorated with mosses and lichens, as in *Contopus* and *Elaenia*. Bulky, ball-shaped globular nests of grasses and twigs are built by Greater Kiskadee, Masked Water Tyrant, Social Flycatcher *Myiozetetes similis*, and others. Pendulous, purse-shaped nests with side entrances characterize the tody-flycatchers (*Todirostrum*) and numerous related genera. All members of the genus *Myiarchus* nest in natural cavities, and line their nests with soft animal matter, virtually always including pieces of shed snake skin. Other cavity-nesters include the genera *Rhytipterna*, *Attila*, *Myiodynastes*, *Machetornis*, and the White-ringed Flycatcher *Conopias parva*.

Clutch size varies from 3–5 in North America (but up to 8 in Great Crested Flycatcher *Myiarchus crinitus*), and is usually 2–3 in the Neotropics. Incubation time typically ranges from 14–20 days, followed by nestling periods of 14–23 days. Independent young of many tropical species remain with their parents to form family groups for nearly a year after fledging. With rare exceptions, both sexes construct the nest and feed the young. Only females incubate eggs or brood young. Many species regularly attempt more than one brood in a single season.

(S.M.) J.W.F.

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FLYCATCHER-SHRIKE: alternative substantive name of some species of Campephagidae (see CUCKOO-SHRIKE).

FLYCATCHER, SILKY: see SILKY FLYCATCHER.

FLYCATCHER-WARBLER: name sometimes given to *Seicercus* spp. (see WARBLER (1)).

FLYEATER: *Gerygone sulphurea*, the only south-east Asian member of the predominantly Australian genus *Gerygone* (see WARBLER, AUSTRALIAN).

FLYWAY: a major route for birds on migration (see MIGRATION).

FODI; FODY: substantive name of *Foudia* spp. (see WEAVER).

FODITANY: substantive name applied to two Madagascan BULBULS of the genus *Phyllastrephus*, and to the aberrant Madagascar BABBLER *Oxylabes madagascariensis*.

FOLIAGE-GLEANER: substantive name of species in several genera (e.g. *Automolus*) of Furnariidae (see OVENBIRD (1)).

FOLKLORE, BIRDS IN: folklore is a term of somewhat imprecise application, mingling as it does with myth, legend, fable and oral literature, and reaching out toward magic and religion. For present purposes bird folklore may be defined as the total corpus of beliefs, half-beliefs, tales and sayings, fanciful or otherwise, orally transmitted and of undetermined authorship, which are referable to genuine species. (For discussion of wholly invented or composite species see FABULOUS BIRDS.) Its origins lie in observation as well as imagination, with misinterpretation in between.

It may be assumed that birds have been the concern of men for as long as humankind has existed: on the material side as a food source for the hunter and later as a competitor for food with the farmer; as a supplier of plumage for adornment and for warmth, and of such accessories as feathers for arrows and bones for beads and whistles; and as practice targets for apprentice hunters (see ORNAMENTATION, BIRDS IN HUMAN). Although true domestication has been accepted by very few species, the keeping of birds as pets may go back to the remote past, to judge by the fondness of 20th century Stone Age peoples in Amazonia for their shoulder-tame macaws *Ara ararauna*, or the young cassowaries *Casuarius* spp. running loose in Papuan villages. On the non-material side, the readiness of men to ascribe human characteristics to other creatures is with us yet. In the minds of preliterate peoples, for whom the barrier between natural and supernatural hardly exists, all animals and often plants must needs live on the spiritual as well as the earthly planes. Thus a bird that is notably wily or swift or cruel or nutritious must possess particular powers, to be courted, countered, revered or borrowed; and upon such relationships myths are built. The antiquity of this preoccupation is illustrated by palaeolithic cave-paintings of bird-men (whether gods, decoys, disguised hunters or all three is not always clear), and its refinement by Horus the Hawk God of dynastic Egypt, who personified the rising sun.

Some myths have the force of religious tenets. For the Hebrews a dove discovered dry land after the Flood, and for the Crow Indians in Montana diving ducks sent down by the Creator brought up mud from below the primaeval waters to make the Earth—to give but two examples of a widespread theme. Over much of native North America rainfall is controlled by the Thunderbird, conceived of usually as an eagle but sometimes as a hawk, and in the interior of British Columbia as a grouse. In all cases it is the flashing eye that generates lightning and the flapping wings that reverberate. As has been said, other creatures besides birds have their mythic roles and, despite his luxuriant plumage, Quetzalcóatl the Plumed Serpent, god of wind and scholarship in ancient Mexico, appears to have been a reptilian rather than an avian mutant. He is much, much older than the eagle with a serpent in its talons which was the sign for the 14th century Aztecs that they had reached their Promised Land.

Not all bird lore is so portentous. Tales told purely for entertainment have abounded in both Old and New Worlds, wherein birds appear as protectors, tricksters or comics. A favourite genre, echoed in Kipling's *Just So Stories*, recounts the origins of particular shapes or plumages: in Europe the Robin *Erithacus rubecula* scorched its breast bright red while stealing fire from the sun, and the Crossbill *Loxia curvirostra* twisted its beak on the nails of the Cross; in Manitoba the Sapsucker *Sphyrapicus varius* acquired its many hues as consolatory gifts from other birds because it had been too tipsy on birch juice to attend the official distribution of colours.

In the Orient some birdlike beings of no clear faunal affinity have entrenched themselves in the great religions (see FABULOUS BIRDS). In the West the bird spirits have been banished by Christianity or diminished, sometimes by way of witchcraft, into mere harbingers of good or bad luck. The dove (when not pronounced 'pigeon') and the crowing cock have maintained an odour of reasonable sanctity, and the Swift *Apus apus* has about lived down a reputed collusion with the Devil, but the superstitious still know that any bird—especially a black-as-night corvid—that strikes at a window is summoning a human soul to the grave.

Attitudes to birds as expressed in British folklore are not always consistent. The Wren *Troglodytes troglodytes*, which shares with the Goldcrest *Regulus regulus* and Firecrest *R. ignicapillus* a variety of ironic European names denoting petty kingship (*Regulus*, Latin; *Roitelet*, French; *Reyezuelo*, Spanish—sometimes downgraded to *Abadejo*, petty abbot), is traditionally killed and paraded on St Stephen's Day in England and Ireland to a satirical refrain dubbing it King of All Birds. This despite the West Country warning that 'Who kills a Robin or a Wran, shall never prosper, boy or man', and similar minatory verses current in Scotland. The Magpie *Pica pica* likewise enjoys a mixed reputation, 'One for sorrow' offset by 'One's a wish'. Owls, highly regarded in Classical Athens and relied upon to deflect lightning in England as in China, are associated with the black arts in both hemispheres and can still induce the crossing of fingers in the role of Shakespeare's 'fatal bellman, that gives the stern'st goodnight'. Perhaps darkness has something to do with it; by daylight the wise old owl is among the most popular of avian symbols.

An important branch of bird folklore is that which may be classed as alternative ornithology, based on day-to-day observation, but leaning heavily on conjectural explanations of what was not, in pre-'scientific' conditions, observable. The empirical approach has engendered some sound proverbs or 'country' sayings; the hypothetical conclusions have been shrivelled by science. It is probably good if expensive husbandry to plant one bean for the rook and one for the crow in addition to the one to grow. It is certainly true that the first Swallow *Hirundo rustica* may arrive in England before the last cold snap, so that one alone does not indeed make a summer. On the other hand it is no longer averred that swallows spend the winter dormant beneath the streams they skim over in autumn; that the Cuckoo *Cuculus canorus* and the Merlin *Falco columbarius* are the summer and winter phases of one and the same species; that the 14 halcyon days during which the seas remain calm are those needed by the Kingfisher or Halcyon *Alcedo atthis* to safeguard the eggs in its floating nest of fish bones; nor yet that the cirriped barnacle is the embryo of the Barnacle Goose *Branta leucopsis*.

Vicariously related to bird lore proper are the Gabriel Hounds, the nocturnal pack whose funereal baying overhead has been explained away as the flight calls of Brent Geese *Branta bernicla*. The ominous function of some other species, notably owls and corvids, has been touched on above; the institutionalized role of birds in augury in S.E. Asia is treated in detail under a separate heading (see OMENS, BIRDS AS).

A wealth of perception, imagination, whimsy and onomatopeia resides in English local or folk-names of birds, and some of it is intriguing. The erroneous reason for calling the Nightjar *Caprimulgus europaeus* a Goatsucker is familiar enough, but why also Corpse-hound (a distinction shared with the Whimbrel *Numenius phaeopus*)? The Wryneck *Jynx torquilla* is Cuckoo's Mate because it arrives a day or two ahead to prepare the way for the Cuckoo—which name itself, amended with the pejorative termination '-old', bespeaks the bird's involvement with fertility. Association with wet weather belongs equally, for differing reasons, to the Green Woodpecker *Picus viridis* and the Red- and Black-throated Divers *Gavia stellata* and *G. arctica*, which are Rain-bird and Rain-geese respectively. The Hooded Crow *Corvus corone cornix* is called a Kentish Crow in Norfolk, an Isle of Wight Crow in Sussex, a Danish Crow in East Anglia and a Dutch Crow in Yorkshire; the North Country's Wetwang Greyback sounds less discriminatory. Storm Witch for the Storm Petrel or Mother Carey's Chicken *Hydrobates pelagicus* reflects the mariner's belief that the bird lived totally invisible until the onset of tempest. The stripling Oxfordshire cronies who taught me Bumbarrel for the Long-tailed Tit *Aegithalos caudatus* cared naught for semantics.

It is very desirable that ornithologists who come across any local or traditional sayings, stories or customs to do with birds should make sure that they are, or that they already have been, recorded. As a counterbalance to the histogram, folklore provides insights both valuable and entertaining into Man's long association with the world of birds. Mainly, to be sure, as it has been in the past—but Her Britannic Majesty's Government still takes precautions against the disaster that would befall the realm were the Tower of London to lose its Ravens *Corvus corax*.

(E.A.A.) G.E.S.T.

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FOLLICLE, FEATHER: see FEATHER.

FOLLICLE, OVARIAN: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

FOLLOWING RESPONSE: see under IMPRINTING.

FOOD: see FEEDING HABITS; FOOD SELECTION; PARENTAL CARE; PIRACY; PREDATION; also ALIMENTARY SYSTEM; GRIT; METABOLISM; NUTRITION; PELLET.

FOOD, BIRDS AS HUMAN: see UTILIZATION BY MAN.

FOOD CHAIN: see ECOLOGY.

FOOD DEFICIENCY: see DISEASE.

FOOD PASS: aerial food presentation by the male raptor to the female, usually taking place during the periods of courtship, incubation, and brooding of the young.

FOOD SELECTION: an aspect of behaviour (see FEEDING HABITS), of interest also from the evolutionary and ecological points of view in that closely related species living in the same habitat do not compete for food (as postulated first by D. Lack and now generally accepted). Although some avian species are specialized for selecting a particular type of food, e.g. the FLAMINGOS, many are rather catholic in their choice and take a variety of items. This wide range of food items is apparently due to an initial response to a few generalized stimulus situations, each characteristic of a variety of objects. The effective stimuli are later narrowed by learning, the course of which is determined not only by the food within the environment, but also by the behaviour patterns, sense organs and body structures available for finding it.

Distantly related species may show marked innate differences in the stimuli that elicit their feeding responses. Between closely related species, however, such innate differences are often more difficult to detect. Sometimes competition is avoided by differences in habit selection or in the selection of the feeding niche within the habitat. In other cases, small differences in behavioural or physical characteristics prevent overlap in diet. Thus tits, but few other species, learn to open milk bottles because they have the necessary motor patterns; and the size of seeds taken by finches is determined in large part by the size of the bill—each species learning to take the most suitable seeds. The ability of many birds—including Jays *Garrulus glandarius*, Magpies *Pica pica*, some finches and tits—to use the foot with the bill is often characteristic of the species, but learning helps towards its perfection. It enables food sources to be tapped that would otherwise be unavailable: thus Magpies pull down and stand on grass stems while they peck out the seeds, and Goldfinches *Carduelis carduelis* use both bill and foot to feed on thistle seeds. The BILL and other structures used in feeding are adapted to conditions in the localities inhabited by the species. Populations adapted to different conditions and meeting later may therefore select different diets, not because of innate differences in responsiveness, but because they learn to eat those foods to which they are structurally adapted (Hinde 1959).

The first appearance of pecking in the young of nidifugous birds is not dependent on learning: they may peck at a number of different items, provided that they contrast with the background, and accuracy improves with experience. Should the object be of a suitable size, it may be swallowed. If the effect is not then unpleasant, the action may be repeated and the animal comes to distinguish the edible from the inedible. In the food selection of most birds, the visual sense is paramount; TASTE and TOUCH are also important, but the other senses less so (although nocturnal birds such as owls hunt by sound, and at least the kiwis and Oilbird *Steatornis caripensis* use an ability to detect ODOUR—see also SMELL).

The stimuli that elicit the greatest pecking response have been tested in a variety of birds. In particular, the newly-emerged young of species that hatch with their eyes open have been found to peck selectively at objects that differ in size, shape, height and in speed of movement. Young birds with little visual experience and no opportunity for direct learning have been tested also for their differential response to colour. It is known that closely-related species tend to have similar colour preferences, and in many cases these preferences have selective advantages. Hence gulls and terns peck at red and orange, and these colours often, but not always, appear on the parents' bill at which the young bird pecks for food. The chicks of the Oystercatcher *Haematopus ostralegus* and Moorhen *Gallinula chloropus* also select red, as does the Coot *Fulica atra* although the adult bill is white. In studies of young ducks and pheasants, which obtain their own food from the start, it has been shown that almost all species prefer green. The preferences of some adult birds can be inferred through a study of bird-pollinated flowers and bird-distributed fruit (see POLLINATORS; SEED DISPERSAL). Some 84% of the former are red or orange, while red, orange and black berries are vastly more common than those of any other colour.

The Browers (1964) suggest that food has a variety of flavours that conveys no information to the naive bird who will accept initially a wide range of items. If the animal eats and then vomits, it will associate the taste of the food being expelled through the mouth with an uncomfortable 'gut reaction'. Originally a gourmand, the bird is now a gourmet, and taste will thereafter convey useful information. Once conditioned, the bird judges potential food by taste. Obviously the next, more efficient, stage is to recognize prey by sight alone before it needs to be caught and tasted.

The complexity of food selection is illustrated by the work of Krebs (1978) among others, on OPTIMAL FORAGING (see also OPTIMALITY THEORY). The hypothesis here is that an animal searching for food must make decisions that maximize its rate of food absorption: it must decide which type of food it will eat, where it will hunt, and what search path it will adopt. Any item eaten has a cost in terms of time taken to find, catch and consume it, and a benefit in terms of net nutritional intake. Predators should (a) prefer more nutritious (profitable) prey, (b) be more selective when such profitable prey items are uncommon and (c) should ignore unprofitable items no matter how common they are. These predictions have been tested and it can be shown that (c) does not apply if the time taken to recognize unprofitable prey lowers the overall rate of food intake. Thus caged Great Tits *Parus major* do not completely ignore unprofitable items if they are abundant and mixed at a high density with profitable ones. Either the birds require time to recognize prey or they need to sacrifice a certain amount of efficiency to acquire information by 'sampling' the relative nutritional value of each food type. Active birds will search where food is clumped or patchy in distribution but, again, the need to collect information through sampling may cause them to deviate from optimal behaviour. In considering the search path that the foraging bird will take, it can be predicted that a non-random route is most likely, at least in situations where the prey is not replenished rapidly, if only so that the bird does not waste time crossing its own path. Blackbirds *Turdus merula*, for instance, will alternate left and right turns in their search path, but after finding an earthworm, tend to make successive turns in the same direction. In a fluctuating environment (and most environments do change with time), the bird's problem is to update continually its estimates of capture rate and availability so that it can always make the 'best' decisions.

Many temperate-latitude species are known to change their diet with the seasons, coinciding with the onset of breeding, migration, the feeding of young, the moult and a changing climate. To some extent this is a matter of food availability, but preferences are governed by internal changes. Domestic hens can learn to select food so as to correct for some deficiencies, and Red Grouse *Lagopus lagopus scoticus* have been found to prefer 3–4 year old heather that is richer in nitrogen and phosphorus.

Parental example and social experience are likely to affect food selection, the latter especially in flocking species. Most parent birds provide potential dietary guidance. Ducks and geese lead their young to suitable feeding grounds, and most gallinaceous birds pick up and drop a morsel of food apparently to draw it to their chicks' attention. Young rails follow their parents and are fed from their bills, and even sometimes obtain food from juveniles of the previous brood. In many other species, the parents bring food to their offspring. The importance of this early experience is not known; in parasitic species, at least, it sometimes appears to be slight. Cuckoos and honeyguides do not parasitize host species that give 'unsuitable' foods or cannot collect enough. Eggs laid by female Cuckoos *Cuculus canorus* 'taken short' in the nests of 'wrong' species often hatch but the young one seldom fledges. Yet no host brings the food that makes the diet of adult cuckoos and honeyguides unique: hairy caterpillars on the one hand and beeswax on the other.

The feeding behaviour of flocking species may be influenced by companions in three ways: by SOCIAL FACILITATION, by imitation and by what has been called 'local enhancement'. Social facilitation usually affects the quantity of food that the individual takes and, apart from vocal mimicry, there is not a lot of evidence for direct imitation in birds. Normally it is 'local enhancement' that accounts for the spread of new feeding habits among birds: one bird happens upon a previously untapped food source and others are led in that direction. Examples are the opening of milk bottles by tits and the appearance of Great Spotted Woodpeckers *Dendrocopos major* at bird tables. Often prolonged severe weather and food scarcity seem to encourage searching and lead to the discovery of new food supplies. Such novel behaviour patterns perhaps originate with young birds during the first year of life; their actions are observed by other juveniles and eventually by their offspring. Thus new habits become traditional, without the usual limits of acquired behaviour that disappears with the death of the individual. The tendency for new feeding behaviour to arise varies from species to species and differences in adaptability seem to be genetic in origin.

Possibilities for interaction between the members of a flock are obviously influenced by the proximity of feeding individuals. Crook (1965) showed how the social organizations of birds are related to the type of food eaten and to its dispersion within the habitat. Food that is scattered or cryptic, difficult to find and difficult to catch, must be searched for by stealth, speed and skill. Birds dependent on this type of food, such as birds-of-prey (Accipitriformes, Falconiformes), are solitary feeders because any gregarious behaviour interferes with individual methods of acquisition, and their feeding methods in consequence tend to be stereotyped. If food is commoner in some parts of the environment than in others, congregation by the birds may be advantageous in increasing the ability to locate and exploit it effectively. In this group are swifts and many nectar-feeders, insectivores with broad diets such as tits, and ground-feeders. These birds normally tolerate other feeding individuals close by, although a change of feeding habit (to feed young, for instance) may change the closeness of foraging, and territorial behaviour develops. It is when food is found sporadically in patches within the habitat and does not require skill to catch it that the greatest gregariousness occurs. Foraging in a flock prevents repeated sampling of areas already covered and this may be of especial value when food is scarce. A member of the flock, by the very act of feeding, indicates where there is food and other birds move towards it—a precise example of 'local enhancement'. This applies especially to fruit-eating birds, such as many parrots, whose frequently bright colours and raucous voices indicate to their own and other species the locality of clumps of ripe fruit which are shared. It is in these social groups that the greatest possibility for change in food selection by demonstration exists. J.K.(1)

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Nutcracker *Nucifraga caryocatactes* digging in the snow for nuts that it has hidden. (*Photo: P.O. Swanberg*).

FOOD STORING: temporary storing ('hoarding') of food in sites other than where it was collected. The time between storing an item and eating it may vary between a few hours in tits and up to a year in certain woodpeckers and corvids. Storing in different forms is well developed among several bird families, notably crows and their allies, tits, nuthatches, shrikes, woodpeckers and also among certain diurnal raptors and owls. For example, Thick-billed Nutcrackers *Nucifraga c. caryocatactes* during autumn collect large numbers of hazelnuts *Corylus avellana* several km from their nesting territories in coniferous forest, storing loads of 15–20 nuts in many different locations on the ground, and carefully covering the sites with vegetation. During winter and spring, the Nutcrackers subsist and raise their young on the stored nuts, which they recover with great precision. Swanberg (1951) found that 86% of the attempts at digging up nuts through thick snow-cover were successful, and the precision did not decrease over the winter. Nutcrackers hence memorize the storing sites, and also which caches they have previously emptied. Food storing is also important in *N. c. macrorhynchos*, and in the North American Clark's Nutcracker *N. columbianus*.

Another species with advanced food storing is the Acorn Woodpecker *Melanerpes formicivorus*. Territorial groups of up to a dozen birds store large numbers of acorns in a few granary trees, in which the woodpeckers have excavated suitable storage holes. The group members communally defend the 'larders' against food competitors of the same and other species. The social organization of Acorn Woodpeckers is related to the feasibility of acorn storage: when food cannot be hoarded in sufficient quantity, the birds do not form social groups but nest in solitary pairs and migrate during winter, a remarkable social flexibility.

Ecological factors promoting hoarding. The survival value of food storing should usually increase with, among other things, the likelihood that (a) food withstands extended storing without decay; (b) food will be less abundant in the period ahead, or the forager will then require more food, for example during reproduction; (c) the storing individual itself will be able to recover the food.

Hoarding seems to fit such a pattern. (a) The most commonly stored items are energy-rich seeds or nuts with protective cover, which are sometimes preserved for over one year without serious decay. Bird's eggs are often hoarded by crows, foxes and martens. Tits store insects mainly during autumn, and low temperatures during the following winter may

Great Spotted Woodpecker *Dendrocopos major* storing cones. (*Photo: H. Schouten*).

retard their decay, but it is doubtful whether hoarded insects remain unused for such a long period. Raptors and owls store small mammals and birds for short periods of usually a few days, both outside and during the breeding period; so do certain shrikes with insects and small vertebrates. (b) Most storing species occur in North Temperate areas, with great differences in food abundance between the autumn storing season and the recovery period during winter and spring. The few known cases of storing in the tropics occur among highland species, for which food abundance may vary due to seasonal fluctuations in rainfall. Further studies in the tropics are needed to test whether hoarding is less common in stable environments with little seasonal variation.

Nesting raptors, owls and shrikes which store food over brief periods might gain two advantages: (1) buffering against temporary food shortage due to, for example, inclement weather which impedes hunting; (2) boosting the growth of chicks when their food requirements are highest and they consume food faster than the parents can gather it. (c) The chances that the hoarder itself will recover the food should be greatest in sedentary species with individual or pair territories. Food storing seems to be crucial for the non-migratory habit in the Acorn Woodpecker. Most hoarding birds are resident species which forage on individual, pair, or group territories. Among colonially nesting birds, the Rook *Corvus frugilegus* regularly and the Jackdaw *C. monedula* sometimes hoard food.

Scatterhoarding and larderhoarding. 'Scatterhoarding' the food in numerous small and dispersed caches, and hiding it in the ground, below vegetation, in bark crevices or tree holes is common among hoarding birds, also among species which live in groups. Scatterhoarding reduces the risk that competitors will discover and consume the stored food.

'Larderhoarding' of food in concentrated, more conspicuous stores occurs in some species which are well equipped to chase away food competitors. Acorn woodpeckers, where the members of a social group store thousands of acorns in one or two prepared trees, jointly defend the larders. Shrikes and birds of prey are morphologically well adapted to protect their larders from other species.

Recovery of stored food. Careful hiding of food reduces the risk that competitors will find it, but also makes recovery by the hoarder more difficult. In some species, this problem is solved by a remarkable memory: several hundred or even thousand storing sites spread over sometimes more than 10 ha are remembered fairly precisely for more than half a year by Thick-billed Nutcrackers and European Jays *Garrulus glandarius*. The jays use conspicuous objects such as saplings and tree trunks as beacons in recovering food. There is strong evidence that the birds do not use smell, but rely on visual cues in recovering stored food. Nutcrackers and jays, like most birds, appear to have poor sense of smell.

Hoarding in groups. Tits, Rook, Clark's Nutcracker, Pinyon Jay *Gymnorhinus cyanocephalus* and several other species hoard in conspecific groups in 'communal areas' where the group members tolerate each other. Hoarding in such situations raises a special problem. Since harvesting and storing food requires time and energy, it has a certain cost which a group member might avoid by refraining from hoarding, yet exploiting the food stored by other group members. When stored food is easily available to each group member, as in the Acorn Woodpecker, such 'cheating' seems particularly likely. In this species all group members except yearlings hoard, but there is no quantitative study of the distribution of storing and consumption of the food among the different members.

In group-living birds which scatterhoard and hide food, cheating may not be advantageous if the hoarder of an item is more likely than any other group member to recover it. This could come about either if individuals remember their own caching sites, or if individuals differ in preferred types of sites. Among group-living tits, both mechanisms may operate. Individual Marsh Tits *Parus palustris* differ in their types of hoarding sites, and have a fairly precise memory of the storing places during at least 24 hours. Contrary to what has been suggested, stored food in many group-living species may not therefore be 'communal property' which all group members have equal chances to eat; the hoarder of an item is often most likely to recover it. Therefore, KIN SELECTION is not necessary for the evolution of hoarding in groups. After juvenile dispersal in late summer, groups of food-storing tits consist of genetically unrelated individuals. But kin selection has possibly been important in other hoarding, group-living birds, as it has apparently been for the evolution of advanced food-storing among bees and other hymenopterous insects.

Evolution of food storing. Among species which do not hoard, a bird, after finding a food item, may move to eat it in a more convenient or protected place, for instance to reduce the risk of discovery by predators or competitors. Food-storing may have evolved from such transportation of food. Woodpeckers and nuthatches often fix their food in holes or bark crevices to make eating easier. Fixation of more food than is immediately needed should be a further easy step in evolution. Many predators may continue hunting even when they have just eaten and will not consume more food. 'Surplus killing' is common among carnivorous mammals, and some birds of prey continue to hunt and store food after they are satiated.

Coevolution of hoarders and food plants. There are several beautiful examples of mutualism and coadaptation between hoarding birds and their food plants. The latter offer the animal a rich food source, while the hoarder 'pays back' by dispersing the seeds (see SEED DISPERSAL). Since the hoarder does not recover all stored seeds, it helps propagate the plant. In some well developed hoarder-plant systems, the bird has evolved a specialized bill and an extensible oesophagus or sublingual pouch for efficient seed transport, and the plant has evolved seeds or fruits which are large, nutritious, easily available, protected against mould by a cover, and otherwise suitable for hoarding. Two examples are Clark's Nutcracker-Piñon Pine *Pinus edulis* and European Jay-Pedunculate Oak *Quercus robur*. But the habits of hoarders are not always advantageous for their food plants; Acorn Woodpeckers and other melanerpine species seldom drop Piñon seeds or acorns, and store them in sites unsuitable for germination. These woodpeckers may therefore be 'parasites' on mutualistic systems developed between other hoarding birds and plants.

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FOOD-WEB: see ECOLOGY.

FOOL HEN: popular name for the Spruce Grouse *Dendragapus canachites* (see GROUSE).

FOOT: see under LEG; SKELETON, POST-CRANIAL.

FOOTEDNESS: a physiological dominance of one foot over the other, comparable with right-handedness or left-handedness in human beings. There is some evidence of this in a few groups of birds.

In 7,259 landings of 11 Domestic Pigeons *Columbia livia*, 7 used the right foot, 3 the left foot, and one showed no particular preference for either (Fisher 1957); biometric analysis revealed a slight departure from bilateral symmetry in the leg bones of the pigeon (McNeil and Martinez 1967). The right leg as a whole, and most of the right limb segments, are significantly longer than the left.

In the Accipitriformes, Bond (1942) found that a young Goshawk *Accipiter gentilis* would sleep on both feet, but would hold its food with the left talon. Hosking (1943) describes the same behaviour for several species of hawks and owls. The parrots manifest a similar type of handedness. Of 20 birds belonging to 7 genera and 16 species observed using right or left foot to bring food to the beak (Friedmann and Davis 1938), the percentage of left-handedness exhibited by the birds as a whole was 72.2%; 3 individuals of *Brotogeris jugularis* were 100% left-handed. Of the genus *Amazona*, 7 species showed 66.97% left-handedness, while the 10 individuals involved were 70.5% left-handed. In *Amazona amazonica*, which is 75% left-handed, McNeil and Martinez showed a significant predominance in the length of the left limb as a whole and in most of the left limb segments. A similar type of left-handedness was reported for the Carolina Parakeet *Conuropsis carolinensis* (Allen 1939). It may be concluded that many genera and species of Psittacidae are left-handed. However, observations on 56 individuals of *Aratinga pertinax* when bringing food to the beak (McNeil *et al* 1971) showed that half the birds were left-handed and half were right-handed. A biometric analysis revealed a slight departure from bilateral symmetry in hindlimbs as a whole and hindlimb segments in close relationship with handedness (left and right).

Among Passeriformes, the occurrence of foot preferences is not well documented. It has been reported (Dobie 1936, and others) that in the Crossbill *Loxia curvirostra* the use of a particular foot to hold a cone is correlated with the direction of crossing of the mandibles. If the lower mandible twists to the right, then the left foot is used and vice versa. When the cone is held with both feet, if the lower mandible twists to the right, the base of the cone lies under the left foot and its tip under the right foot and vice versa. Great Tits *Parus major* showed marked preferences, about half the birds being right- and half left-footed, when holding insect food (Vince 1964). The preferences were however more marked in some individuals than others and broke down in the more complex task of string-pulling.

There is no evidence to show whether such foot preferences are individually acquired or not. A close relationship between skeletal bilateral asymmetry and footedness has been shown but the results do not demonstrate any causal relationship. McNeil and Martinez (1967) believe that bilateral symmetry in external organs (limbs and sense organs) may be interpreted as a locomotor adaptation in the sense that it would make it easier for an animal to reach its goal directly, while departures from bilateral symmetry may have other functions in, for example food handling or prey catching. R.McN.

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FOOT-PADDLING: see FEEDING HABITS.

FOOT PAPILLAE AND PADS: thickenings of plantar skin; pads are covered with papillae and are separated from other pads by furrows. In various birds pads and papillae, making contact with the substrate, show great variety in structure as adaptations to the way of living. The papillae are often called scales or reticulate scales. In embryonic studies they are called radially symmetrical scales in contrast to the overlapping scales of tarsometatarsus and toes. The morphology, histology, and function of papillae deviate from scales and justify the term papilla.

Embryonic development. Pads, furrows, and papillae develop by three separate processes in the embryo (see Fig. 1). The furrows develop through a thickening of epidermal cells, followed by a folding; they appear during days 10–12 of the domestic chick's embryo development. Pads swell by cell proliferation in the deep dermis; the large pad in the centre of the foot appears on day 8 of the embryo, and the pads in the toes on days 10–12. The papillae develop through a condensation of dermal cells close to a thickening of epidermal cells; they appear on days 11–14. The embryonic development of papillae shows similarities to that of scales and feathers; factors in the dermis control the differentiation of the skin.

Papillae. Tree-living birds often have papillae with the microscopic structure shown in Fig. 2. The primary dermal papilla is divided into several secondary dermal papillae. This implies an increased surface of

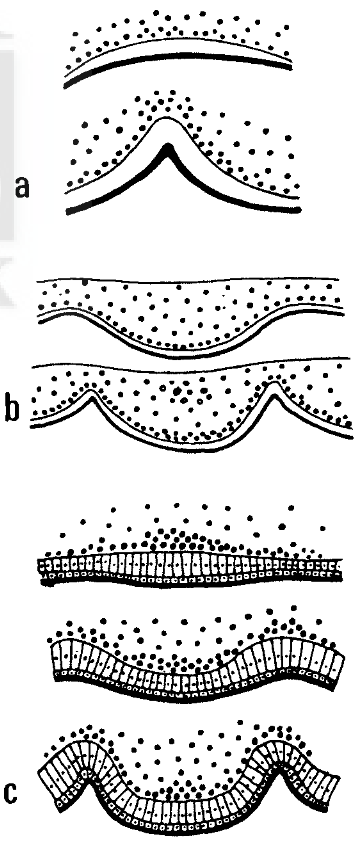

Fig. 1. Development of (a) furrow, (b) pad, and (c) papilla. The periderm is indicated black; the basal epidermal cells are unshadowed in (a) and (b); the epidermis is two-layered in (c); the superficial dense dermal cells are indicated by dots, and the deep dermal cells by rings. A line in (b) shows the deep border of the dermis.

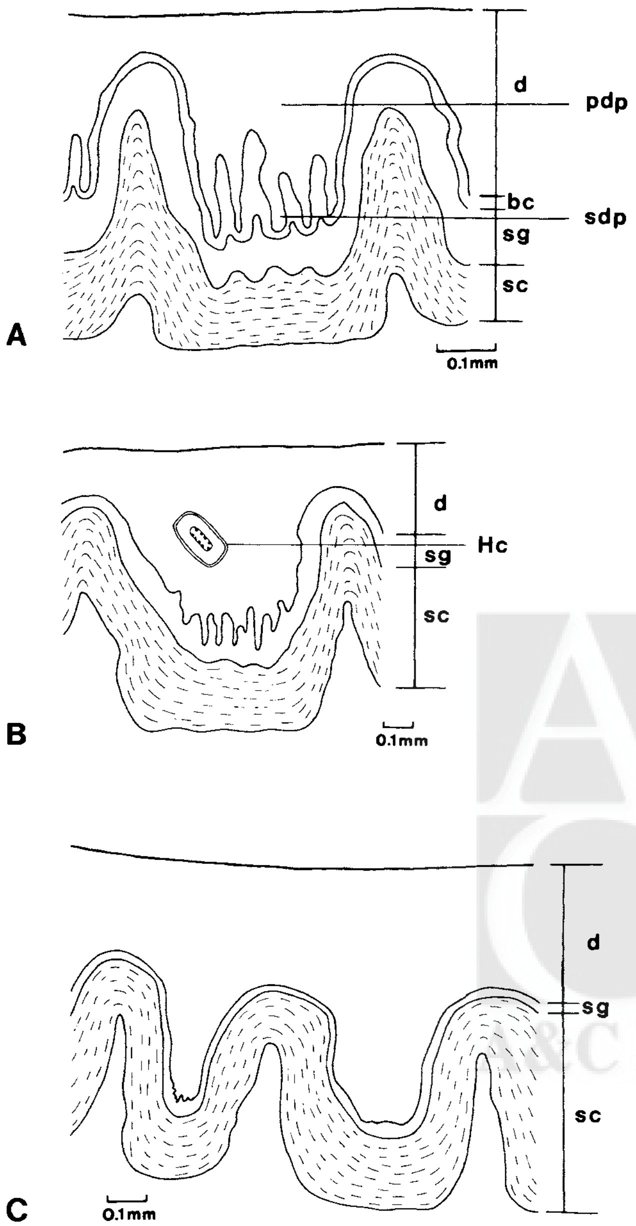

Fig. 2. Diagrams of papilla in (a) a passerine, (b) a parrot, and (c) an owl. The skin consists of the dermis (d), which projects into the papilla with a primary dermal papilla (pdp) and several secondary dermal papillae (sdp). The epidermis has a basal cell layer (bc) where mitotic activity renews the epidermis, the cells moving through the stratum germinativum (sg) and the stratum corneum (sc) to be worn off at the surface. Many papillae in parrots have Herbst sensory corpuscles (Hc). Scales 0.1 mm.

contact between dermis and epidermis and space for a large number of basal epidermal cells, which divide and renew the epidermis. Papillary arteries and veins branch from a network of blood vessels in the dermis and continue as capillaries to the top of the secondary dermal papillae. Arteriovenous anastomoses occur at the base, regulating the blood flow to the papilla. There is obviously a heat exchange between arteries and veins, generating a temperature gradient in the papilla.

The pads and papillae of tree-living birds are often subjected to strong external forces when the bird lands or grasps a branch. They are connected to each other by a thick layer of stratum corneum, forming a thick skin which covers the pad. This skin is flexible but only slightly stretchable. The distal end of the papillae in some birds projects and is pointed, suitable to penetrate roughnesses in the substrate.

Ground-living birds such as waders, bustards, cranes, grouse and storks have a similar connection of papillae to a skin plate, although the surface of the papillae is flat.

Parrots have separate papillae. Many papillae have Herbst sensory corpuscles in the dermis. The free papillae and the sensory corpuscles indicate a touch function of the papillae, comparable to the touch function of the epidermal ridges in primates.

Birds-of-prey have separate or connected papillae. The stratum germinativum is often thin and the stratum corneum is thick, indicating a different condition of wear and renewal. Herbst sensory corpuscles are sparse and scattered in the dermis of owls *Asio* and buzzard *Buteo*. The Osprey *Pandion* and the fishing owls *Ketupa* and *Scotopelia* have pointed, spiny papillae adapted to grasping slippery fishes.

Palearctic passerines wintering within the region have generally few and large papillae, whereas passerines of similar size wintering in tropical Africa have many and small papillae. The Redpoll *Carduelis flammea* and the Goldcrest *Regulus regulus* have exceptionally few papillae, but some of them are very large and the stratum corneum is thick. This reduces the area of contact with the substrate during cold winter conditions. Some birds wintering in temperate climates have a thicker stratum corneum in winter than in summer, an insulative acclimatization. Passerines living on the ground such as the Skylark *Alauda arvensis* also have few papillae.

Pads. The pads are defined by the furrows: gaps between the papillae, which open and close when the digits are bent. Some furrows are developed in the early embryo and occur in every individual of the species; other furrows develop later in the embryo or early in the nestling, and they show individual variation in occurrence.

The pads in the toes are anchored by connective tissue to the phalanges or to the joints and are therefore termed phalanx pads and joint pads. One pad in the central part of the foot is close to the trochleas of the tarsometatarsus: the central pad.

Figure 3 shows the feet of 6 birds. The Grey Heron *Ardea cinerea* has small joint pads and long narrow phalanx pads. This pattern occurs in

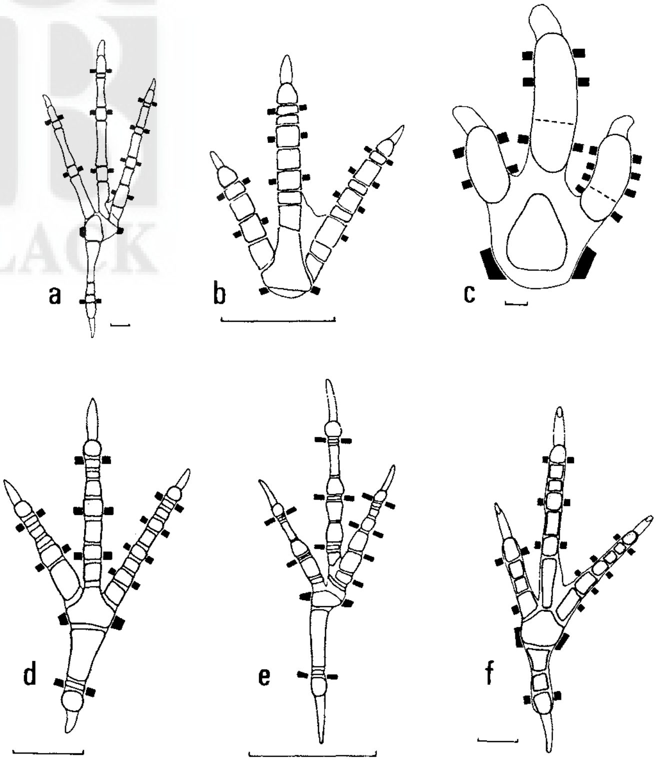

Fig. 3. Pads in the feet of 3 ground-living birds (upper row) and 3 tree-living birds (lower row): (a) Grey Heron *Ardea cinerea*; (b) Ringed Plover *Charadrius hiaticula*; (c) Kori Bustard *Choriotis kori*; (d) Roller *Coracias garrulus*; (e) Redstart *Phoenicurus phoenicurus*; (f) Sparrowhawk *Accipiter nisus*. Each pad is represented by a line showing the margin of the pad. Black areas at the side of the digit show the position of joints. Scales 1 cm.

many ground-living birds such as waders and gamebirds. Some of them, such as the Ringed Plover *Charadrius hiaticula*, walking mostly on hard substrates, have phalanx and joint paids about equal in size. This also occurs in the Little Bustard *Otis tetrax*. The great Kori Bustard *Ardeotis kori* has only 4 pads: one in the centre of the foot and one in each of the anterior toes, the latter being fusions of several pads. Similar fusions of pads occur in sandgrouse and in flightless birds such as the Ostrich *Struthio camelus*.

Many ducks and gulls have joint pads and a central pad but lack furrows. The Eider *Somateria mollissima* has a large phalanx pad at the base of the second toe, obviously important in standing. The Scaup *Aythya marila* and the divers have only a central pad and no sign of pads in the toes. The papillae and pads of the petrels are very similar to these groups.

The Roller *Coracias garrulus* has phalanx and joint pads; some phalanx pads in the distal part of second and third toe are divided into 2 or 3 pads. Kingfishers and other birds with toes connected by skin have fewer pads due to fusions. Pigeons and doves have pads comparable to those in the Roller, but certain species have fewer pads.

Passerines, e.g. the Redstart *Phoenicurus phoenicurus*, have a basic pattern of 12 phalanx pads and one central pad. The joint pads are reduced to folds, which have a few papillae or a smooth skin surface without any papillae. Certain joints may even lack folds. Woodpeckers and cuckoos have prominent phalanx pads and small folds at many joints.

Many diurnal raptors have phalanx and joint pads, but not so many as in the Roller. The Sparrowhawk *Accipiter nisus* has some projecting joint pads in the third and fourth toe adapted to penetrate the feathers of its prey. The owls have joint pads, but the furrows are unclear or absent.

Pads and papillae are mostly characteristic of the species. In fragments of birds including the leg, e.g. from a raptor's prey, the species may sometimes be recognized by comparison with wet-prepared museum specimens. I.L.

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FORAGING STRATEGY: see STRATEGY.

FORAMEN: an aperture (plural 'foramina') in a bone or other bodily structure (see SKELETON, POST-CRANIAL).

FOREHEAD: see TOPOGRAPHY.

FORENECK: see TOPOGRAPHY.

FORKTAIL: substantive name of *Enicurus* spp. (see THRUSH).

FORM: in taxonomy, a loose or deliberately neutral term for a species or a subdivision thereof, non-committal as regards the rank or status to be assigned to it; sometimes used more precisely to embrace subspecies and monotypic species, e.g. in giving the total number of 'forms' included in a genus or found in an area. For nomenclatural purposes, however, it is now (after 1960) assumed that a 'form' or 'variety' designated as such is infrasubspecific (presumably where the context admits).

FORMENKREIS: term introduced by Kleinschmidt in 1900 for a taxonomic grouping between the wide Linnean genus and the narrowly defined species of his own day; the nearest equivalent in current parlance is 'superspecies'. The author's views, although based on theoretical considerations that are unacceptable, had a useful influence on the development of taxonomic thought. See also SUPERSPECIES.

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FORMICARIIDAE: see under PASSERIFORMES, suborder Deutero-Oscines; ANTBIRD.

FOSSA: a depression in a bone, e.g. temporal fossa, tympanic fossa (see SKELETON, POST-CRANIAL).

FOSSIL BIRDS: any members of the class Aves whose remains have been preserved in a palaeontological context. Fossil birds range in age from the Jurassic Period up to only several hundred years old and may be taken to include all avian remains that are not accompanied by written historical documentation. Bone, both mineralized and unmineralized, is the most common and the most important type of avian fossil, although feathers, feather impressions, eggshells, gizzard stones, footprints, and mummified skin and bare parts have also contributed to our knowledge of birds of the past.

Chronological framework. A clear understanding of geological time and its associated biological events is essential to interpret the fossil record of birds. Recent years have witnessed great advances in geochronology and biochronology, especially through the application of radiometric and palaeomagnetic dating methods to many fossil localities. Figures 1 and 2 present a synthesis of much recent information on

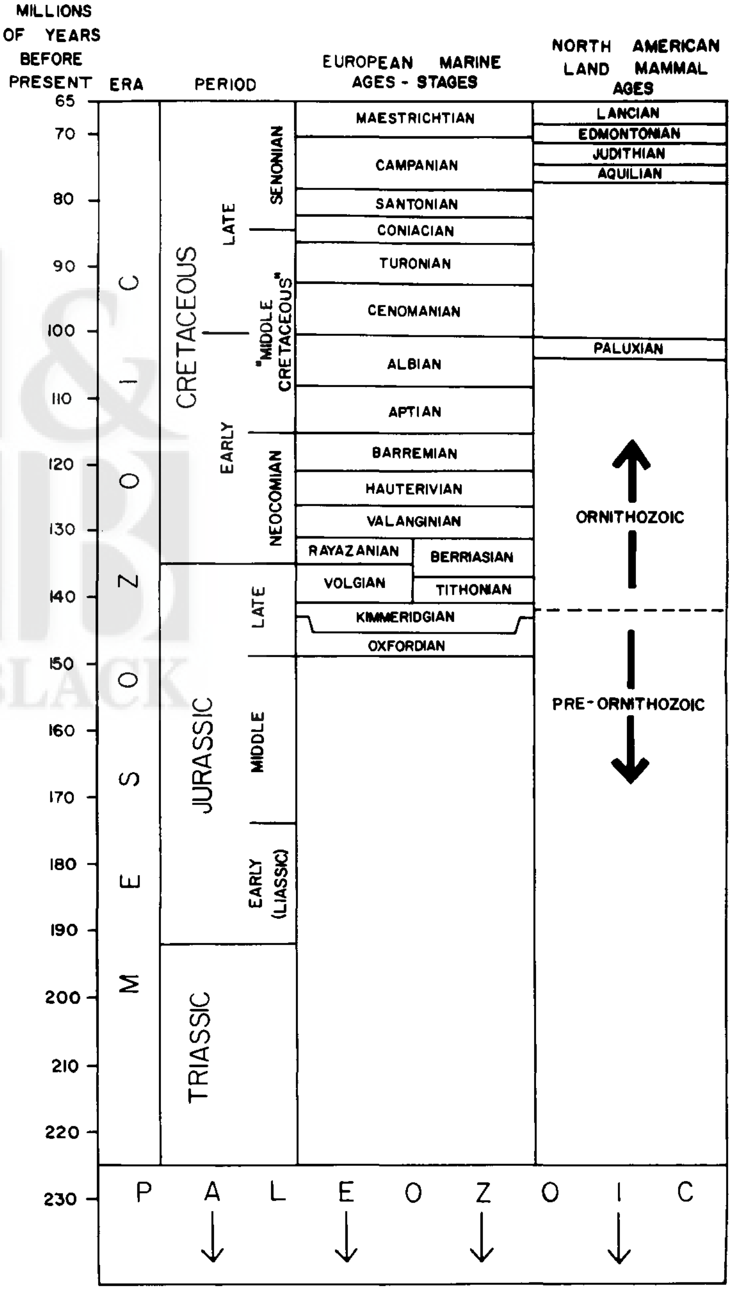

Fig. 1. Mesozoic time scale, as related to birds. (Largely derived from Clemens *et al* 1979. Acknowledgment to Dr E.H. Lindsay, University of Arizona).

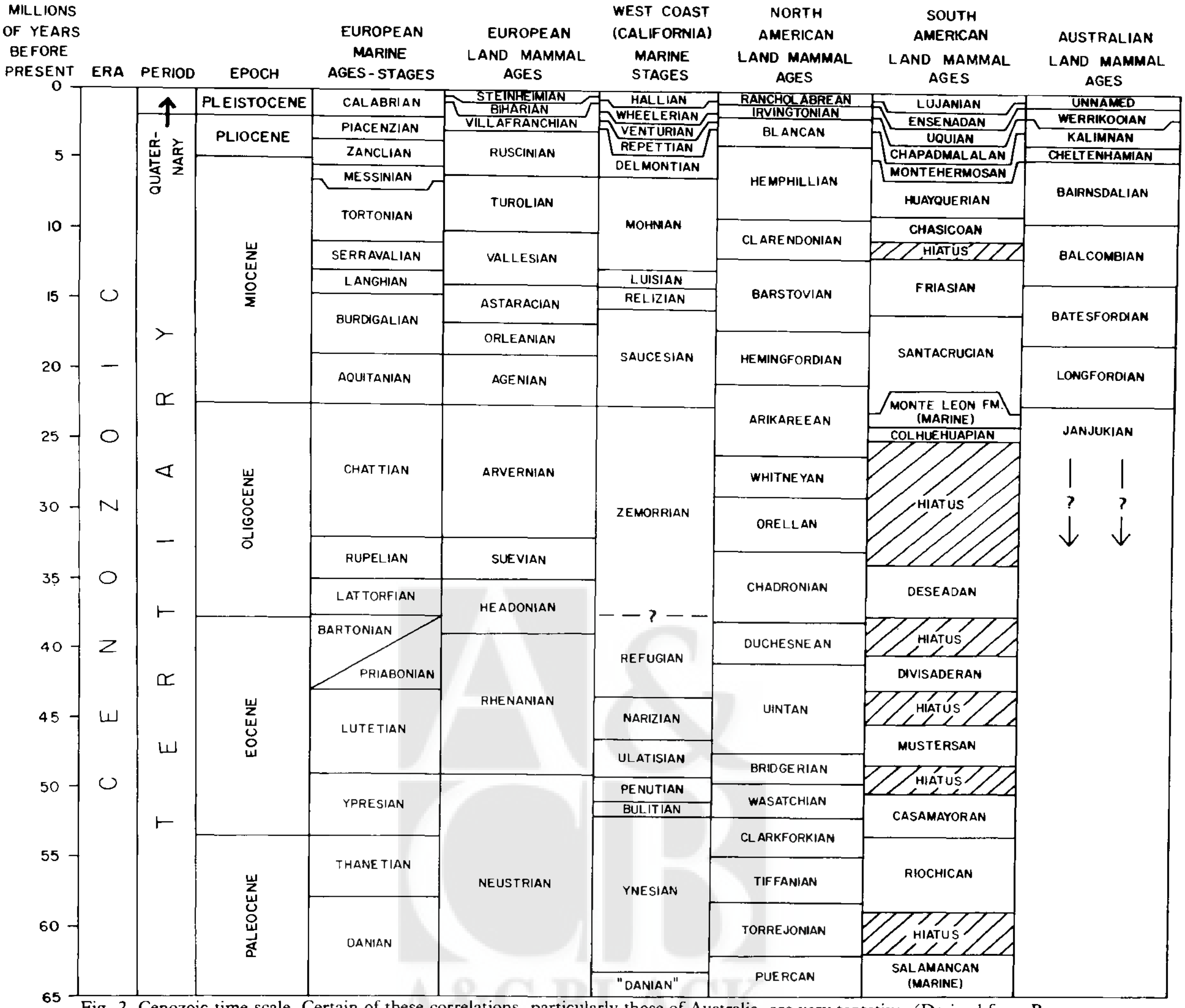

Fig. 2. Cenozoic time scale. Certain of these correlations, particularly those of Australia, are very tentative. (Derived from Berggren 1972, Berggren *et al* 1978, Berggren & van Couvering 1974, Lindsay & Tessman 1974, Marshall *et al* 1977, Stirton *et al* 1968).

geological time as it relates to fossil vertebrates. It is fortunate that essentially all terrestrial deposits of the Cenozoic Era that contain fossil birds have also yielded mammalian fossils, thus permitting biochronological correlation with other fossil sites in a sequence of land mammal ages. Likewise, most marine deposits with avian fossils have been temporally correlated on the basis of various invertebrate fossils or planktonic assemblages. In Africa and Asia, the fossil record of Cenozoic vertebrates has not yet been resolved into a system of land mammal ages.

The discovery and detailed study of new Mesozoic and Cenozoic vertebrate localities is proceeding rapidly on a world-wide basis, resulting in continuing significant changes and improvements in the temporal resolution of the fossil record. But much of the literature on fossil birds either ignores or deals inadequately with geochronology.

Archaeopteryx and the origin of birds. Birds evolved from archosaurian reptiles, as evidenced by the diapsid condition of the skull, the foraminate lower jaw, the shape and placement of the teeth, and the pelvic structure (see EARLY EVOLUTION OF BIRDS). The subclass Archosauria includes the following orders: Thecodontia (thecodonts), Crocodilia (crocodiles), Pterosauria (flying reptiles), Saurischia ('reptile-hipped' dinosaurs), and Ornithischia ('bird-hipped' dinosaurs). Crocodilians are the only surviving archosaurs, the other 4 orders being known only from Mesozoic fossils.

The ancestry of birds is a problem not yet resolved. A meaningful assessment of relationships of birds to various reptilian groups is very difficult in our present state of knowledge of avian osteology. For example, it has been shown that the names of certain palatal bones in the avian skull are probably not homologous with those of reptiles. Nevertheless, a close relationship to birds has been proposed at one time or another for each order of archosaurs. It appears, however, that all presently known archosaurs except thecodonts of the suborder Pseudosuchia are too specialized to qualify as possible ancestors. Evidence against a theory of avian origins from saurischians includes differences in their tarsal and dental morphology. Cranial and dental similarities have been used to suggest a rather close relationship between birds and crocodilians, but these similarities may be traced back to their thecodont ancestors, thus leaving no solid evidence to support an origin of birds via the crocodilians. The ornithischians differ from *Archaeopteryx* in the absence of sternal ribs, the presence of supraorbitals, and dental morphology, while the pterosaurs are different from birds in many ways, particularly in the tremendous elongation of the digits of the manus to form the main bony support for the wings.

A generalized pseudosuchian, perhaps similar to *Euparkeria* of the early Triassic of South Africa, has been suggested by various workers to be near the ancestry of birds. One must keep in mind, however, that nearly 100 million years separates *Euparkeria* from the earliest certain bird, ARCHAEOPTERYX of the late Jurassic (Tithonian) of Germany. It is in this long interval of time that we should search for reptiles with various sorts of avian characters that will provide new insights into the origin of birds.

The hypothesis of a pseudosuchian origin of birds has been strengthened recently by the discovery of 2 pseudosuchians that appear to have birdlike features. The first is *Cosesaurus aviceps* of the late Triassic of Spain, a very small reptile (skull length *c.* 18 mm) with a rather birdlike skull and indistinct linear structures near its long tail that may represent proto-feathers. The second new pseudosuchian is *Longisquama insignis* of the early Triassic of south-central USSR. The skull of *Longisquama* is 23 mm long and is less bird-like than that of *Cosesaurus*. The most interesting features of *Longisquama* are its fused clavicles that resemble an avian furcula and its greatly elongated mid-dorsal scales that roughly resemble feathers.

Stimulated by the discovery of several new specimens, there has been a strong renewal of interest in *Archaeopteryx* among palaeontologists of the past decade, especially in regard to its role in the origin and subsequent evolution of birds in general. The presence of highly developed feathers capable of sustaining flight leaves no doubt as to the avian nature of *Archaeopteryx*, in spite of the many reptilian characters in its skeleton. The toothed skull of *Archaeopteryx* is about 45 mm long and much more reptilian than avian in appearance. Other reptilian features of *Archaeopteryx* are the shape of the coracoid, the absence of an ossified sternum, the presence of gastralia, unfused carpals and metacarpals, clawed digits of the manus, and a long tail of many unfused caudal vertebrae. Avian characters of *Archaeopteryx* include the robust furcula, the elongated forelimb, and, most importantly, feathers that are very similar to those of modern birds.

Cretaceous birds. Most known birds of the Cretaceous are toothed, marine forms that are not clearly related to any birds recorded thus far from the Cenozoic Era. Large, flightless, diving birds inhabited the warm, shallow Cretaceous seas and include *Enaliornis* of the early Cretaceous (Albian) of England, and *Baptornis* and *Hesperornis* of the late Cretaceous (Coniacian) of North America. Another well known Cretaceous bird is the volant *Ichthyornis*, a sympatric contemporary of *Baptornis* and *Hesperornis*. The jaws of *Enaliornis* and *Baptornis* are not known, but *Hesperornis* and *Ichthyornis* had teeth that are basically similar to those of *Archaeopteryx*. All of the Cretaceous birds discussed thus far are probably specialized, dead-end groups. Many types of birds probably were toothless by the end of the Mesozoic, but *Gobipteryx* of the late Cretaceous of Mongolia is the only known avian skull of this period that lacks teeth.

Ambiortus, of the Neocomian of Mongolia, is very similar in overall structure to modern volant birds. Although it occurred only shortly after *Archaeopteryx*, *Ambiortus* possessed none of the reptilian features of *Archaeopteryx*. *Alexornis* (Campanian of Baja California) is the only other Cretaceous bird that may have any bearing on the evolution of modern land birds. *Alexornis* is a small bird that may be related to both the Momotidae (motmots) and the Bucconidae (puffbirds), but is different enough to warrant its own order.

Many named birds of the Cretaceous are of indeterminable systematic affinities because of the incomplete and undiagnostic nature of the fossils upon which they were based. Among such forms are *Gallornis* (Neocomian of France), *Parascaniornis* (Campanian of Sweden), *Torotix* (Lancian of Wyoming), and *Elopteryx* (Maestrichtian of Rumania), the first 3 of which have previously been regarded as early flamingos, and the last a pelecaniform. *Lonchodytes* and *Cimolopteryx* (both Lancian of Wyoming), as well as *Telmatornis* and *Palaeotringa* (both Maestrichtian of New Jersey) may be primitive charadriiforms. If so, they are among the few Cretaceous birds that seem referable to an existing order.

Tertiary birds. The fossil record of birds in the Tertiary Era is much more complete than that of the Cretaceous. Nearly all living orders of birds are first recorded in Paleogene (Paleocene to Oligocene) deposits, important exceptions being the passerines and the 'ratites', except possibly the Struthioniformes. Birds that are safely referable to living families appear from the early Eocene to the Oligocene. Thus the chronology of the first appearances of modern higher taxa of birds roughly parallels that of mammals, for which a more complete fossil record exists. Much caution should be used in stating the chronologies of various families and orders of birds because many fossils that have hitherto been thought to represent a modern family or order are actually too fragmentary to be diagnostic at even these levels.

Avian fossils of the Paleocene are relatively rare and are dominated by large, flightless, cursorial birds of possible gruiform affinities. Among such forms are *Gastornis* of the late Paleocene in Europe, and *Diatryma* of the late Paleocene to middle Eocene in Europe and North America. A single bone of a primitive owl is known from the late Paleocene of Colorado. The fossil record of Eocene birds is much more complete than that of the Paleocene, and includes the first appearances of many modern orders and families, but no fossils that can be assigned to living genera. Late Eocene penguins have been found in several areas within their modern range. Well known birds of the North American early Eocene include *Limnofregata*, a frigatebird; *Gallinuloides*, a galliform; *Presbyornis*, a colonial shorebird with a charadriiform post-cranial skeleton and a duck-like skull; a variety of large gruiforms, most of which were, however, much smaller than *Diatryma*; and the primobucconids, small arboreal birds that were similar to modern puffbirds. Eocene birds of Europe include *Colymboides*, a late Eocene diver; the early Eocene pelecaniforms *Prophaethon* and *Odontopteryx*, the latter with many bony tooth-like projections on its bill; and various small, non-passerine land birds. There is no unequivocal evidence for the occurrence of cracids in the Tertiary of Europe, as has been suggested in the past. The extensive terrestrial avifauna of the phosphorites of Quercy, France, is composed of fossils that are both late Eocene and early Oligocene in age. Among the birds of this site are galliforms, gruiforms such as *Idiornis* and *Elaphrocnemus*, the caprimulgiform *Aegialornis*, and the trogon-like *Archaeotrogon*. The few Paleogene records of birds in South America predominantly comprise a variety of gruiforms. Except for penguins, there are no fossil birds known from the Paleogene of Australia. There is no published record of Paleocene birds from Africa and only a single specimen of a pelecaniform (*Gigantornis*) is known from the Eocene. All reports of elephant-birds (Aepyornithidae) from the Tertiary of Africa are unreliable.

The fossil record of Oligocene birds is less complete than that of the Eocene. No fossil passerines are known from Oligocene deposits, although primitive passerines may have existed at this time. Nearly all families of non-passerines were probably established before the close of the Oligocene, but substantiation by fossils is lacking for many of them, particularly certain charadriiforms. Although palaeobotanists rightly regard the Oligocene as a time of significant world-wide cooling, the occurrence of cracids in South Dakota (*Procrax*, Chadronian), todies in Wyoming (*Palaeotodus*, Orellan), and motmots in Switzerland (*Protornis*, early Oligocene) is evidence that Oligocene climates were not extremely harsh.

Giant penguins were well represented in both Oligocene and Miocene times. Their contemporaneous ecological counterparts in the North Pacific were the plotopterids, a family of huge, flightless pelecaniforms. Both the plotopterids and the giant penguins were wing-propelled diving birds whose extinction may have been caused by competition with seals and porpoises, two groups of marine mammals that diversified greatly in the Miocene. The bony-toothed pseudodontorns were a family of pelecaniforms that inhabited lower Eocene to upper Miocene seas.

Fossil birds of the Neogene (Miocene and Pliocene) are known much better than those of the Paleogene. Many living families of birds first occur in Miocene deposits, but this is almost certainly a bias due to the relative scarcity of bird-bearing Oligocene sediments, especially marine deposits. The birds of Neogene waters present a combination of ancient and modern groups. A number of Miocene birds can be assigned to living genera, and many additional modern genera are first recorded from Pliocene deposits. Living genera of aquatic birds recorded from the Miocene include *Gavia*, *Diomedea*, *Puffinus*, *Oceanodroma*, *Phalacrocorax*, *Sula*, *Morus*, *Pelecanus*, *Phoenicopterus*, *Mergus*, and *Larus*. Among the well known extinct Neogene genera are *Palaeolodus*, a possibly natatorial flamingo of the Aquitanian of Europe, and the alcids *Praemancalla* (Miocene) and *Mancalla* (Pliocene), wing-propelled divers of the eastern Pacific.

Many Neogene land birds have been found outside of the modern range of their family. For example, temperate North America supported accipitrid vultures (*Palaeoborus*, *Neophrontops*) and cracids (*Boreortalis*, *Ortalis*) in the Miocene and Pliocene, and a pratincole (*Paractiornis*) in the Miocene. The Miocene avifauna of Europe included parrots (*Archaeopsittacus*), turacos (*Apopempsis*), mousebirds (*Colius*), trogons (*Paratrogon*), hornbills (*Homalopus*), barbets (Capitonidae), and broadbills (Eurylaimidae).

The Neogene record of birds in Australia comprises many families of non-passerines, of which only the endemic Dromornithidae are extinct. The dromornithids were huge, flightless birds that are known from the middle Miocene to the Pleistocene. Five genera and 8 species of dromornithids are currently recognized, but their relationships to other families of birds are not resolved. The Neogene avifaunas of South America and Africa are poorly known at present. That of Africa is particularly incomplete and contains only forms that are closely related to modern African species. That of South America includes penguins, tinamous, rheas, large cursorial gruiforms such as *Brontornis* and *Phor-*

orhacos, a variety of seriema-like gruiforms, and the spectacular teratorn *Argentavis*, which is the largest known flying bird. *Argentavis*, from the Huayquerian of Argentina, had a wing-span of *c.* 7.0–7.6 m and an estimated weight of 120 kg.

The first certain passerine fossils occur in Miocene deposits, but no rich fauna of passerines is known before the Pleistocene. The only Miocene passerines are an indeterminate broadbill from Germany, 2 corvids (*Miocitta* from Colorado and *Corvus* from France), a possible shrike from France, a sparrow from Kansas, and *Palaeoscinis* from California, which is thought to represent an extinct family perhaps related to bulbuls, waxwings, corvids, or dippers. The Pliocene record of passerines is somewhat better than that of the Miocene, but still is extremely incomplete and includes no species of major evolutionary or zoogeographic consequence.

Pleistocene birds. Although Pleistocene avifaunas are dominated by living species, they also contain a significant number of extinct ones. The record of late Pleistocene birds is much more complete than that of the early Pleistocene. Probably the single most important late Pleistocene site is Rancho La Brea, California, where past avian life is recorded in thousands of beautifully preserved, tar-impregnated bones. The teratorns were perhaps the most spectacular birds of the North American Pleistocene. *Teratornis incredibilis* had an estimated wing-span of about 5 m, greater than in any living bird. Although somewhat vulture-like in their post-cranial skeleton, the teratorns had a large, sharply hooked bill unlike that of any cathartid vulture. Other noteworthy extinct birds of the late Pleistocene in North America include 2 species of storks (*Ciconia maltha*, *Mycteria wetmorei*), a cathartid vulture (*Breagyps*), 2 accipitrid vultures (*Neogyps*, *Neophrontops*), a variety of large eagles of uncertain taxonomic position, 2 small turkeys (*Meleagris californica*, *M. crassipes*), a shelduck *Anabernicula*, and a flightless eider *Chendytes*.

The advance and retreat of continental ice sheets in the Holarctic Region had a profound effect upon the distributions of temperate and arctic birds. Fossil localities of glacial age have recorded northern birds such as ptarmigan *Lagopus* and jays *Perisoreus* hundreds of km south of their modern southern limits. It appears that many areas in tropical latitudes were more arid during glacial advances than during interglacial intervals, such as exists today. These changes in tropical climates and habitats had a great influence on avian evolution and distribution during the Quaternary. This subject has been analyzed in detail for tropical South America, based on the systematics and distributions of modern species. A useful fossil record of Pleistocene birds in South America is emerging; two recently studied late Pleistocene sites from Ecuador and Peru have yielded extinct species of cathartid vultures, hawks, a caracara, a heron, plovers, scolopacids, a seedsnipe, a phalarope, ducks, and a nightjar. The Pleistocene avifauna of Africa is still very poorly known, pending completion of study of a large number of avian fossils from Olduvai Gorge. Pleistocene birds from Australia consist mainly of living species of non-passerines, but extinct species include megapodes, a flamingo, and the dromornithids.

Quaternary fossil birds from oceanic islands. Fossil birds are known from many oceanic islands throughout the world. These ancient insular avifaunas are usually characterized by a high percentage of extinct forms, particularly flightless species (see FLIGHTLESSNESS). The age of many insular sites cannot be refined beyond 'Quaternary' because absolute age determinations are seldom available for sites that contain fossil birds but no cultural remains. Archaeological sites on islands often do contain extinct birds, however, and many of these sites have now been dated by radiocarbon. Past changes in climate (wind patterns, moisture regimes, oceanic currents) have affected avian extinctions on oceanic islands, but man has been the principal agent of extinction in island birds during the Holocene, through the combined forces of habitat destruction, hunting, and introduced mammalian predators. The numerous archaeological associations of man and extinct birds in New Zealand are particularly convincing evidence of man's ability to disrupt an island's avifauna (see EXTINCT BIRDS).

Flightless RAILS are especially characteristic of islands, although flightless species of many other families are also known. For example, flightless or nearly flightless fossil birds of the West Indies include an ibis from Jamaica (*Xenicibis*), and *Ornimegalonyx* from Cuba, the largest known owl. In addition, several volant extinct species of West Indian barn owls *Tyto* are larger than any living tytonids. Flightless geese *Thambetochen* and a flightless ibis *Apteribis* are known from Hawaii. Among New Zealand's endemic ancient birds are the huge MOAS, various anseriforms and rails, and *Megaegotheles*, a large owlet-nightjar. The fossil birds of Madagascar are dominated by the elephant-birds *Aepyornis*, a group of massive, ground-dwelling birds that are unknown outside Madagascar (see ELEPHANT-BIRD).

Prospects. Avian fossils have provided a wealth of data bearing on the evolution, systematics, and zoogeography of birds. Through careful work by modern avian palaeontologists, our knowledge in these subjects can only improve with time. An important duty in current avian palaeontology is to re-examine many fossils that have been mistreated taxonomically, either because they were described in the absence of adequate comparative skeletons, or because the fossil itself was simply too fragmentary to permit an accurate assessment of its taxonomic position. The relative scarcity of avian fossils as compared to mammalian fossils has promoted the philosophy that every avian fossil, no matter how badly damaged or incomplete, can and should be identified and named. As a result, there is an abundance of generic and specific names of fossil birds that are based on specimens that cannot be safely assigned even to a family or order.

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FOSSORIAL: term applied to the habit of digging (not just scratching or probing) or burrowing in the soil, exhibited by various birds in preparing nesting holes (see NEST).

FOSTER PARENTS: see BROOD-PARASITISM.

FOUNDER PRINCIPLE: the thesis that the founders of a new population (e.g. breeding colony) contain only a small fraction of the total genetic variation of the parental population.

FOVEA: part of the retina of the eye (see VISION).

FOWL, DOMESTIC: see DOMESTICATION.

FOWLING: see TRAPPING; WILDFOWL.

FOWL PLAGUE: see DISEASE.

FRANCOLIN: substantive name of *Francolinus* and *Pternistis* spp. (see under PHEASANT).

FRATERCULINI: see AUK.

FREGATAE; FREGATIDAE: see under PELECANIFORMES; FRIGATEBIRD.

FREQUENCY-DEPENDENT SELECTION: a process which causes a character to be advantageous to an individual when it is rare in the population and disadvantageous when it is common. Differences between individuals in their ability to survive and reproduce may be due to genetic differences between them (see NATURAL SELECTION). When the superiority of a particular genotype depends upon the genetic composition of the population and the genotype is at a selective advantage when rare, then the rarer forms will increase in frequency until they reach an equilibrium level at which they no longer gain an advantage. Such selection can occur if a predator or parasite attacks a disproportionately large number of the commonest individuals, or where individuals preferentially mate with those which possess a rare allele (disassortative mating). Frequency-dependent selection, also known as apostatic selection, may be an important factor in maintaining genetic diversity (Clarke 1979).

Most avian studies of frequency-dependent selection have concentrated on the feeding behaviour of predators and its effect on the visual polymorphisms of prey. Imagine a bird feeding on a prey species which can be one of two colours, pink or brown. When the pink morphs are common and brown ones rare, predators consume pink prey in a greater proportion than expected from their frequency in the population. As a result, the overlooked brown ones gain a reproductive advantage and begin to increase in relative frequency. At some stage they may become so common that the predator switches its attention to the brown individuals, ignoring the pink which will now have the advantage. This process will continue until eventually a balanced mixture of the two morphs will arise which is maintained by frequency-dependent predation.

A tendency to take disproportionately more of the common varieties of prey and overlook rare ones has been shown experimentally with studies of chicks and quail feeding on coloured mixtures of artificial baits. Frequency-dependent predation has been invoked to explain the maintenance of colour polymorphisms in prey species e.g. snails, mimetic butterflies. This mode of predation may be advantageous to the predator. By switching to the commoner prey types the predator may maximize its rate of food intake (see OPTIMAL FORAGING). One proximate means of producing this preference is through the formation of a searching image for particular forms of prey.

Frequency-dependent factors may also select for colour polymorphism in predators. Diurnal birds of prey which feed on relatively intelligent prey with good visual acuity (e.g. birds and mammals) are more polymorphic for colour than other predators (see POLYMORPHISM). One possible explanation is that it may be advantageous for the predator to differ from the visual norm. The success of the character in deceiving the prey will depend on its relative frequency in the population (Paulson 1973). P.J.G.

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FREQUENCY DISTRIBUTION: see BIOSTATISTICS.

FRIARBIRD: substantive name, alternatively 'leatherhead', of the HONEYEATERS of the genus *Philemon* (see also MIMICRY).

FRIGATEBIRD: substantive name of the species of Freigatidae (Pelecaniformes, suborder Fregatae); in the plural, general term for the family. Five species and some 14 subspecies are listed, but the taxonomy of the group requires revision. There is a single genus *Fregata*.

Characteristics. Frigatebirds range in length from 70–80 cm (*F. ariel*) to over 110 cm (*F. minor* and *F. magnificens*); females tend to be larger than males, and there is marked sexual dimorphism in all species. The enormous black wings (spanning over 2 m in the larger species), long hooked bill and forked tail provide an unmistakeable flight silhouette. Frigatebirds have a low wing-loading and soar effortlessly, taking advantage of updraughts to gain height and remaining semi-motionless on the wing for hours at a time (see also FLIGHT). In pursuit of prey they are speedy and highly manoeuvrable; the large tail twists and turns for steering and braking. On the ground the wings are an encumbrance, and in strong winds the birds have difficulty in landing. The legs are small and the feet, with reduced webbing, and sharp claws, are appropriate more for perching than for swimming.

Lesser Frigatebird *Fregata ariel*. (*J.B.*).

Habitat and distribution. Frigatebirds (or Man-of-war birds) occur in tropical and subtropical oceanic areas, particularly where flying fish are abundant. Breeding birds tend to stay close to their breeding grounds throughout the year; non-breeding young disperse widely and may appear over 800 km from the nearest land. The presence of several frigatebirds together is often an indication that their breeding ground is not far away.

The sedentary habit of frigatebirds and their isolation on islands has led to the formation of many small, isolated populations. The Ascension I. Frigatebird *Fregata aquila* is peculiar to Ascension, where a population of 2,000 to 3,000 adults breed on nearby Boatswainbird Island. The total population has been estimated at 8,000 to 10,000 birds. *F. andrewsi* the Christmas I. Frigatebird breeds on Christmas I. and other islands in the eastern Indian Ocean. The Magnificent Frigatebird *F. magnificens*, largest of the genus, ranges from the Galapagos Is. and eastern Pacific Ocean to the Caribbean, Cape Verde Is. and the coast of West Africa. The Lesser Frigatebird *F. ariel* and Great Frigatebird *F. minor* breed on islands of the Indian and Pacific Oceans and also at South Trinidad in the southern Atlantic Ocean.

Food. The skill of frigatebirds in chasing home-coming boobies, forcing them to disgorge fish and then catching the food in mid-air, has been described by many observers. Frigatebirds are, however, fully capable of fishing for themselves. They seldom settle on the sea; their oil glands are small and the plumage seems inadequately coated, readily becoming saturated. Instead they fly above shoals of hunting tuna or dolphins and catch on the wing the flying fish that leap out of the water ahead of their pursuers. They also snap up refuse from the surface of the sea, and may swoop low over open breeding colonies of terns and other small birds, taking unwary chicks; chicks of their own species may be taken if left unattended.

Behaviour. In the courtship season males develop an inflatable crimson gular sac, which they display prominently. In splendid iridescent black plumage they take up nest sites on the colony; with wings spread and sac inflated like a balloon, they posture to females flying overhead, shivering violently and rattling bills and quills as potential partners approach.

Resting adults and juveniles seek shade from strong tropical sun, but in exposed places they take up a 'sunning' posture with wings extended and turned so that the concave under-surface lies uppermost, possibly as a means of shedding heat.

Breeding. Frigatebirds nest typically in trees or low shrubs, but in the absence of vegetation they breed successfully on the ground. There is strong competition for sites or for nesting material on the colonies, which are often crowded, with special areas of concentration. Nest material, including sticks, feathers and bones, accumulated by both parents during courtship and incubation, is often lost to neighbours. A single large white egg is laid, and both parents incubate. The chick is hatched after some 55 days' incubation, and closely brooded for a further 2 or more weeks until covered with pale grey down. The chicks defend themselves from intrusions of neighbours while both parents search for food; nest losses at this stage may be very high when competition for sites is keen. Fully feathered after 4–5 months, the juveniles (in all species distinguished by a white head) remain dependent on their parents for a further 2–6 months, sometimes augmenting food brought to them by scavenging on the colony. They fly together in small bands, picking up feathers and seaweed from the surface of the sea, snatching small unattended chicks of their own species, occasionally attacking boobies and other flying birds, and gradually acquiring the skills necessary for catching food on the wing. B.S.

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FRIGATE-PETREL: substantive name of *Pelagodroma* ('*Fregetta*') spp. (see PETREL).

FRINGILLIDAE; FRINGILLINAE: a family and subfamily of PASSERIFORMES, suborder Oscines; FINCH.

FROGMOUTH: substantive name of the species of Podargidae (Caprimulgiformes, suborder Caprimulgi); in the plural, general term for the family.

Systematics and distribution. This is a group of large 'nightjars' (in the ordinal sense) confined to the Oriental and Australasian Regions (not New Zealand); it comprises 2 genera: *Podargus* (3 species, 33–58 cm long), restricted to Australia, New Guinea and the Solomon Islands, and *Batrachostomus* (9 species, 23–40 cm long), occurring from India to Malaya.

Characteristics. Frogmouths have the same marbled grey-brown and rufous cryptic colouring and soft plumage as true nightjars, but differ considerably in some of their habits and structural characters. Anatomical peculiarities, as compared with the true nightjars, include a desmognathous instead of an aegithognathous palate, no functional basipterygoid processes, 13 instead of 14 cervical vertebrae, sternum double-notched on each side, outer toe with 5 phalanges, a single carotid, and a bronchial syrinx. The tongue is large and paper-like. In both genera there is a pair of remarkably well-developed powder-down tufts arranged on either side of the rump. *Podargus* lacks an oil gland, while *Batrachostomus* possesses a very small one. The bills are wide and boat-like, so that earlier naturalists surmised that they were superbly adapted for hawking after nocturnal flying insects. However, it has been demonstrated that frogmouths capture most of their prey on the ground or from branches. Frogmouths are comparatively fast fliers for short distances, but they are inferior to the Nightjar *Caprimulgus europeaus* for sustained FLIGHT owing to their lower aspect-ratio. Manoeuvring ability, as judged by relative tail area, has been lost by *Podargus* in greater degree than by *Batrachostomus*.

Podargus has a characteristic alarm posture in daylight; the bird stretches out, with its bill pointed obliquely upward, and the resemblance to a broken branch is remarkable. It freezes into this rigid 'broken branch' stance only if flushed unawares by day and does not adopt the attitude at night. The birds are active after dusk and before dawn.

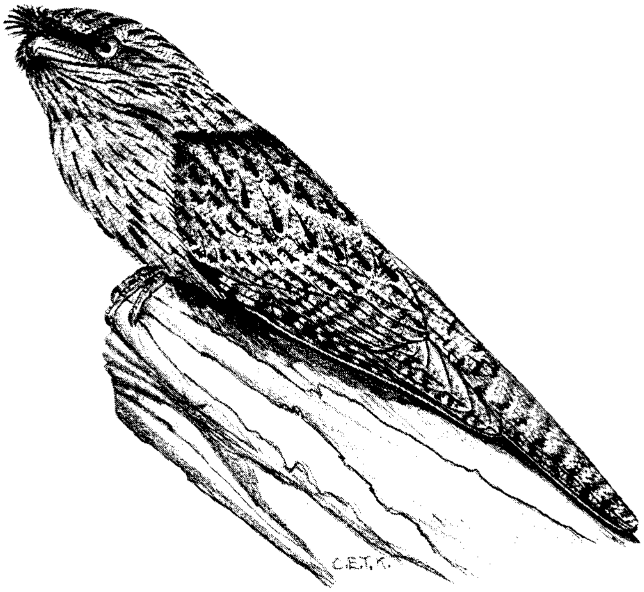
Habitat. Frogmouths are arboreal, occurring in forested country.

Population. Frogmouths occur in pairs, but they are nowhere particularly numerous, and, in the Australasian Region, are never seen in the great densities reported of nightjars in Africa and tropical America.

Food. Frogmouths make short flights from a sally point to take a resting beetle, scorpion, centipede, snail, or frog from the ground or a branch. Mice and small birds, and occasionally fruits, are also eaten. They have to a large extent lost the aerial feeding habit.

Voice. Calls include repeated low-pitched hoots, also hissing and screeching notes.

Breeding. *Podargus* builds a flimsy stick nest on the horizontal bough of a tree, *Batrachostomus* a pad-like structure made up of its own down and with an external covering of spider-web and lichens. The eggs are white, *Batrachostomus* lays one, and *Podargus* 2, occasionally 3. Both incubation and fledging periods are about 30 days. The young are covered with long white down. Probably only the female incubates, but both parents share in the feeding of the young.



Tawny Frogmouth *Podargus strigoides*. (*C.E.T.K.*).

See photo NOCTURNAL HABITS. D.L.S.

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Schodde, R. & Mason, I.J. 1980. Nocturnal Birds of Australia. Melbourne.
Serventy, D.L. 1936. Feeding methods of Podargus—with remarks on the possible causes of its aberrant habits. Emu 36: 74–90.
Stresemann, E. 1937. Studien über die Gattung *Batrachostomus*. Mitt. Zool. Mus. Berlin 22: 304–329.

FROGMOUTH, OWLET: see OWLET-FROGMOUTH.

FRONTAL: pertaining to the forehead (for the frontal bones see SKELETON, POST-CRANIAL); also used on occasion (e.g. aerodynamically) in its ordinary more general sense of entire forward-facing aspect.

FRONTED: refers to the forehead (in such combinations as 'white-fronted').

FRUGIVOROUS: fruit eating.

FRUITCROW: substantive name of *Querula purpurata* and *Pyroderus scutatus*, also applied as a general term to other large COTINGAS.

FRUITEATER: substantive name of COTINGAS of the genera *Pipreola* and *Ampelioides*.

FULICINAE: see under RAIL.

FULL-WINGED: having the power of flight.

FULMAR: substantive name of *Fulmarus* spp. and *Macronectes giganteus*, and often applied without qualification to *F. glacialis*; in the plural, a general term for these and allied genera of the Procellariidae (see PETREL). See photos DISPLAY; FEEDING HABITS.

FULMAR-OIL: see PETREL.

FURCULA: bony structure ('wishbone' or 'merrythought') formed by fusion, in birds, of the right and left clavicles (see SKELETON, POST-CRANIAL).

FURNARII: infraorder of PASSERIFORMES, suborder Deutero-Oscines.

FURNARIIDAE: see under PASSERIFORMES, suborder Deutero-Oscines; OVENBIRD (1).

G

GADWALL: *Anas strepera* (see DUCK).

GAGGLE: see ASSEMBLY, NOUN OF.

GAIT: see LOCOMOTION, TERRESTRIAL.

GALAH: name now generally used (formerly Roseate Cockatoo) for the small Australian cockatoo *Cacatua roseicapilla* (see PARROT).

GALAPAGOS FINCHES: see DARWIN'S FINCHES.

GALBULAE; GALBULIDAE: see under PICIFORMES; JACAMAR.

GALBULOIDEA: see under PICIFORMES.

GALL-BLADDER: not always present in birds (see LIVER).

GALLERY FOREST: a type of riverine forest consisting of trees whose roots need wet conditions and are adapted to resist flooding. The tree canopy may extend over the water, hiding the bank from view.

GALLI: see below.

GALLIFORMES: an order, alternatively 'Galli', comprising 2 suborders: Galli, Opisthocomi; 4 families: Megapodiidae (MEGAPODE), Cracidae (CURASSOW), Phasianidae (PHEASANT; GROUSE; GUINEAFOWL; TURKEY), Opisthocomidae (HOATZIN). They are often referred to as 'gallinaceous birds', the domestic fowl being a characteristic member; and they are sometimes loosely called GAME-BIRDS, which some of the most familiar species notably are. The order is a cosmopolitan one, but Megapodiidae and Numidinae have restricted distribution in the Old World and the Cracidae, Meleagridinae, and Opisthocomidae in the New; the Tetraoninae are confined to the Northern Hemisphere. Several species have been domesticated and others are often kept in captivity as ornamental birds (see DOMESTICATION).

GALLINACEOUS: resembling a domestic fowl (see GALLIFORMES).

GALLINULE: substantive name of species of *Porphyrio*, *Porphyrula*, and sometimes (alternatively to 'moorhen') *Gallinula* (see RAIL).

GALLITO: substantive name of *Rhinocrypta lanceolata* (see TAPACULO).

GALLOPHEASANT: in the plural, term for *Lophura* spp. (see PHEASANT).

GAME-BIRDS: sometimes used ornithologically to denote the Galliformes, but properly a general term for certain quarry species belonging for the most part to the subfamilies Tetraoninae and Phasianinae (see GROUSE; PHEASANT). In certain parts of the world others of the Galliformes are included, such as turkeys (Meleagridinae), guineafowl (Numidinae), megapodes (Megapodiidae) and guans (Cracidae). Bustards (Otididae) of the order Gruiformes, tinamous (Tinamiformes), and certain 'waders' (Charadrii)—notably snipe and woodcock (Scolopacidae)—are usually regarded as game-birds, although the ducks, geese, and swans (Anatidae) are not (see WILDFOWL); but in New Zealand the introduced Black Swan *Cygnus atratus* and Canada Goose *Branta canadensis* are sometimes referred to as 'game', and 'game ducks' was formerly used for dabbling ducks of the tribe Anatini (see DUCK).

The term 'game' has a legal connotation in Britain, and a game licence is required to shoot Partridge *Perdix perdix*, Pheasant *Phasianus colchicus*, grouse (Red Grouse *Lagopus lagopus* and Ptarmigan *L. mutus*), and 'black game' (Black Grouse *Tetrao tetrix*); bustards *Otis* spp. were also included, anachronistically, in this list until 1954. In addition, the Woodcock *Scolopax rusticola* and snipe *Gallinago* spp., etc., have a more limited status under the game laws, and until 1954 this was true also of the Quail *Coturnix coturnix* and the Corncrake *Crex crex*. The need for special game laws to protect sporting rights originated from the fact that in the common law of England (not Scotland) wild animals in general were nobody's property until brought into possession by killing or capture. In America, game laws have had the object of protecting the birds rather than of preserving enclosure rights (see CONSERVATION).

The shooting of game-birds in most parts of the world consists of 'walking-up' ('jump shooting' is the American phrase), and dogs—setters and pointers—have been bred specially for giving advance warning of crouching game-birds. A more complicated system known as 'driving' was evolved and brought to a high pitch of efficiency in Britain at the end of the 19th century; grouse, pheasant, and partridge 'drives' became and have remained a feature of British country life, and are conducted strictly in accordance with tradition. The breeding and training of dogs for 'pointing', 'setting', and particularly for 'retrieving' wounded birds, is regarded by devotees of the sport as one of the most satisfying aspects of game shooting. P.S.

GAMES THEORY: the mathematical theory of decision making by individuals in circumstances where interests are at least in part conflicting. In the study of bird behaviour, games theory models have been used to analyze questions such as why birds obey conventional signals to settle contests for resources, and why prior residence seems to lead to dominance in territorial combat.

GAMETE: general term for a germ-cell, whether spermatozoon or ovum (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; GENETICS).

GAMOSEMATIC: term for appearance or behaviour that helps members of a pair to find each other.

GANDER: special term for a male GOOSE (1).

GANNET: substantive name for the 3 members (allospecies) of the gannet superspecies—Atlantic, *Sula bassana*, African, *S. capensis*, and Australasian, *S. serrator*—which with the 6 booby species comprise the Sulidae (Pelecaniformes, suborder Pelecani). The 9 species comprise some 17–19 forms, though 6 of the species are monotypic (the 3 polytypics are Masked or White (*Sula dactylatra*), Brown (*S. leucogaster*) and Red-footed Booby (*S. sula*). Sulids are sometimes split into 2 genera, *Morus* (gannets) and *Sula* (boobies).

Characteristics. Gannets and boobies have torpedo-shaped bodies, strong, tapering and slightly hooked bills (no external nostrils) which can gape extremely widely; long, fairly narrow wings and a variable but generally long and wedge-shaped tail. The heaviest sulid (length 90 cm) is the Atlantic Gannet (3,100 g) and the lightest is the Red-footed Booby (940 g). Variable combinations of morphological characters indicate the adaptive radiation which has developed within the family and which relates mainly to their different modes of foraging and feeding, though all plunge-dive deeply. The legs are fairly short and strong, and the feet are webbed between all 4 toes. All adult sulids except the Brown Booby and brown forms of the Red-footed are completely white on belly and breast and the 3 gannets and the Masked Booby are mainly white above. The facial skin, iris, bill and feet may be brightly coloured. All juveniles except Abbott's *Sula abbotti* differ in plumage, varying in degree from adults; the juvenile Atlantic Gannet is mainly black and its parents mainly white. Adult plumage is gained, according to species, in the 3rd to 6th year.

Habitat. Gannets and boobies are so well adapted to life at sea that they can spend long periods without approaching land. Atlantic Gannets nest mainly on cliffs, including precipitous faces; the other 2 gannets nest mainly on flat ground, as do Blue-footed *S. nebouxii* and Masked Boobies. Brown Boobies prefer slopes or semi-cliffs and Peruvian Boobies *S. variegata* utilize cliffs, slopes and flat ground. Red-footed Boobies nest in low scrub or in trees, and Abbott's Booby is restricted to tall jungle trees.

Distribution and populations. Sulids breed from the Arctic (Atlantic Gannets in Norway) almost to the sub-Antarctic (the Australasian Gannet breeds at 46° 36′S). But the boobies are essentially tropical to subtropical, 3 species breeding on islands at these latitudes, across the

Blue-footed Booby *Sula nebouxii*, landing salute. (*J.B.*).

world's oceans. The commonest sulids are undoubtedly the Red-footed and Brown Boobies and the rarest is Abbott's, which is confined to the Indian Ocean Christmas Island. The Peruvian Booby is confined almost entirely to the Guano Islands of the Humboldt current off Peru; the Blue-footed is restricted to 3 areas on the fringes of cold water (Northern Peru and north to Panama; the Galapagos Islands; the Gulf of California and islands off Mexico). Apart from Abbott's Booby, the most accurately censused sulids are the 3 gannets, especially the Atlantic. There are 6 colonies of African Gannets off the southern tip of Africa (some 166,000 pairs at the last census in 1956), approximately 25 colonies and roughly 35,000 pairs of Australasian Gannets and 34 colonies containing some 213,000 pairs of Atlantic Gannets (6 of these colonies, some 33,000 pairs, are in Canada).

Movements. All sulids disperse widely from their breeding stations and the tropical trio may be encountered thousands of kilometres from the nearest land. The Atlantic Gannet is occasionally seen in mid-Atlantic.

The juveniles disperse most widely and in the 3 gannets this movement is a genuine migration which takes virtually all the year's young more than 5,000 km away from their birthplace, to warmer waters. Thus, the E. Atlantic young migrate almost to the Equator off West Africa and those from Canadian colonies to the Gulf of Mexico. The young African Gannets move north as far as the Gulf of Guinea and the Australasian juveniles cross the Tasman Sea mainly to the east and south coasts of Australia. The most stay-at-home is probably the Peruvian Booby, but even it may move thousands of kilometres under certain conditions.

Food. Gannets and boobies eat mainly fish and squid. Of the species for which there is reasonable information (which excludes Abbott's and the Blue-foot) all have both a wide spectrum but also preferred prey. Thus the Atlantic Gannet takes at least 50 species on occasion, but herring *Clupea harengus*, mackerel *Scomber scombrus*, sprat *Sprattus sprattus* and sand-eels *Ammodytes* are probably most important. The trio of tropical boobies all depend heavily on flying fish and squid species; the Peruvian Booby is virtually dependent on the anchovy *Engraulis encrasicholus*, and so on. But probably all are highly opportunistic and will take unusual species or hunt in an unusual manner. Thus, whilst sulids plunge-dive from various heights (up to 45 m in the Atlantic Gannet) they also dive from the surface, pursue prey by underwater swimming and may even hunt on foot in shallow water. Following a plunge, the fish is often taken from beneath as the bird comes up. Even the Atlantic Gannet probably rarely penetrates beyond some 3 m by diving, and perhaps 5–15 m by swimming. Several boobies capture flying fish and squid on the wing. Whilst all sulids (except perhaps Abbott's, for which there is no information) occasionally, or usually, dive in groups which may exceed 1,000 birds, only the Blue-foot is known to co-operate in feeding, by diving synchronously upon a vocalization from a member of the group. This species, and especially the male, also has a marked tendency to plunge-dive into extremely shallow, inshore water. Scavenging is probably not important for any sulid, but is practised by several.

Voice. The Atlantic Gannet's basic call is a rasping *aarah-arrah* given at about 2 calls per second when flying on to the site, and when displaying and (intermittently and with variants) when fighting. Calls given during communal activities (gathering nest material or fishing) are shorter, gruffer but less metallic and quicker. In flight a raven-like *krok krok* is occasionally uttered. During the skypointing display with the bill which precedes and accompanies take-off, a sighing groan, *oo-ah*, is given and is a true vocalization rather than an involuntary expiration caused by the looped-up posture. Individual voices are recognized by mates, neighbours and chicks. The boobies whistle, honk, quack and (Abbott's) call in a deep sonorous bellow.

Breeding and behaviour. All sulids except Abbott's Booby nest in colonies; the largest are those of the Peruvian Booby (up to at least 750,000 pairs) but all except Abbott's may number thousands of pairs. The densest breeding colonies are those of the African Gannet (up to 6.8 nests/m^2). Perhaps the most widely dispersed ground nesting sulid is typically the Masked Booby, which at its densest occupies 3.3 m^2 per pair and has a suggested optimal spacing of 1 pair per 200 m^2. In all the ground-nesting boobies density is much affected by terrain, whereas in the 3 gannets it is relatively inflexible.

All sulids possess a rich repertoire of ritualized behaviour which communicates to fellow members their 'mood' and 'intention'. Thus, upon returning to the colony after a period of sea-wandering, the experienced male breeder typically resumes occupancy of his old site and displays there.

Sulid displays have family characters. Though often complex, their ritualized displays derive from simple movements such as head-shaking, biting or touching the ground or nest material, and so on. In functional terms, display usually substitutes for overt fighting in declaring and preserving the territory (which may be no more than the actual nest site) and in forming and maintaining the pair-bond. Sulids, and especially the 3 gannets, are unusual among seabirds in the extent to which they have developed both of these functional groups of displays, and particularly the pair-bonding ones. There is no courtship feeding. Movement around the territory, and particularly away from the mate, is accompanied by ritualized postures derived from intention-movements. Ritualized appeasement behaviour involves placing the bill in non-attack positions. Comfort behaviour includes oiling, by which the bird transfers the secretion from the preen gland above the roots of the tail feathers to the plumage; various shaking movements; scratching; wing-stretching (never both together) and various forms of heat-regulating movements. These include exposing and excreting on the webs for evaporative cooling, panting and fluttering the throat-skin and hanging the wings loosely away from the body.

Sulids incubate by applying their webs to the egg(s), until these begin to pip at 43–45 days, whereupon they are transferred to the tops of the webs. Egg-shells are not carried away from the nest. The new chick, with but a few sparse tracts of down, is brooded on top of the webs. No sulid chick can regulate its own body temperature until it is about a month old. It takes food directly from the parent's mouth and throat. Later, the chick's begging behaviour varies with species; it is frenzied in the 3 tropical boobies, but highly restrained in the Atlantic Gannet and in Abbott's Booby, in both of which falling from the nest is a major danger.

The detailed breeding ecology of each species of sulid is largely determined by the nature of its food supply. The Peruvian Booby on the doorstep of the prolific Humboldt upwelling rears up to 4 young; the Blue-foot, on the fringes of productive cold water, often rears 2; two of the boobies from impoverished tropical blue-water (the Masked and the Brown) often hatch 2 eggs but the brood is invariably reduced to 1 by sibling-murder; the third tropical booby (the Red-foot) always lays 1 egg. All 3 frequently lose their young by starvation due to the unpredictable food shortages which occur in their relatively unseasonal areas. The 3 gannets all lay one-egg clutches although the Atlantic Gannet, especially, breeds in food-rich waters. However, it (and to a lesser extent its 2 allospecies) invests much of its feeding in the production of young with large fat reserves, since the newly-fledged young are thrown entirely on to their own resources when *c.* 15 weeks old; all the others are fed as free-flying juveniles, the young Abbott's Booby for between 6–12 months.

All sulids except Abbott's Booby are known to be able to rear to fledging one chick from up to 70% of all clutches laid; some can do considerably better. However, among the 3 tropical boobies and Abbott's, breeding success in some areas can fall well below 20%, and although the Peruvian Booby is normally most productive of all, its success can be zero, and the vast majority of adults can die, in (Niño) years in which the upwelling fails and warm water drives the cold-loving anchovies to inaccessible depths.

Responses to the nature of the feeding environment largely determine breeding regime. Thus, Abbott's Booby clearly cannot lay each year, since each cycle occupies far more than 12 months. On the other hand, Brown Boobies on Ascension and Galapagos Blue-footed Boobies may lay only some 9 months apart even when successful; but, typically, sulids lay once a year. The sulid most closely tied to laying at a particular time each year is the Atlantic Gannet, though this time varies by up to 3 weeks even between British colonies.

Sulids breed for the first time at ages ranging from 2–6 years. Some apparently have 'rest' years, when the pair remains together but does not attempt to breed. Atlantic Gannets do not rest in this way. Mortality rate figures lie between 6–10% but are probably lower in some cases. Fidelity to site and mate is very high in the Atlantic Gannet, but much lower in the boobies (possibly excepting Abbott's). Even erstwhile successful pairs of Masked Boobies may split up, though both partners return to the colony and though such divorce tends to reduce breeding success. See photo RITUALIZATION. J.B.N.

Fisher, J. & Vevers, H.G. 1943–44. The breeding distribution, history and population of the North Atlantic Gannet *Sula bassana*. J. Anim. Ecol., 12: 173–213; 13: 49–62.

Gurney, J.H. 1913. The Gannet, a Bird with a History. London.

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GAPE: GAPE FLANGES: see BILL; FLANGES; PARENTAL CARE.

GAPES: see DISEASE.

GAPING: see BEHAVIOUR, DEVELOPMENT OF.

GARDENER: substantive name of *Amblyornis* spp. (see BOWERBIRD).

GAREFOWL: alternative name of the extinct Great Auk *Pinguinus impennis* (see AUK; EXTINCT BIRDS).

GARGANEY: *Anas querquedula* (see DUCK).

GARROD'S FORMULA: see MUSCULATURE.

GARRULINAE: see CROW (I).

GARUDA: see FABULOUS BIRDS.

GASTRULATION: see DEVELOPMENT, EMBRYONIC.

GAUSE'S RULE: in 1934 G.F. Gause wrote: 'As a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of foods and modes of life in which it has an advantage over its competitor'. Gause's rule is often paraphrased as: 'Species with similar (or the same) ecological niches cannot coexist'; and as its corollary 'Coexisting species differ in their ecology'.

Gause's rule is useful as a general statement: but it is not a testable hypothesis in normal scientific terms, because its reasoning is circular. If species coexist, they must be sufficiently different: if they do not coexist, they are too similar. Unless the terms 'similar' and 'different' can be made more precise, there is no way out of this impasse.

Gause, G.F. 1934. The Struggle for Existence. Baltimore.

GAVIAE: alternative ordinal name (see below); but 'almost from the beginning of systematic Ornithology the word *Gavia* has been used in several senses' (Newton); one of the more recent usages of 'Gaviae' was for an order equivalent to the present suborder Lari of the Charadriiformes.

GAVIIDAE: see below.

GAVIIFORMES: an order, alternatively 'Gaviae', comprising only the Holarctic family Gaviidae (see DIVER). For the question of nomenclature see under COLYMBIDAE.

GENE: see GENETICS.

GENE FLOW: the movement of genes from one population to another, resulting from an individual breeding in a population other than that in which it was born. (In plants, dispersal of pollen or seeds may result in gene flow.)

GENERA: plural of GENUS.

GENERIC NAME: see NOMENCLATURE.

GENETIC DRIFT: change in the frequency of a gene or genes in a population—or, more generally, change in the whole gene-complex—as a result of random processes of reproduction and survival of individuals, independent of NATURAL SELECTION. The importance of genetic drift in evolution has long been a matter of dispute, but it is now generally agreed that it is unlikely to be important except in very small populations.

GENETICS: the study of how characters are passed from parent to offspring, and thus one of the fundamental parts of biology. The basic laws of inheritance were discovered by the Abbot Gregor Mendel (1822–84), but lay unrecognized until their rediscovery in 1900. Relatively little experimental genetic work has been undertaken with birds because of the difficulty of controlling the breeding of many species either in the wild or in captivity.

Simple Mendelian inheritance. It is easiest to begin with the inheritance of simple alternative plumage features such as the presence or absence of bridling in the Guillemot *Uria aalge*, and white or tan crown stripe in the White-throated Sparrow *Zonotrichia albicollis*. These are examples of the simplest system of heredity where the character is inherited as one of two alternative forms. The basic principle in this case is that every individual possesses two factors relating to the character, one of which was inherited from the father and one from the mother. If they are the same, then the individual is said to be 'homozygous', if different then it is said to be 'heterozygous'. A copy of one of the factors is passed on to each of the individual's offspring. We can see how this happens by considering the inheritance of one aspect of coloration in the Budgerigar *Melopsittacus undulatus*. Native Australian Budgerigars are predominantly green, but there is a cage variety that is blue. If we cross a pure-breeding green bird with one from a pure blue stock, the offspring will be 'wild type' green. If some of these individuals are mated together, brother to sister, both wild type and blue forms will be produced in a ratio that will be very close to 3:1 if a large number of progeny are examined.

The explanation is that the green form was pure-bred, and possessed two of the wild-type factors, one received from each of its parents. Its genetic constitution can be designated as the homozygote BB and the blue bird, also pure bred, can be designated as the homozygote bb. These two birds produce ova or sperms each containing a single factor for colour, and the offspring produced by any fertilization of an ovum by a sperm must be the heterozygote Bb. In this example, and many others, the heterozygous individuals closely resemble one of the parents, and are not intermediate between them. Here they resemble the wild-type green parent, a situation described by the statement that the wild-type plumage is 'dominant' to blue plumage, and that blue is 'recessive' to green.

The hereditary factors that are transmitted in the ovum and sperm are called 'genes'. Alternative forms of genes such as the ones giving rise to green or blue plumage are termed 'allelomorphs' or 'alleles' for short. There may of course be many more than two allelic forms of a single gene, but any bird can only carry two of them.

The genetic make-up of an individual is called its 'genotype', while its external appearance is its 'phenotype'. Thus, in the Budgerigar example, the genotypes BB and Bb both give rise to a green phenotype.

When the heterozygous offspring are mated together, each parent can produce two sorts of ova or sperm, one sort carrying B and the other b. However many ova or sperms a bird may produce, half of them will carry each allele, and it is very unusual for the ova and sperms not to fuse at random. This can be shown diagrammatically, as in Fig. 1, where it can be seen that three different genotypes are produced in the next (second filial or F2) generation. Since wild-type is dominant over blue, there are only two phenotypes, the green, including both BB and Bb genotypes, and the blue, including only bb. In this mating, the blue character that had been 'lost' in the F1 generation has reappeared (of course, the gene for blue had not really been lost; its effects were concealed in the heterozygote). This segregation of grandparental types, without con-

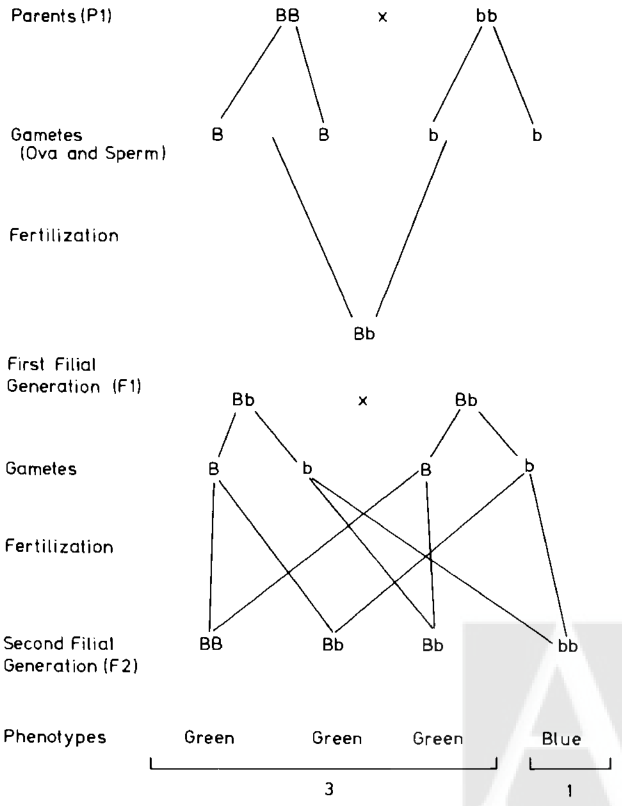

Fig. 1.

tamination or dilution, is one of the fundamental discoveries of genetics. A recessive character may disappear, but its allele still exists, masked by dominance in the heterozygotes, and able to reappear whenever two such heterozygotes mate and produce offspring.

From this example, it is relatively straightforward to see what would happen if one of the heterozygotes were mated with either homozygote. Such a mating is called a 'back-cross' and gives rise to the two parental genotypes in approximately equal numbers. In general, however, the mating of an individual showing the dominant phenotype with a homozygous recessive is called a 'test-cross' because the genotype of the 'dominant' individual can be determined from the resulting progeny. If the recessive phenotype is present among the offspring, then the parent must have been heterozygous. If the offspring are all of the dominant phenotype, then the parent may have been a homozygote. However, this can only be established with certainty if a reasonable number of offspring (say 10 or more) have been produced, for when there are few young a heterozygote could by chance produce nothing but offspring of the dominant phenotype.

The bodies of most animals are made up of many cells each of which contains a nucleus. Within the nucleus are minute thread-like bodies called 'chromosomes'. The genes are carried on these chromosomes, each gene being associated with a definite position or 'locus' on a particular chromosome. A complete set of chromosomes is carried within the ovum and the sperm, so that a fertilized egg carries a double set in which there are two (one from each parent) of each kind of chromosome (excepting the sex chromosome—see below). Normally, all the cells produced by division from the egg during development have a double set each. The nuclear division used by a cell to produce two daughter nuclei each with a double set of chromosomes is called 'mitosis'. However, when the sex cells or 'gametes' are to be produced, there is a special 'reduction division' or 'meiosis' whereby only a single complete set is put into each ripe sperm or ovum. One representative of each pair of chromosomes passes into a single gamete, and as a rule the choice is random from the mixture of grandfather's and grandmother's chromosomes.

If there are two pairs of contrasting characters in a mating, there may be two separate genes each with two alleles. These genes are at separate loci which may or may not be on the same chromosome. If the loci are on separate chromosomes, then the inheritance of the two pairs of alleles proceeds independently of each other.

Returning to the Budgerigar, there is a second locus which also controls colour. Again, a dominant allele at this locus allows the development of a wild-type plumage. The recessive allele in this case, however, produces a yellow bird when it is in the homozygous state. In this case the alleles can be called Y and y, with yy producing the recessive yellow phenotype.

Suppose that two parents with the constitution BB, yy and bb, YY are now crossed. These birds are, respectively, yellow and blue. All of the offspring will be Bb, Yy and thus have a green phenotype. When these birds are 'sib-mated'—i.e. brother to sister—there will simultaneously be two crosses of the same kind as that between the F1 siblings in the first example. The genes will assort independently, and the best way to work out the combination of possible offspring is to tabulate the constitution of possible gametes. Clearly, any individual can produce gametes with alleles B and Y, B and y, b and Y and b and y, since either B or b can occur with Y or y. In male birds, these will be sperms, and in females they will be ova. Thus any one of these combinations can fuse with any other to produce the kinds of zygotes shown in Fig. 2.

		OVA			
		BY	By	bY	by
SPERMS	BY	BBYY Green	BBYy Green	Bb YY Green	Bb Yy Green
	By	BBYy Green	BB yy Yellow	Bb Yy Green	Bb yy Yellow
	bY	Bb YY Green	Bb Yy Green	bb YY Blue	bb Yy Blue
	by	Bb Yy Green	Bb yy Yellow	bb Yy Blue	bb yy White

Fig. 2.

Such a diagram is called a 'Punnet square' after the early geneticist R.C. Punnet. There are clearly many possible genetic constitutions resulting from this cross. If only the genotypes for B and b are counted (Y and y being disregarded), a ratio of 1 BB:2 Bb:1 bb will be found as in the first example. A similar result is obtained if only Y and y are counted. With bb homozygotes producing blue Budgerigars, and yy producing yellows, the proportions of phenotypes from the double cross can be worked out using the table, and they are found to be:

9 B and Y: 3 b and Y: 3 B and y: 1 b and y.

There are actually 9 genotypes, but only 4 phenotypes. The first three are respectively green, blue and yellow. The last, the double recessive homozygote, is in fact white.

It is easy to work out the results of crosses that involve more than two alleles at one locus using the same methods as in the examples above.

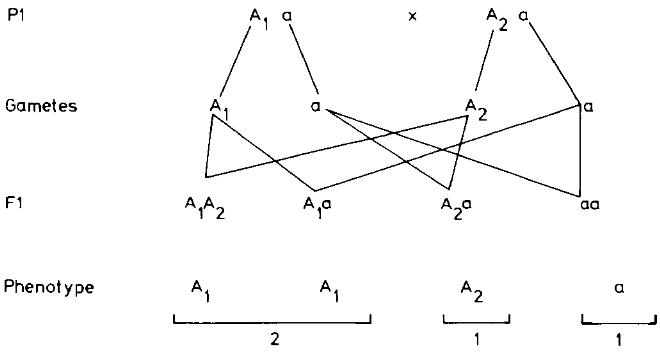

Fig. 3.

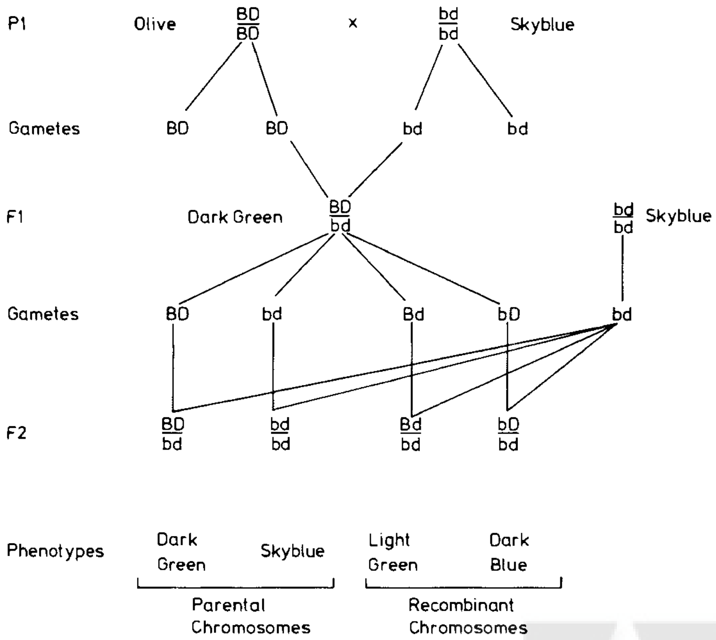

Fig. 4.

Suppose we have a cross that involves three alleles A_1, A_2 and a, in which A_1 is dominant to A_2, and both are dominant to a. If the parents are A_1a and A_2a, then the results of a simple cross are as shown in Fig. 3.

Linkage. It sometimes happens that two or more loci lie on the same chromosome. These are then said to be 'linked', and the rule that the genes assort independently of each other no longer holds. A gene in the Budgerigar has the effect of modifying the action of the wild-type and blue genes, turning light green into dark green or olive and sky blue into cobalt or mauve. Its locus is on the same chromosome as that of the blue gene. This dark gene is also interesting since it has a greater effect when homozygous than when it is present in the heterozygous condition. It is thus said to exhibit intermediate or, to be more precise, an absence of dominance, since the heterozygote Dd is intermediate between the two homozygotes DD and dd.

When an olive bird which is genetically BBDD is crossed with a sky blue bbdd, the offspring are all dark green BbDd. If some of these are backcrossed to sky blues the resulting progeny are as shown in Fig. 4. Because the loci for blue and dark are linked, their alleles do not assort independently. However, linkage is seldom perfect. This is a consequence of the fact that, during the production of eggs and sperms, the chromosomes in the nucleus of their precursor cells come close together in pairs (they have, of course, a double set like almost all the other cells in the body). While the chromosomes lie together in their 'homologous' pairs, they may break and exchange pieces of material (see Fig. 5). Consequently, in the production of some ova or sperms, a process of 'crossing-over' may occur, and a few (or perhaps many) of the crossover classes of gametes may be produced. The closer the two loci lie on the same chromosome, the less likely it is that crossing-over will occur between them. The new combinations of alleles are called recombinants and, in the blue/dark example in Budgerigars, about 14% of the chromosomes produced by the heterozygous parent are recombinant. The results of crossing-over are very consistent, and so maps of the chromosomes have been produced in a few species by observing crossover values and working out in what order the loci are arranged along a chromosome. Perhaps not surprisingly, the best avian genetic map is that of the domestic fowl.

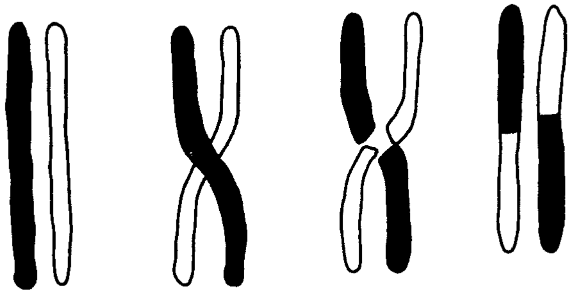

Fig. 5. Diagram to illustrate the interchange of material between the members of a chromosome pair by breakage and recombination.

Quantitative variation. The examples so far quoted all refer to simple alternative characters. However, a considerable amount of variation exists that is of a more continuous nature, such as weight, wing length, tarsal length or clutch-size. This variation is often used for discriminating between subspecies or higher taxa, and the assumption is made that it has some kind of underlying genetic basis. Very little field genetical analysis has been undertaken of such characters in birds, a notable exception being the work of Perrins and Jones (1974) on the inheritance of clutch size in the Great Tit *Parus major.*

Quantitative characters are of particular interest to the poultry industry, and attributes such as egg weight, growth rate and food conversion have been extensively studied. Research indicates that quantitative variation is usually under multi-locus control. Breeding data suggest that a series of loci may be involved, each of which may have several alleles that are individually of rather small effect. Such inheritance has been termed 'polygenic' in the past. Recent studies have suggested that a polygenic locus for one character may be a major locus of large effect for another.

Artificial selection can produce strains of chickens that lay eggs of a larger or smaller size, or that have an increased growth rate or a greater mature body size. The selection presumably acts to produce genotypes that are homozygous for alleles that have the desired phenotypic effect. Interestingly, and perhaps not surprisingly, evidence suggests that the control of egg size and egg number are quite closely related. So it is easier to select for large eggs or larger numbers of eggs than to select for both; presumably limitations are imposed on egg production by the energy metabolism of the bird.

Sex and linkage. The control of sex in most animals is by means of the sex chromosomes. In female birds (but in male mammals and many other vertebrates), the members of one of the chromosome pairs are not identical in appearance; in the male bird or female mammal one of this dissimilar pair is absent and the other is represented twice. In birds, the odd chromosome is called W and the other Z, so that the genetic constitution of females is WZ and of males is ZZ. The W chromosome carries fewer genes and is often largely inert. Since males can mate only with females, every mating in respect of the sex chromosomes is between a heterozygote and a homozygote. Consequently a 1:1 ratio of phenotypes is always produced genetically (although this may be modified somewhat by other factors). The Z chromosome carries genes that affect characters besides the purely sexual ones, and these are then said to be sex-linked. A very few are known on the W chromosome, and such genes may be useful to breeders for sexing young chicks, provided that their effects are seen very early in life. It is also possible that egg colour in the CUCKOO *Cuculus canorus* is controlled by a locus on the W chromosome.

Modification of dominance. It is implied above that a gene may control a character. This, however, is really an oversimplification. The genes that are easiest to work with in genetical investigations are those that always have a definite effect upon a particular character. However, even this apparent independence is achieved by a precise adjustment of some of the other genes themselves, and there is often very considerable modification by genes of each others' action. For example, dominance has been shown in some cases (including genes in the domestic fowl) not to be a property residing in a particular allele, but a result of modifying genes acting upon it. It has been possible to take a stock that is segregating for two alleles, in which the heterozygote is normally intermediate between the two homozygotes (i.e. there is no dominance—see above), and to exercise selection in two lines so as to make one allele dominant over its partner in one line, and recessive to it in the other. Dominance, whether brought about by the action of modifiers, or in other ways, is a device that allows a beneficial allele to express itself even in a single dose, while suppressing a less useful one. It is otherwise remarkable that so many deleterious alleles are recessive, and many geneticists believe that the properties of genes, and of genetic mechanisms such as meiosis or sex, have all evolved through natural selection.

The significance of sexual reproduction. The whole point of sexual reproduction seems to be to pass on to the offspring sufficient genetic information to allow them to survive through to maturity and to breed. It operates by transmitting linked groups of genes in particular allelomorphic states that have by and large been favoured in the past by natural selection. These genes work together to build up the enormously complex systems that comprise an individual, and to adapt it for its role in nature. At the same time, however, the sophisticated process of meiosis and crossing-over allows new combinations of alleles to be developed that might prove superior in performance in the environmental conditions to which they are exposed.

The production of an entirely new inheritable variation is called a 'mutation', and this may occur in one of several ways. For example, one of the constituent parts of the complex biological molecule that forms a gene may actually be lost as a consequence of radiation damage. Alternatively, an extra piece of material may be inserted inside a gene, or a part of it may be replaced by a different fragment. It has become clear recently that crossing over can even occur within individual genes, again possibly producing novel allelic forms.

New arrangements, whether of genes or chromosomes, are not in general likely to be advantageous if their effects are at all considerable; the chances of a sudden large random change in a delicate and complex organism being actually beneficial are very slight. Consequently, mutation rates need to be kept very low (one of the dangers of atomic radiation is that it raises mutation rates), or the individual or population may suffer serious damage. But a slow trickle of mutations maintains variability, and allows the species the possibility of adapting to changing conditions.

Genetical study in the field. Birds are not particularly suitable material for genetical research, because of the length of their generations, and because of the difficulty and expense of maintaining breeding stocks in captivity. The majority of research has concerned the analysis of phenotypic variation between populations, without troubling too much about its genetic basis. However, distinct characters, controlled by one or a few genes, occur in a number of species and the study of these can often illuminate the evolution of a species or species group. Since most birds lay a fair number of eggs, it is possible to determine the genetic control of such characters from field observations of matings and progeny without excessive labour. This type of variation has been studied extensively in some species, and gives useful information about many aspects of avian biology.

One question that can be studied in the field is the amount of genetic variation in nature, or what proportion of loci have multiple allelic forms in a population? Recent developments in biochemical genetics have allowed an approach to this question, for it transpires that many enzymes can be analyzed by a technique called gel electrophoresis. Essentially, this process separates enzyme molecules according to various physicochemical properties, and allows the detection of variant forms. The application of electrophoresis to species such as American thrushes and the House Sparrow *Passer domesticus* suggests that about 10–20% of enzyme loci may be polymorphic. The discovery of this variation, which is of a similar frequency to that in other homeotherms, allows an assessment of the similarity of populations at a genic level, as opposed to the more traditional approach of measuring the means and variance of quantitative phenotypes. (A.J.C.) D.T.P.

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GENETIC SEQUENCE: see DNA-DNA HYBRIDIZATION.

GENITAL SYSTEM: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

GENOTYPE: the group in which an individual falls by reason of its genetic constitution (compare PHENOTYPE). The term was at one time misapplied (also 'generitype', 'generotype') in ornithological nomenclature to the type species of a genus (see TYPE SPECIES).

GENS: literally 'race' (plural 'gentes'); has been used in various contexts for infrasubspecific categories, and especially for the divisions of the European Cuckoo *Cuculus canorus* population that lay eggs of particular colours; also 'a chronological series of populations forming a single evolutionary lineage (divisible into palaeospecies) and biospecifically separated at any time from its closest relatives' (Cain); see EVOLUTION.

GENUS: a taxonomic category representing a grouping of species; also a particular example or (plural 'genera') examples of that category. In Mayr's words, a genus is 'a systematic category including one species or a group of species of presumably common phylogenetic origin, which is separated from other similar units by a decided gap'. The category is a primary one in nomenclature, in that it is obligatory that every species should be placed in a genus. If there is only one species in the genus, the latter is 'monotypic'; if there are two or more species, these are said to be 'congeneric'. The name of the genus (which must be unique in the Animal Kingdom, a matter in which the *Nomenclator Zoologicus* is helpful) constitutes the first word of the scientific name (binomen or trinomen) of an included species or subspecies. Every genus has a 'type species'; and a genus may itself be the type of a higher taxon. See NOMENCLATURE; SPECIES; TAXON; TYPE GENUS; TYPE SPECIES.

The genus is a purely subjective concept, and taxonomists vary widely in the standards of difference that they regard as calling for generic separation. The original Linnaean genus was a broad category; and the general tendency now seems to be a swing back for some distance in that direction. This follows an era during which many authors have indulged in a great deal of splitting of genera in accordance with their own standards of difference and ideas of relationship. Apart from this, but accentuated by it, has been the transfer of species from one genus to another in the light of new information or changing views. Unfortunately, all these revisions involve changes in the naming of species—a notable defect of the binominal system. For this reason it is sometimes necessary to show a discarded but familiar generic name in parenthesis.

Subgenus. A genus may be divided into subgenera where the included species appear to fall into well-marked groups; but the subgenus is not a primary category. Taxonomists who use narrow genera naturally have little occasion for such subdivision; in wider genera it serves to express ideas about interspecific relationships, with the advantage that it does not affect the names of species. For particular purposes, however, a subgeneric name may be shown in parenthesis after the generic name in a binomen or trinomen. In each divided genus, one of the subgenera is 'nominotypical', having the same type species as the genus and a name identical with the generic name. A category of 'superspecies' may be interpolated between subgenus and species, but this has no nomenclatural status (see SUPERSPECIES; also SPECIES GROUP (2)).

Neave, S.A. 1939–40, 1950. Nomenclator Zoologicus (Index of generic and subgeneric names in the Animal Kingdom proposed from 1758 onwards), vols. 1–4 and 5. 1966, Vol. 6 (Edwards, M.A. & Hopwood, A.T. eds.) covering 1946–1955. London.

GENUS GROUP: with reference to the ranks of taxa, term embracing genus and subgenus (see NOMENCLATURE).

GEOGRAPHICAL DISTRIBUTION: see DISTRIBUTION, GEOGRAPHICAL.

GEOGRAPHICAL VARIATION: see CLINE; SUBSPECIES.

GEOLOGICAL FACTORS: those relating to the history of the earth's surface as far as they are relevant to the distribution and evolution of the biota (specifically birds). Chief among such geological factors are (a) palaeogeographic changes in the distribution of land and sea and (b) changes of climate and vegetation on the continents since the Cretaceous period (when birds began to occupy many areas of the world). Palaeogeographic changes in the distribution of land and sea were caused by

—vertical movements of portions of the earth's crust either on a broad and fairly gentle scale (epeirogenesis) or on a regionally more restricted and violent scale (mountain building [=orogenesis] and vulcanism),

—lateral movements of the earth's crust due to continental rifting and drift, or

—changes in world sea-level unrelated to vertical movements of the land.

Paleogeographic changes in the distribution of vegetation zones due to changes in the palaeoclimate were caused, e.g., by

—rain shadow effects on the leeward side of rising mountain ranges,

—drift of a continent into or across latitudes with a different climatic regime, or

—periods of glaciation such as those during the Quaternary.

Changes in the distribution of land and sea. Rather gentle, large-scale vertical movements of portions of the continents led to the repeated invasion (and later retreat) of the oceans when varyingly extensive epicontinental seas were formed (which later disappeared again). Continental coastlines in, e.g., Europe and America, differed conspicuously from those of today during the Cretaceous and Tertiary periods when representatives of many extant families of birds were evolving. Populations of land birds were repeatedly isolated on extensive islands and later reconnected through changing coastlines. The large mountain systems of the Alps to the Himalayas and of the Andes-Rocky Mountains developed during the Cretaceous and Tertiary periods from fairly narrow sedimentary basins covered by shallow seas. These mountains rose above sea-level as strings of islands which became connected and were increasingly uplifted through compression, folding and faulting of geological strata (orogenesis), often associated with vulcanism. The movements continued from the Tertiary into Pleistocene and Recent times as indicated by uplifted river terraces, tilted or faulted gravel and fan deposits, and heavy earthquakes. Oceanic vulcanism led to the formation of islands and archipelagos through the build-up of volcanos from the ocean floor which reached the surface of the sea. Such 'oceanic' islands never had any connection with a continent and must have received their flora and fauna across the water (in contrast to 'continental' islands formed by the disappearance of a previous land connection).

Until some 25 years ago the majority of earth scientists accepted the existence of temporary landbridges between certain continents, but denied the former direct connection and later separation and drift of continents (as proposed by Alfred Wegener toward the beginning of this century). However, the collection of new geoscientific data, particularly over the ocean basins, during the last two decades led to the formulation of the concept of Plate Tectonics or New Global Tectonics which offers a unifying interpretation of observable geologic features on a global scale. Basically, several large rigid plates or spherical caps of the earth's crust are supposedly moved relative to one another by convection currents in the underlying mantle. The main phenomena and interactions assumed are (1) extensional zones where plates originate and move away from 'spreading centres', mostly oceanic rift systems, (2) faults where plates move past each other along vertical shears, and (3) compressional zones where plates are thrust under adjoining plates along 'subduction zones', which are usually associated with deep sea trenches. Continents represent the lighter (upper) portion of the crustal plates and are assumed to be rafted passively over the surface of the globe together with the denser lower crustal layer that forms the 'oceanic basement'. The margins of the continents may or may not coincide with plate boundaries.

The history of the continents started in the Triassic period (200 million years ago) when the previous supercontinent (Pangaea) separated into southern Gondwana and northern Laurasia; subsequently, Gondwana split into a western portion (Africa + South America) and an eastern portion (Australia + Antarctica). The opening of the South Atlantic began in the late Jurassic and early Cretaceous. Portions of present tropical South America and western Africa were in rather close proximity into late Cretaceous times, when the east/west directed coastlines passed by each other. The proto-Antilles may have provided a discontinuous connection between North and South America during the early Cretaceous and later were relatively displaced eastward (due to westward drift of North and South America) to form the Greater Antilles. A Tertiary volcanic arc in southern Central America was progressively more uplifted until a continuous landbridge through Panamá was eventually formed during the late Pliocene only about 3 million years ago. Separation of North America and Eurasia commenced in the late Cretaceous but was not complete until the early Eocene. Australia did not separate from Antarctica until the earliest Eocene or latest Paleocene. India probably began a northward drift from a previous connection with Madagascar–Africa–Antarctica in the middle Cretaceous and collided with Asia during the Eocene.

Since many bird families originated in the Cretaceous, these families were in existence when most of the southern continents were still more or less interconnected and when the high latitudes had equable climates. Study of the higher taxa of birds may indicate an influence of the late Mesozoic palaeogeography on avian evolution. Most families of passerine birds and many Recent genera originated during the middle and late Tertiary when the configuration of the continental land masses was approaching that of the present time.

World sea-level fell and rose during the glacial and interglacial periods of the Pleistocene, respectively, when large amounts of water were alternately tied up in the polar ice caps and again released into the oceans. During the glacial periods, world sea-level was about 80–100 m lower than today, thus joining many islands on the continental shelves with the mainland. These connections were again severed and extensive present coastal lowlands flooded when sea-level rose during a following interglacial. High stands of interglacial world sea-level compared to present sea-level ranged between +60 m during the Günz/Mindel interglacial and +17 m during the Riss/Würm interglacial periods.

Changes of climate and vegetation. Rising mountain ranges often caused a change of climate over the lowlands on the leeward side through a 'rainshadow effect'. Thus forests retreated northward in temperate South America during the second half of the Tertiary when the Andes were gradually uplifted and the climate became cooler and drier. With the uplift of the Himalayas from the Miocene onward, climates were altered in some surrounding areas, causing severe aridity in places. Climatic changes observed in some areas, e.g. Australia or India, during the Tertiary may have been due to the drift of these continents into latitudes with a different climatic regime.

The Pleistocene fluctuations of world climate led to alternating advances of the polar ice caps into middle latitudes and retreats to their present position (and beyond). Montane glaciers extended during cold periods and covered many mountains in the temperate zones and in the tropics. Polar steppe and tundra vegetation in front of the glacial north-polar ice sheet extended through central Asia and Europe to Britain and across North America. In the Mediterranean area, cool steppes had a wide distribution during full glacial times. Because of the cool–arid climate of the glacial periods, forests and forested steppes were restricted to the base or lower slopes of some mountain ranges in the western Iberian Peninsula, in Italy, and in the Balkan Peninsula. Isolated forest areas (forest 'refugia') also existed in the Caucasian region, along the base and lower slopes of the Tianshan Mountains, in south–central Siberia as well as in other portions of eastern Asia. Similarly, isolated forest regions existed in various portions of North America (southeastern United States, California, Mexico, Alaska).

Four main glacial/interglacial cycles during the Pleistocene are recognized with many smaller climatic cycles superimposed. The deterioration of the Cenozoic world climate commenced with glaciations which occurred in the polar regions during the Miocene and Pliocene, gradually influencing the climate of the temperate zones and eventually affecting also the tropical latitudes during the Pleistocene.

For several decades many scientists assumed that the Pleistocene climatic fluctuations did not influence the tropical lowlands to any major degree. The rainforest and savanna flora and fauna of tropical South America, Africa and south-east Asia supposedly survived in an equable climate relatively unchanged since Tertiary times. Intensified fieldwork during the last 20 years has shown the concept of environmental stability in the tropics during the Quaternary to be incorrect. Although the temperature fluctuations in the equatorial lowlands were rather small (3–5°C lower than today during glacial maxima), alternating dry and humid climatic periods led to vast changes in the distribution of forest and savanna vegetation. Forests expanded during humid periods and survived in restricted 'refugia' during dry periods; the opposite was true for savanna regions.

Data for a reconstruction of the history of the distribution of tropical vegetation during the last 2 million years come from several different sources: from geological investigations of Pleistocene and post-Pleistocene deposits, from geomorphological interpretations of extant landforms, from analyses of the pollen content of Quaternary strata and from palaeoclimatological modelling and interpretations. Field data are available from only a few study areas in the vast tropical lowlands and many additional surveys are needed to substantiate the basic model of environmental changes and, especially, to map the details of vegetational changes during each of the numerous climatic periods. Their correlation with the glacial and interglacial periods of mid-latitudes is not well established, although the maxima of dry periods probably coincided with the glacial maxima and pronounced humid periods correlated with the peak of the interglacial periods. A number of ecological refugia during adverse climatic periods have been mapped in tropical South America, Africa and in Australia; they have been interpreted as dispersal centres of plants and animals during the post-Pleistocene.

Tectonic or palaeoecological events during the geological history of a particular region led to the separation of portions of the avifauna and later permitted all or part of the species to rejoin their ranges. In a historic–biogeographical analysis of a fauna, attempts are made to relate the origin of extant species and their distribution areas (or of biogeographical features such as secondary contact zones) to particular events or processes during the geological history of the region studied. It is especially difficult to judge the relative importance of ancient and modern causes of particular patterns of differentiation and distribution. For example: how many of the extant species originated in Pleistocene refugia during periods of geographic isolation and how many merely survived in these refugia having originated earlier during the Tertiary through an isolating event caused by some other geological process? If a cluster of secondary contact zones of birds cannot be correlated with any geological feature in the area (e.g. narrow zones of uplift and subsidence, because the contact zones cross the geological units at right angles; or the zoological contact zones are located over a uniform and geologically stable unit, such as a basement shield) then it is unlikely that the processes responsible for the formation of the geological features and those which led to the formation of the contact zones are causally related. If conspecific populations of an upland bird species inhabit mountains with independent geological histories, dispersal of this species from one mountain region where the species originated to the other mountain must be assumed to have occurred (either through the intervening lowlands or by flying, 'hopping', across the lowland barrier); it is very unlikely that the same montane species could have been differentiated from a common lowland ancestor independently several times in these isolated mountain regions. In this example the known independent geological origin (uplift) of the presently isolated mountains rules out the alternative interpretation of a previously continuous species population on a continuous mountain range, which was later subdivided into isolated units through partial subsidence and/or differential erosion. Also, decrease of temperatures in the tropical lowlands during Pleistocene glacial phases was insufficient to have permitted the formation of a continuous lowland population of the montane species (which might have retreated upslope on the isolated mountains during a following warmer interglacial period).

Accepting these premises, a number of montane hummingbirds, toucans, trogons, antbirds, finches and tanagers which inhabit the Andes and the table mountains of southern Venezuela at a distance of over 500 km must have originated in one of these two montane regions (the majority probably in the Andes) and later dispersed to the other mountains, colonizing them like 'islands' in the 'sea' of the tropical lowlands. The widening of the Amazon basin during the early Tertiary separated the fauna of the ancient land area to the north (Guayana Shield) from that of the Brazilian Shield to the south. This event may have isolated the ancestors of certain contemporary birds which, mostly as monotypic genera, survive in the area of the Guayana Shield (*Rupicola rupicola*, *Perissocephalus tricolor* and others) and of the Brazilian Shield (*Rhea americana*, *Cariama cristata*, *Chunga burmeisteri* and others). A large number of extant bird species and subspecies of the tropics and of higher latitudes probably originated in ecological refugia (forest and nonforest) which repeatedly resulted from recurrent climatic–vegetational changes of the last 2 million years (Quaternary period), e.g. the following European species and subspecies pairs (in each case the western representative is listed first): Carrion Crow *Corvus corone corone* and Hooded Crow *C. c. cornix*, Nightingale *Luscinia megarhynchos* and Thrush Nightingale *L. luscinia*, Blue Tit *Parus caeruleus* and Azure Tit *P. cyanus*, Short-toed Treecreeper *Certhia brachydactyla* and Treecreeper *C. familiaris*, and many other pairs. J.H.H.

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GEOSPIZINAE: see DARWIN'S FINCHES.

GERM-CELL: a gamete (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

GERMINAL VESICLE: the nucleus of the ovum (see DEVELOPMENT, EMBRYONIC; EGG).

GERYGONE: see WARBLERS, AUSTRALIAN.

GIBBER-BIRD: *Ashbyia lovensis*, one of the Australian chats (see CHAT (3)).

GILL-SLIT: see DEVELOPMENT, EMBRYONIC.

GIZZARD: the ventriculus (see ALIMENTARY SYSTEM).

GLACIATION: see GEOLOGICAL FACTORS.

GLADIATOR: name, alternatively 'Gladiator Shrike', of *Malaconotus blanchoti*, and also of the rare *M. gladiator* (see SHRIKE).

GLAND: a secretory organ. Some glands discharge their secretions through openings or ducts, e.g., those associated with digestion—see ALIMENTARY SYSTEM; the secretions of others are internal, i.e., absorbed into the blood stream (hormones)—see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM. The body-surface of birds has few glands (see OIL GLAND; SKIN).

GLAND, SALIVARY: see ALIMENTARY SYSTEM; PALATE; TONGUE.

GLAREOLIDAE: see under CHARADRIIFORMES. There are 2 subfamilies, Glareolinae (see PRATINCOLE), and Cursoriinae (see COURSER).

GLAREOLOIDEA: see under CHARADRIIFORMES.

GLEDE: old name (also spelt 'glead' and 'gled') in Britain for the Kite *Milvus milvus* (see under HAWK).

GLENOID CAVITY: articulation of the head of the humerus with the pectoral girdle (see SKELETON, POST-CRANIAL).

GLIDING: see FLIGHT.

GLOGER'S RULE: that, in a given species, races in warm and humid areas are apt to be more heavily pigmented than those in cool and dry areas (see ENERGETICS).

GLOMERULUS: part of a nephron (excretory unit of a kidney)—see EXCRETORY SYSTEM.

GLOTTIS: see RESPIRATORY SYSTEM.

GLYCOGEN: see LIVER; METABOLISM.

GNATCATCHER: substantive name of species of the subfamily Polioptilinae of the Sylviidae (Passeriformes, suborder Oscines); in the plural, general term for the subfamily. The Neotropical 'gnatwrens' (*Microbates* spp., *Ramphocaenus* sp.) have arbitrarily been placed in this subfamily but it is possible that their closest affinity is with some other Old World group. The gnatcatchers are distinctive, containing *c.* 8 species that are all placed in the genus *Polioptila*.

Characteristics. Gnatcatchers are tiny birds (ranging from 10–12 cm in length and usually weighing less than 7 g) with long tails and slender bills. Most have pale blue-grey backs, white undersides, and a black tail edged by white outer feathers. The Slate-throated Gnatcatcher *P. schistaceigula* departs furthest from this pattern; it has a darker back and throat and lacks white in the tail. During the breeding season, the males of most species can be distinguished from females by the presence of black markings on the head.

Habitat. Gnatcatchers are typically found in woody, broad-leaved vegetation where the canopy is deep and broken into discrete clumps. These characteristic features of the habitat are provided by a broad array of environments, including desert scrub, dry woodland, cypress swamp, tropical second growth, and, within dense forests, by the edges formed around windfalls and along the crowns of trees that tower above their neighbours.

Distribution and movements. The group is restricted to the warmer regions of the New World. The northernmost populations of the Blue-grey Gnatcatcher *P. caerulea* occur in northern California, Minnesota, and New England during the breeding season and in the southern United States during the winter. This is the only species to undertake extensive migrations. The southernmost species, the Masked Gnatcatcher *P. dumicola*, breeds as far south as Buenos Aires, Argentina.

Food. The diet consists of small insects and spiders. Foraging gnatcatchers are extremely active; as they flit from twig to twig, they move the tail in wide jerks. Even though they pick much of their prey off the surfaces of leaves and twigs, feeding is a strenuous activity for these tiny predators because they must hover to reach many of the insects they spot. Frequently they rush and tumble after insects they have flushed and sally out, flycatcher fashion, to snatch flying insects. Gnatcatchers do not manipulate objects with the foot, so they subdue large prey by thrashing and wiping them against the perch.

Behaviour and voice. Each breeding pair defends a territory (*c.* 1–3 ha in extent) against all other adults. Members of a pair maintain contact with each other by giving *speee* calls every minute or so. These calls, which are usually what first draws an observer's attention, have a sibilant quality, difficult to describe, that is characteristic of all the species. Gnatcatcher songs are relatively faint and are composed of a variable series of brief phrases.

Breeding. Nests are open cups placed above the ground where the bottom and a sector of the wall can be attached to woody surfaces. Gnatcatchers incorporate much spider web in their nests; this sticky material is used to bind the nest to its supports and to attach the bits of lichen that usually cover the outer walls. Blue-grey Gnatcatchers and Black-tailed Gnatcatchers *P. melanura* frequently reuse material from their previous nests. This habit, which serves to speed construction of a new nest, may also foster the infestations of mites that plague some broods. Both sexes build the nest, although the male may do most of the work if the female is occupied feeding fledglings from a previous brood.

Both parents commit a similar effort to incubation and to feeding the young. Clutches contain 3–5 eggs. The incubation period is 13–15 days and the nestlings normally leave the nest after 11–14 days. Typical feeding rates to a brood of older nestlings are 30–40 visits per hour. Fledglings of the Blue-grey Gnatcatcher depend on the adults for the bulk of their food until about the 16th day after leaving the nest but strike out on their own after the 3rd week. (J.C.G.Jr.) R.B.R.

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GNATEATER: substantive name of the species of *Conopophaga* (Passeriformes, suborder Deutero-Oscines) (alternatively 'antpipit', but this name is best restricted to *Corythopis* spp.—see ANTPIPIT), now included in the ANTBIRD family but formerly placed with *Corythopis* in a separate family Conopophagidae.

The principal morphological characters of the gnateaters (skull, sternum, syrinx and pterylosis) were studied in detail only recently, and proved to lie within the wide range of variation found in the Formicariidae, as that family is now understood. In spite of this, it is obvious that gnateaters differ outstandingly from the other antbirds. This is immediately evident from their general appearance and behaviour, and is confirmed by morphological features such as the structure of the skull, the form of the bill, and the presence of sound-producing flight feathers in the male in certain species. There is no similarity with the antpittas (*Grallaria*, *Hylopezus*, etc.), but a certain resemblance to *Myrmoborus*. There are also several similarities with the tapaculos in structure (sternum, coracoid, scapula, pelvis) and in behaviour.

Characteristics. The 9 species of *Conopophaga* are rotund 'neck-less' little birds (*c.* 14 cm long) with long, thin legs and long toes, rounded wings, short soft tail, and body thickly covered with long feathers. Their shape, and in some cases colour, is reminiscent of the Robin *Erithacus rubecula* of Europe, but they are bigger and heavier. Behind the eye there is a slightly protruding tuft of rather elongated silky feathers, frequently of a brilliant white, normally more or less hidden but puffed out when the bird is excited and then strikingly visible. The sexes are usually quite differently coloured.

Habitat, behaviour and voice. Gnateaters live in pairs in shrubby habitats and forest undergrowth, for much of the time perching on low branches where they stay motionless for a long time and are easily overlooked. They drop to the ground to pick up an insect, then fly to another perch. On the ground they move little, but occasionally hop and sometimes scratch, not unlike a tapaculo *Scytalopus*. The name 'cuspidor' (spitter), used in south-eastern Brazil, refers to the short, rasping alarm note. Generally they are silent.

Distribution and breeding. The Rufous Gnateater *C. lineata*, distributed from Brazil to Paraguay and northern Argentina, is about 14 cm long (weight 21 g), generally earth-brown in colour with a rusty foreneck and nearly white belly; the post-ocular tuft is white in the male and grey in the female. During the breeding season, towards the end of the calendar year, the male emits a simple whistling melody ending in a few lower and more accentuated notes. In the dusk the male persistently flies around his territory, sometimes quite high up, producing a surprisingly loud rattling noise with the wings. The outer primaries (5th to 9th, especially 8th and 9th) are apically enlarged (i.e. the opposite of attenuated), and are evidently under the bird's control, as the sound is made only at the time of pair-formation and only in a certain degree of darkness. The female's wing is normally shaped and her flight is always silent.

The nest of this species is placed on a firm base in low vegetation close to the ground; it is bowl-shaped, open at the top, neatly constructed of large dry leaves and lined with fibres. The 2 eggs are yellowish with light brown, partly smudged spots, especially towards the broad end.

In the Black-cheeked Gnateater *C. melanops* of Brazil the male has a cinnamon crown, the sides of the head black, and the underparts ash-grey and white; the female resembles that of *C. lineata*. It has a full melodious song that ascends in a long drawn-out scale, also the alarm note mentioned above. The nest and eggs are similar to those of *C. lineata*; the sexes seem to share in incubation and, if disturbed at the nest, the parent leaves, feigning injury. H.S.

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GNATHOTHECA: term sometimes applied to the part of the rhamphotheca covering the lower mandible (see BILL).

GNATWREN: see under GNATCATCHER.

GOAL-ORIENTATION: term proposed by Lack and Williamson for the directing of flight to compensate for lateral displacement, so that the normal goal is reached; distinguished from 'one-directional navigation', in which flight is directed on a constant heading without compensating for drift, diversion, or artificial displacement (see MIGRATION; NAVIGATION).

GOATSUCKER: now mainly in American usage; in the plural, an alternative general term for the Caprimulgidae and more particularly for the nominotypical subfamily (see NIGHTJAR).

GO-AWAY-BIRD substantive name of some species of Musophagidae (see TURACO).

GOBBLING GROUND: special term in North America for the social display ground of the Lesser Prairie Chicken *Tympanuchus pallidicinctus* (see GROUSE; LEK).

GODWIT: substantive name of *Limosa* spp. (see under SANDPIPER). See photo COMFORT BEHAVIOUR.

GOLDCREST: name (formerly 'Golden-crested Wren', a misnomer) of *Regulus regulus* (see WARBLER (1)).

GOLDENEYE: substantive name of *Bucephala* spp.; used without qualification, in Britain, for *B. clangula* (see DUCK).

GOLDENTAIL: *Hylocharis eliciae* (for family see HUMMINGBIRD).

GOLDENTHROAT: substantive name of *Polytmus guainumbi* and *Smaragdites theresiae* (for family see HUMMINGBIRD).

GOLDFINCH: substantive name of some *Carduelis* or '*Spinus*' spp.; used without qualification, in Britain, for *C. carduelis* (see FINCH).

GONAD: general term for the primary sex organs, testes (paired) in the male and ovary (single) in the female (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

GONOLEK: substantive name of some *Laniarius* spp. (see SHRIKE).

GONYS: the ridge formed by the junction of the two rami of the lower mandible near its tip (see BILL).

GOOSANDER: name used in Britain for *Mergus merganser*, in North America called 'Common Merganser' (see DUCK).

GOOSE (1): substantive name (plural 'geese') of many species of Anatidae; the 'true geese' are placed, with the swans, in the tribe Anserini of the subfamily Anserinae, but the name is also used in 3 other tribes (and both other subfamilies) in such a way that 'ducks' and 'geese' cannot be taxonomically separated (see DUCK). Ornithologically, 'goose' is applied irrespective of sex, but one usage restricts it to the female in contradistinction to the 'gander' or male; the diminutive 'gosling' is used for the young.

GOOSE (2): misnomer sometimes (not in current ornithological usage) applied to certain large sea birds unrelated to the geese, as 'Solan Goose' for *Sula bassana* (see GANNET), and 'Ember Goose' or 'Immer Goose' for *Gavia immer* (see DIVER).

GORGET: a band of colour, in some plumage patterns, on the throat or upper breast.

GOSHAWK: substantive name of *Accipiter gentilis* and nearly related congeners; also of the chanting goshawks *Melierax* spp. and the Gabar Goshawk *Micronisus gabar* (see HAWK).

GOSLING: special term for a young (not full-grown) GOOSE (1).

GOURINAE: see PIGEON.

GRACKLE: substantive name of species in several genera (*Quiscalus*, etc.) of Icteridae (see ORIOLE (2)); also, sometimes applied in Asia to mynahs of the genus *Gracula* (see STARLING).

GRALLAE: the fourth avian order of Linnaeus, but later used in a restricted sense for an order approximating to the Gruiformes.

GRALLINIDAE: a family of PASSERIFORMES, suborder Oscines; MAGPIE-LARK.

GRAMINIVOROUS: feeding on grass.

GRANDALA: generic name used as substantive name of *Grandala coelicolor* (for subfamily see THRUSH).

GRANIVOROUS: feeding on grain or seeds.

GRANULATE: covered with small tubercles, as on the podothecae of some birds (see LEG).

GRASSBIRD: substantive name, in Australia, of *Megalurus* spp. (see WARBLER (1)).

GRASSFINCH: in the plural, general term for a tribe (Erythrurini) of the Estrildidae (see ESTRILDID FINCH). Also, 'Grassfinch' is used sometimes in America as substantive name of *Sicalis* spp. (for family see FINCH).

GRASSQUIT: substantive name of species of *Tiaris*, *Volatinia* and *Loxipasser* (for family see FINCH).

GRASSWREN: substantive name of Maluridae spp. (see WREN (2)).

GREATER COVERTS: see TOPOGRAPHY.

GREBE: substantive name for all species of the Podicipedidae, sole family of the Podicipediformes; in the plural general term for both family and order. Grebes are an isolated, closely homogeneous group of diving, foot-propelled waterbirds. Taking the ornithologically convenient view, there are 22 species of recent grebes in 8 genera, though 20 species in 6 genera were recognized in the latest review.

Characteristics. Grebes vary from *c.* 23 cm to *c.* 76 cm in length and from less than 150 g to nearly 1,500 g in weight. All have thick waterproof plumage of up to 20,000 feathers, those on the underparts being particularly dense. The tufted oil-gland is well developed. The sexes look alike though males tend to be brighter, also bigger, with longer bills. Non-breeding plumages are usually counter-shaded: brown, blackish or grey above, and white or whitish below. Many show white on the wing. In breeding plumage grebes develop special colours, markings or plumes above; some also remain white below, but others become more mottled, even showing no white at all. The grebes that are really plumed—mostly in the genera *Rollandia*, *Poliocephalus*, and *Podiceps*—have crests, tippets (ruffs), auricular fans or hair-like filaments; the necks of some of these species may be red (as also in 2 *Tachybaptus*) or black, and the nuptial colour may extend to breast, flanks or vent, or there may be a white patch under or on each side of the tail tuft. *Podilymbus* grebes also have white under tail-coverts, but are otherwise drab-looking, with no real plumes. The head feathers of most *Tachybaptus* lack plumes but tend to be more elongated than *Podilymbus*; all have a dark cap, contrasting with rufous, grey and/or white on the rest of the head. A striking feature is the yellowish green patch of swollen skin on the gape and base of the lower mandible, lacking only in *T. pelzelni* of Madagascar. This feature is also absent in the Least Grebe *Lymnodytes dominicus*, a drab greyish bird with black chin and throat and head feathers slightly elongated. The slightly crested Western Grebe *Aechmophorus occidentalis* has a sharply contrasting black-and-white plumage. At hatching, grebe chicks have a short, soft coat of dense down, most with a longitudinally striped dorsal pattern, particularly on head and neck. Juveniles resemble adults in non-breeding plumage, but retain the striped pattern about the head and neck to a greater or lesser extent until the post-juvenile moult.

Grebes are almost exclusively aquatic, adapted for diving and swimming under water, the feet placed at the rear of the body and the wings (with 12 primaries and 17–22 secondaries) relatively small and concealed in the plumage. The tail tuft is vestigial, lacking stiff rectrices. Under water, grebes strike out powerfully with both feet together and, because of the very flexible tarsometatarsal joint, are highly manoeuvrable. The 3 front toes are broadly lobed and slightly webbed, the raised hind toe is vestigial. The nails are wide and flat, pectinated on the middle toe. The hind edge of the laterally compressed tarsus is serrated. In flight, the wing-beats are rapid because of the high loading. Grebes shed their flight-feathers simultaneously during the post-breeding moult or later and are flightless for 3–4 weeks. The Short-winged Grebe *Rollandia microptera* is permanently flightless and neither the Atitlan Grebe *Podilymbus gigas* nor the Junin Grebe *Podiceps taczanowskii* have been seen to fly. Grebe bills, with narrow slits for nostrils, vary in size and shape. Variation in the length of bill and neck, as well as in the streamlining of the body, is adaptably correlated with food and feeding habits and the depth of effective diving.

Habitat and movements. At least during the breeding season, grebes inhabit standing fresh water, particularly shallow eutrophic lakes and ponds with emergent, floating or submerged vegetation, but sometimes slow-moving rivers, or occasionally sheltered coastal inlets. Outside the breeding season, especially when forced by cold or drought, many populations move to large inland waters or close in shore on the sea. Here large gatherings of flightless birds may also form during the wing moult. More northerly populations are truly migratory.

Distribution. Grebes, though of nearly world-wide distribution, are largely birds of temperate areas; in the tropics, most species frequent montane lakes only. The centre of origin seems to have been in the New World, where there are now 15 indigenous species, of which 12 are endemic. Though some populations readily colonize gravel pits and reservoirs, many have been adversely affected by modern human pressures; among threatened or endangered species are the Atitlan, Hooded *Podiceps gallardoi* and Colombian *P. andinus* Grebes, the last of these now possibly extinct.

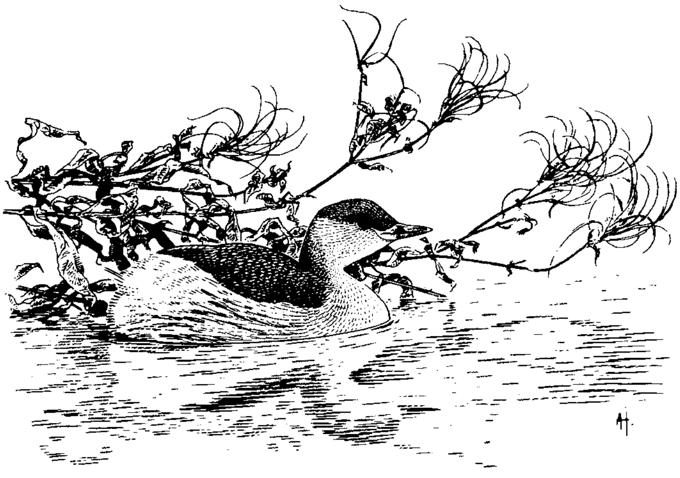
The 2 *Podilymbus* grebes are restricted to the New World: the Pied-billed *P. podiceps* is widely distributed in North, Central and South America (including the West Indies); its quasi-sibling the Atitlan Grebe is confined to Lake Atitlan in Guatemala where the Pied-billed also breeds. Four *Tachybaptus* species are confined to the Old World, where the Little Grebe or Dabchick *T. ruficollis* occurs widely in the Paleartic Afrotropical and Oriental Regions. The Black-throated Dabchick *T. novaehollandiae* is found in Australia, Tasmania, some Australian islands, and has recently nested in New Zealand. There are 2 endemic species on Madagascar, *T. pelzelni* and the tiny Aloatra Dabchick *T. rufolavatus*, which hybridizes with *T. ruficollis*, now occurring on the island. The Least Grebe, often classified as *T. dominicus*, though it differs from the true dabchicks in a number of respects, is a New World species, found from Mexico to northern Argentina and in some West Indies.

The 3 *Rollandia* grebes are South American. The Lesser Golden or White-tufted Grebe *R. chilensis* occurs widely from northern Peru and southern Brazil southwards, forming a superspecies with the much larger Rolland's Grebe *R. rolland*, endemic to the Falkland Islands. The Short-winged Grebe *R. microptera* is confined to Lakes Titicaca, Umayo and Poopo, and their river system in the Titicaca basin. The 2 *Poliocephalus* grebes, the Hoary-headed *P. poliocephalus* of Australia and Tasmania and the New Zealand 'Dabchick' *P. rufopectus* form a superspecies confined to the Antipodes. The Great Grebe, still classified as *Podiceps major*, differs significantly from the rest of the genus; it is found only in South America, from Paraguay and southern Brazil south to Tierra del Fuego.

The 8 other *Podiceps* grebes fall into 2 main sub-groups. There are 4 eared grebes: the Silver Grebe *P. occidentalis* of western and southern South America and the Falklands; its sibling the Junin Grebe, confined to Lake Junin, Peru; the small Colombian Grebe, perhaps now confined just to Lake Tota or even extinct; and the Black-necked or Eared Grebe *P. nigricollis*, widely distributed in North America, Eurasia and Africa. The other main group consists of 3 distinctive, sometimes sympatric species: the Slavonian or Horned Grebe *P. auritus* and the Red-necked *P. grisegena*, both with a Holarctic range; and the Great Crested Grebe *P. cristatus*, an Old World species occurring widely in the Palearctic, Afrotropical and Australasian Regions. The Hooded Grebe is known only from southern Patagonia. Finally, the Western Grebe is restricted to North America.

Food. Though some food is obtained by grebes at water level, most is caught by diving, searching and pursuit below the surface. But even the larger species only remain submerged for less than a minute. On surfacing, the bird often head-shakes laterally but may also drain water from the bill with a special throat-touching movement. The diet consists mainly of aquatic animals, but the food spectrum may vary locally and in the presence of competing species. Those grebes that eat mainly invertebrates tend to be rotund with fairly short necks and bills. Fish-eaters have more elongated bodies and longer necks and bills. Fish-eating species, especially, have the unique habit of eating their own feathers in large quantities and of feeding them to their young. While pellet-formation and regurgitation have been recorded, mainly by insect- and crustacean-eating species, some grebes eat their own helminths and feed them to the chicks.

Behaviour. Grebes pass much of their day between clear-cut spells of food-seeking and loafing, spending much time on feather maintenance (see COMFORT BEHAVIOUR). When resting, they insert the bill frontally into the side of the neck and stow away one or both feet into the flank 'pocket' under the wing. Sun-basking (see SUNNING) is a habit of the smaller species and of the Short-winged, Junin and Hooded Grebes. Grebes typically feed singly but may congregate over dense sources of food. Loose gatherings may form, usually outside the breeding season. A monogamous mating system is the rule, with both parents tending the young. The pair-bond is often only seasonal, but is typically initiated in winter, the birds taking up a nesting territory well before breeding. Pair formation is accompanied by water-courtship, often organized into a number of mutual display chains, male and female playing similar roles simultaneously or reciprocally, or different roles interchangeably, either sex taking the initiative. The rituals continue after pairing, especially at meeting, and are particularly complex and clear-cut in *Podiceps* and *Aechmophorus*, the former having an elaborate 'discovery' and the latter a fantastic 'rushing' ceremony. The pair also engage in platform-courtship, building mating structures together and taking turns in soliciting and mounting each other. Such ceremonies grade into true nest-building (by both sexes) and functional copulation (by the male only) shortly before egg-laying. Regular courtship feeding (male to female) has so far been observed only in the Western Grebe, but casual presentation has been reported for a number of other species.


Little Grebe *Tachybaptus ruficollis*. (*A.H.*).

Voice. Grebes utter a variety of barking, trilling, braying, whistling and wailing calls but, while some species are highly vocal, others are almost silent, even in the breeding season. Many have a vocabulary of about 10–12 calls. An 'advertising' call when alone is often the most distinctive vocalization of the species and frequently leads to water-courtship; and calling may play an important part in courtship itself in species such as the Little and Least Grebes. Dependent young give high-pitched piping calls.

Breeding. The nests of territorial grebes are usually well dispersed in concealing or protected sites, but may sometimes be loosely grouped; 7 species, including the Western Grebe, are true colonial breeders. Breeding is seasonal in higher latitudes, but tends to be less so elsewhere; most grebes have an extended laying period and are opportunistic, e.g. timing laying to coincide with the growth of emergent vegetation for the safe siting of the nest of plant stems and leaves, which is usually built in the water, anchored to vegetation, raised up from the bottom or partly floating. Clutches range from 2–6 eggs, elongated in shape, unmarked white or cream-coloured when laid, but quickly stained brown. Lost clutches and even broods may be replaced; some grebes will raise 2 broods in a season, smaller species even 3. Eggs are laid at intervals of 1–2 days. Incubation, starting from the first or second egg, is by male and female equally, each having a large median brood-patch; when disturbed, the sitting grebe typically covers the clutch with nest material. Incubation lasts 3–4 weeks. Though precocial, the chicks depend on their parents for food as well as warmth and protection, riding on their backs when small or being kept in a nursery nest. Both parents carry and feed the young; later, they tend to divide the brood between them and to give special attention each to their favourite chick. Sometimes the two family groups maintain only loose contact, or even separate entirely. The Hooded Grebe is unique: it lays 2 eggs but takes only a single chick away with it from the nest, abandoning the second egg if the first hatches successfully. Chicks show elaborate begging and appeasement behaviour; in species with a bare crown-spot, this becomes engorged with blood at times and spreads, quilt-like, over the top of the head like a crimson tonsure. Similar flushing signals appear and disappear at will on the bare areas of the face. The young become independent about the time of fledging, or later in the case of favourite chicks. Fledging periods are variable; in west Palearctic grebes they range from 6–7 to 10–12 weeks. Juveniles of some species have been reported to feed or carry younger siblings of a later brood. The age of first breeding is 1 or 2 years. See photo PARENTAL CARE. K.E.L.S.

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GREBE, SUN-: see FINFOOT.

GREENBUL: substantive name of species of Pycnonotidae in several genera (see BULBUL).

GREENFINCH: substantive name of some *Carduelis* spp.; used without qualification, in Britain, for *Carduelis* (*'Chloris'*) *chloris* (see FINCH).

GREENHEAD: a name in North America for the Mallard *Anas platyrhynchos* (see DUCK).

GREENHEART-BIRD: alternative name, used in Guyana, of the Screaming Piha *Lipaugus vociferans* (see COTINGA).

GREENLET: substantive name now restricted to *Hylophilus* spp. (see VIREO).

GREENSHANK: *Tringa nebularia* (see SANDPIPER).

GREGARIOUSNESS: see COLONIALITY; FLOCKING; and under MIGRATION.

GRENADIER: alternative substantive name of 2 species of waxbills *Estrilda* (*'Granatina'*) spp. (see ESTRILDID FINCH).

GRESSORES: see CICONIIFORMES.

GREYBIRD: alternative substantive name of some *Coracina* spp. (see CUCKOO-SHRIKE).

GREYHEN: see under BLACKCOCK; GROUSE.

GREYLAG: colloquial short name for the Greylag Goose *Anser anser* (see under DUCK).

GREYTAIL: substantive name of the 2 species of *Xenerpestes* (for family see OVENBIRD (1)).

GREYWING: substantive name of some African francolins (see PHEASANT).

GRIFFON: substantive name of *Gyps* spp.; used without qualification for *G. fulvus* (see VULTURE (1)).

GRIT: particles of stones taken in by birds that eat vegetable matter, to grind the food to pulp through the action of the powerful stomach muscles (see ALIMENTARY SYSTEM). Grit taken passes direct to the stomach through the crop, by-passing the food in the crop. Serviceable grit is not evacuated from the stomach with digested food, and is seldom found in faeces. Birds with stomachs completely free of food retain their quota of grit or sand.

Hard parts of the diet, such as shells of molluscs or crustacea, may replace the grit, e.g. in diving ducks, Dippers *Cinclus cinclus* or Starlings *Sturnus vulgaris*. Birds with a variable diet take in grit when feeding on seeds but little or none when eating insects or fruit (e.g. some Columbidae, Fringillidae). For the swallowing of feathers see GREBE.

Birds resort to regular places at regular times for grit; the Red Grouse *Lagopus l. scoticus*, very dependent on coarse grit, will undertake mass movements after heavy snow when their grit supply is covered. The size and amount of grit ingested is in direct relation to the coarseness of food. Coots *Fulica atra* feeding on soft, growing shoots in spring have less sand in their gizzard than in autumn when eating tougher plant parts. Birds that eat very coarse food (e.g. Capercaillie *Tetrao urogallus* or Himalayan Phasianidae) consume large quantities of coarse grit, whilst swans *Cygnus* spp. and geese *Anser*, etc., eating soft vegetable matter, take in little but coarse sand. The Greater Flamingo *Phoenicopterus ruber*, eating gastropods among other things, takes a fairly coarse grit; whilst the Lesser Flamingo *Phoeniconaias minor*, eating algae and diatoms, takes a very fine sand. The Ostrich *Struthio camelus*, eating very coarse vegetable matter, takes in up to 1 kg of grit composed of pebbles up to 2.5 cm in diameter. Moas (Dinornithidae) of New Zealand consumed coarse plant matter; up to 200 stones weighing 2.5 kg have been found in a stomach. The regular occurrence of small pebbles in adult divers *Gavia* spp. and nestling cormorants *Phalacrocorax* spp. remains to be explained satisfactorily.

Bright-coloured grit is preferred to dull. The discovery of the famous ruby mines in Burma originated with the finding of a ruby in the stomach of a pheasant. The structure of grit can determine the source whence migratory birds commence their flight. Both Whooper Swans *Cygnus cygnus* and Pink-footed Geese *Anser fabalis brachyrhynchus* shot in Scotland have been found to contain black lava grit which can have derived only from Iceland.

Regular duck shooting in traditional sites produces a high proportion of lead pellets in the ground where ducks consume grit. Of Mallard *Anas platyrhynchos* gizzards examined in England, Denmark, Switzerland, Sweden and the USA, 2–17% contained lead pellets. Autopsy of Danish Mallards found dead indicated lead poisoning in 20% of cases. A high pollution of soil by lead pellets exists also in the neighbourhood of grouse-butts that have been used for many years.

Calcareous material (grit, shells of molluscs) is also fed to nestlings in many species, presumably to supply the calcium needed when forming the skeleton (see SKELETON, POST-CRANIAL). Females of many species, including those not normally taking grit, selectively eat material rich in calcium, such as shells of snails, during laying, presumably to build up the egg shell (see EGGSHELL, ULTRASTRUCTURE OF): snail shell fragments were found in the gizzards of female House Sparrows *Passer domesticus* in 10–20% of non-laying birds, in 37.5% of prelaying birds, in 95% of laying females and in 27% of sparrows just after clutch-completion. It has been argued that the availability of calcareous material might influence the limits of distribution in some species such as the Pheasant *Phasianus colchicus* in North America. (R.M.) L.S.

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GROSBEAK: substantive name of species of Carduelinae (Fringillidae) in the genera *Pinicola*, *Chaunoproctus*, *Mycerobas* and *Hesperiphona*, and sometimes, in the form of Scarlet Grosbeak, as a poor alternative for Common Rosefinch *Carpodacus erythrinus* or for all members of the genus *Carpodacus* (see FINCH); also of species of Cardinalinae (Emberizidae)—see CARDINAL-GROSBEAK; and sometimes of certain of the Ploceidae—see WEAVER.

GROUND-CHOUGH: alternative, less appropriate name for the GROUND-JAYS.

GROUNDCREEPER: substantive name of the furnariid *Clibanornis dendrocolaptoides* (see OVENBIRD (1)).

GROUND-CUCKOO: general term for most members of the subfamily Neomorphinae (see CUCKOO).

GROUND-JAY: substantive name of the largely terrestrial Asian crows of the genus *Podoces*; preferable to ground-chough, the name formerly used (see CROW).

GROUND-ROLLER: name used for 5 species in 3 genera (*Brachypteracias*, *Atelornis* and *Uratelornis*) in the family Brachypteraciidae (order Coraciiformes), perhaps correctly placed in the same superfamily as the ROLLERS.

Characteristics. By contrast with the cuckoo-rollers Leptosomatidae, this family may represent a second, rather than a first, invasion of Madagascar by roller stock. *Brachypteracias* is perhaps the most primitive genus, and *Uratelornis* possibly synonymous with *Atelornis*. The family is endemic to Madagascar. All 5 species are stout-bodied ground birds, 24–45 cm long; all with a large stout bill, large head, large eyes, short wings, a moderate to long tail and legs. The colours are soft and rich, variously patterned. The sexes are alike in colour.

Four of the species are confined to eastern Madagascar, all 25–30 cm long. These are the Short-legged Ground-roller *Brachypteracias leptosomus*, with crown chestnut, nape washed deep blue, mantle olive-green, rump blue-green, tail tawny with black subapical and white apical markings, chin and throat buffish streaked with brown, an unmarked pale chest band, rest of underparts buffish barred with brown; the Scaled Ground-roller *B. squamigera*, with underparts and head buffish, heavily marked with dark crescents on each feather, the head having a black median stripe and another one behind each eye, the upper back rufous, the rest of the upper-parts mostly green; the Blue-headed Ground-roller *Atelornis pittoides*, with crown blue, mantle green, chin and throat-patch white surrounded with blue, breast and flanks pale rufous; and Crossley's Ground-roller *A. crossleyi*, with head and underparts mostly rufous, a black, white-streaked patch on the throat, and the mantle, rump and tail deep green.

The fifth species, the Long-tailed Ground-roller *Uratelornis chimaera*, seems most closely related to *A. pittoides*. It is *c.* 45 cm long, with a very long tail and long legs. It is confined to the southwest. The upperparts are dull brown variegated with blackish, with some pale blue on the wing-coverts and outer rectrices; the underparts are white with a black breast-band.

Habitat. The first 4 of these species are confined to dense evergreen forest, where the foliage above casts a continual shade, and the ground is nearly bare of vegetation. The fifth is confined to subdesert scrub.

Distribution. The two *Brachypteracias* spp. and *Atelornis crossleyi* are only known from the central and northern parts of the humid east. *Atelornis pittoides* is more widespread in the humid east, and is also known from the Sambirano, in the northwest. *Uratelornis chimaera* is confined to the coastal southwest, from north of Tulear to the Mangoky River.

Populations. Due to habitat destruction, the status of all 5 species is a matter for deep concern. This applies in particular to *U. chimaera*, of which there may not remain more than 250 pairs.

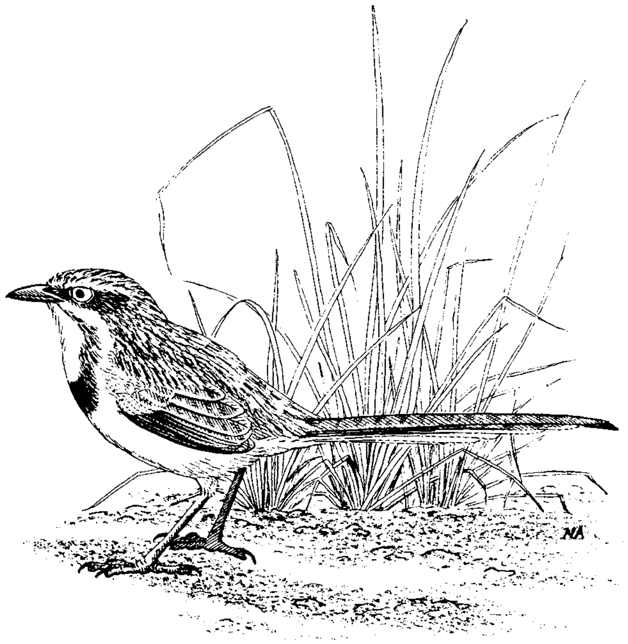
Movements. Probably all are strictly sedentary.

Food. All are insectivorous, although a snake, a snail and chameleons have also been recorded in the stomach-contents of *B. leptosomus*.

Behaviour. Very little known, but all are essentially terrestrial (in feeding probably entirely so), and usually solitary, although *U. chimaera* has been noted in groups of 4 or 5. When alarmed, they may run a few steps, to stand quietly watching. By contrast, however, *B. leptosomus* flies to a low perch, where unless further disturbed it may remain indefinitely, tranquil, and easily approached. Nor at least are *A. pittoides* or *U. chimaera* entirely terrestrial, while the latter is known to be partially active at night.

Voice. A *coee coee* has been heard from *B. leptosomus*, a 'low clucking' from *A. pittoides*.

Breeding. *Atelornis pittoides* lays its white eggs at the end of a horizontal tunnel burrowed by the parents into a bank. The same applies to *U. chimaera*, but the tunnel is gently sloping (into flat sandy ground). In both, the normal clutch-size may be 3 or 4. *Brachypteracias leptosomus* is also said to lay at the end of a burrow, but no information at all is available for the other two species. (A.L.R.) C.W.B.



Long-tailed Ground-roller *Uratelornis chimaera*. (*N.A.*).

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GROUND SPEED: see FLIGHT, SPEEDS OF.

GROUND-THRUSH: see QUAIL-THRUSH; RAIL-BABBLER.

GROUND-TYRANT: substantive name of the terrestrial tyrant-flycatchers of the genus *Muscisaxicola* (see FLYCATCHER (2)).

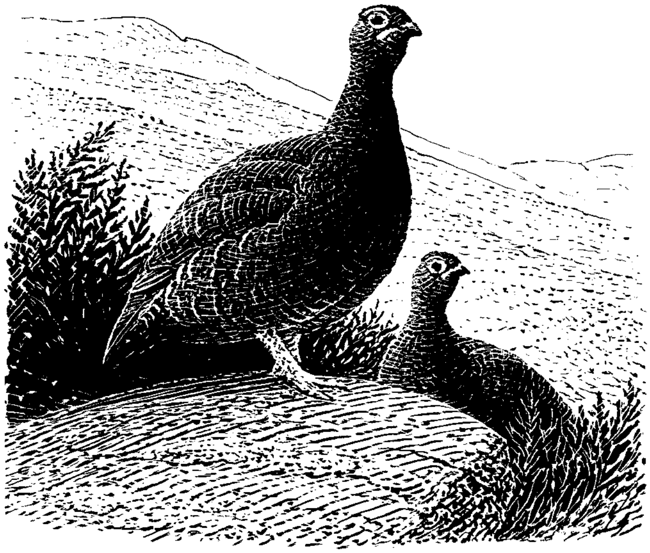
GROUP (1): in nomenclature, 'an assemblage of co-ordinate categories' (see FAMILY GROUP; GENUS GROUP; SPECIES GROUP (1)); and NOMENCLATURE).

GROUP (2): in taxonomy, a loose or deliberately neutral term for a taxon or collection of taxa, non-committal as regards the precise rank or status to be assigned to it.

GROUP SELECTION: processes leading to systematic differences in the survival of different populations of a species, beyond those resulting simply from differences in fitness of the individuals within each population. Rarely of importance in EVOLUTION.

GROUSE: substantive name of most species of Tetraoninae (Galliformes, Phasianinae); in the plural (unchanged), general term for the subfamily. Several arctic or montane species of grouse are called 'ptarmigan', and several other vernacular names are regionally or locally applied to various grouse species. The family has a circumpolar distribution, from about 26°N to about 81°N. From 16–18 species are usually recognized, and are now usually placed in 6 genera. Two species are of Holarctic distribution; 7 additional species are limited to the Nearctic, while 7 are confined to the Palearctic.

Characteristics. Grouse are fowl-like birds ranging in length from 30–90 cm and in weight from 0.3–7.0 kg. Their nostrils are hidden by feathers, their unspurred tarsi are at least partially (usually fully) feathered, and the toes are either feathered seasonally (ptarmigan) or have pectinations 2–3 mm along the sides of each toe; these features are probably associated with the group's northerly distribution. The hind toe is elevated, the bill is fowl-like and relatively short, with a rounded culmen, the wings are short and rounded, and the tail is rather varied in form. In most species the males have seasonally engorged combs over the



Red Grouse *Lagopus lagopus scoticus*. (*D.W.*).

eyes, and can inflate the upper oesophagus to form 'air sacs' during display. The most northerly forms have white winter plumages, and cryptic coloration is typical of all. The downy young are typically galliform, having a variegated brown and light-coloured back pattern, the dark colour usually extending forward on to the crown, various facial markings, and pale underparts. The probable nearest relatives of the grouse are the Old World pheasants, in particular the snowcocks (*Tetraogallus*).

Habitat and distribution. Grouse are essentially terrestrial birds, but many perch readily, and some forest-dwelling species spend much time roosting in trees or foraging arboreally on buds, fruit or berries. Of the 16 species now generally recognized, 3 (the ptarmigans) are arctic or montane-adapted, 3 are grassland or sage semidesert species, 3 are largely associated with deciduous forest, and the remainder are primarily associated with mixed or coniferous forests. There is a considerable degree of ecological segregation in the grouse, and it is rare to find 2 species sharing the same habitat. Several species are associated with forest-edge or successional stages of forest development, and in such situations habitat sharing may occur.

In North America, the Canadian boreal forests support 2 species of *Dendragapus*, the Blue Grouse *D. obscurus* and the Spruce Grouse *D. canachites*, from which the western form *franklinii* is sometimes specifically separated. Of these, the Spruce Grouse is especially associated with rather dense coniferous forests, while the Blue Grouse occupies more open coniferous forests during winter and tends to move into edge situations or even into open grassland-dominated habitats during the breeding period. The Willow Grouse or Ptarmigan *Lagopus lagopus* is a timberline and sub-arctic form while the (Rock) Ptarmigan *L. mutus* is the high-arctic replacement form. In montane areas, the White-tailed Ptarmigan *L. leucurus* occurs in alpine tundra. In western areas of relatively cool, sage-dominated plains the Sage Grouse *Centrocercus urophasianus* represents the most arid-adapted of the grouse group, while in the drier grasslands, forest openings, and early stages of forest succession the Sharp-tailed Grouse *Tympanuchus phasianellus* is widespread. In somewhat older successional stands of forests, supporting aspens, poplars and other hardwoods the Ruffed Grouse *Bonasa umbellus* is prevalent. Originally, the Pinnated Grouse or Prairie Chicken *Tympanuchus cupido* ranged widely over the grasslands of central and eastern North America, with the drier and western areas occupied by the Lesser Prairie Chicken, which is often given species status (*pallidocinctus*).

In Eurasia, all of the grouse except for the 2 ptarmigans can be considered 'forest grouse'; the Red Grouse *L. lagopus scoticus*, occupies moors and peat bogs in the British Isles and is a race of the more widespread Willow Ptarmigan that does not assume the usual white plumage of ptarmigans during winter. The ecological counterparts of the Ruffed Grouse in Eurasia are the Hazel Grouse *Bonasa bonasia* of Europe and *B. sewerzowi* of China, which occupy mature stands of hardwoods, especially those rich in alder, birch and other suitable winter foods. Likewise, the counterpart of the North American Spruce Grouse is the Sharp-winged Grouse *Dendragapus falcipennis* of eastern Siberia and China, similarly associated with relatively dense coniferous forests. The Eurasian Capercaillies, *Tetrao urogallus* of Europe and western Asia, and *T. parvirostris* of Siberia, are also essentially coniferous forest species, occupying a similar ecological role to the North American Blue Grouse. Lastly, the 2 Black Grouse *Tetrao* (or *Lyrurus*) *tetrix* of Europe and Asia, and the Caucasian Black Grouse *T. mlokosiewiczi*, tend to be forest-edge species. In some respects they are similar to the Sharp-tailed Grouse of North America, but also occupy low-altitude heathlands and bogs, subalpine grasslands, and sometimes even montane habitats. At times *T. tetrix* also occurs seasonally in fairly dense coniferous forests where there is a well-developed shrub understory, but like the North American prairie-adapted grouse it always requires rather open areas nearby for display sites.

Population. The densities of grouse are highly variable among species and habitats, but probably exceed a pair per hectare only under the best late-summer conditions. The 3 ptarmigans often have spring and summer densities of from 10–50 ha per pair or territorial male, and about the same is true of the 3 grassland and sage-adapted species of grouse. Densities of the forest-dwelling grouse seem to be highly variable, with breeding populations in North America ranging from about 2–90 males per km^2. There are regional and temporal variations in population densities that are often quite large and still of controversial origin; the apparent cyclical fluctuations of such species as Ruffed Grouse have received considerable attention but have yet to be explained adequately. Such factors as variations in weather, food, disease, and predation levels have all been advanced with varying degrees of success to account for these density changes. There also seem to be behavioural differences in aggressiveness, breeding behaviour, and perhaps such things as dispersal tendencies that are associated with differing population densities, although whether these are the causes or effects of differences in population densities is still to be established.

In most areas, populations of grouse have suffered considerably and many species have vanished from much of their original ranges. Over much of Europe the populations of Black Grouse and Capercaillie have declined greatly, and in Great Britain the Capercaillie had been eliminated by 1760, but has since been successfully re-introduced into Scotland. On the continent, the Capercaillie has also suffered greatly from forestry operations, while the Black Grouse benefits from increased forest clearings produced by limited forestry. Likewise, the Hazel Grouse also copes fairly well with limited forest removal. Perhaps the rarest of the Eurasian grouse are the Caucasian Black Grouse and Sewerzow's Hazel Hen; both have remote and extremely limited distributions, and their status is not known at present. In North America the Pinnated Grouse has been seriously affected by human activities. The Atlantic coast population of this species (called the 'Heath hen') became extinct by 1930, and the Gulf Coast population (Attwater's Prairie Chicken) is now considered endangered. Both of the other forms, the Greater Prairie Chicken and the Lesser Prairie Chicken, are on the Federal list of threatened species. The Sharp-tailed Grouse has been eliminated from much of its original prairie range in the United States, but is still widespread in Canada and Alaska. The Sage Grouse is also probably declining throughout its range as more sage desert areas are converted to irrigated croplands or otherwise cleared of original sagebrush cover. Hunting, pesticide use, and general human disturbance have contributed to population declines in some areas.

Movements. Most of the grouse are relatively sedentary, moving no more than a few km between summer and winter ranges, but the Sage Grouse may move as far as 90–150 km. The forest-dwelling grouse are generally less mobile than are the prairie grouse, the maximum movement in Blue Grouse being about 50 km. The Spruce Grouse is even more sedentary, and males tend to remain on or near their territories for most of the year. Of all the grouse, the ptarmigans are the most mobile. In the alpine White-tailed Ptarmigan the seasonal movements tend to be altitudinal, although autumn movements may exceed 16 km. The Willow Ptarmigan and Rock Ptarmigan are partial migrants, but exhibit true migrations in many northern areas, such as in northern Scandinavia and the USSR. In arctic Canada the Rock Ptarmigan often moves 15–25 km between breeding and wintering grounds, and in northern Alaska the Willow Ptarmigans nesting on the north slope of the Brooks Range regularly migrate to areas about 50 km south of Anaktuvuk Pass in this range. Probably females and juvenile males migrate the greater distances, while adult males tend to winter as close as possible to their breeding territories. The Red Grouse, however, is essentially sedentary, and not many individuals move more than a few km in their lifetimes.

Food. All of the grouse are primarily vegetarian, feeding on leaves, buds, berries and other vegetation for much of the year, particularly during winter, when each species concentrates on rather specific foods for survival. In the forest grouse the food is the buds, leaves and needles of woody species, such as conifers and ericaceous evergreen plants. In spring, the catkins of aspens, birches and alders are important foods, especially for species such as the Ruffed Grouse and Hazel Hen. The young shoots and flowering cones of larches are often eaten in spring by black grouse and capercaillies. Insects are the major foods of young grouse, and sometimes are consumed in considerable quantity by adults during summer. Most species concentrate on berries and fruits during the autumn. All grouse ingest gravel to aid in digestion. Variations in the yearly amounts and nutritional quality of foods are one of the areas that have been investigated with respect to the possible causes of population fluctuations.

Behaviour and voice. In their social organization grouse exhibit a remarkable diversity of mating systems for so small a group of species. These range from essentially monogamous matings (in some ptarmigans) to polygamy or total promiscuity, with promiscuity the most typical. In conjunction with their diverse mating systems, the degree of plumage and size dimorphism varies accordingly, with little or no dimorphism in monogamous species, but a high degree in promiscuous forms. The relatively restricted degree of plumage dimorphism in the grouse as compared with many other promiscuous-mating birds, such as the pheasants, seems to be associated with rather strong ecological pressures for retaining protective coloration patterns that closely match the environment. Perhaps to compensate for their limited ornamental plumage, grouse exhibit a considerable development of variable exposed combs or wattles above the eyes and areas of colourful bare skin in the neck region that can be temporarily exposed by oesophageal inflation. Additionally, mechanical sound production by tail shaking, rapid tail fanning, wing-dropping and scraping, and foot-stamping are frequent devices for male identification and advertisement. Vocally, the *go-back go-back* of the cock Red Grouse is one of the distinctive sounds of British moorlands.

Only in the black grouse and capercaillies is there a fairly strong degree of sexual dimorphism in plumage; the males have iridescent blues and blackish coloration, while the females retain the cryptic brown and buff tones typical of the group. In both of these the contrast between the dark blackish colours and adjoining white spots or larger feather areas appear to be important components of male postural display.

The males of all grouse species are distinctly territorial, although the size of the territory and the length of time that it is held and advertised varies greatly in the group. The sedentary forest-dwelling species tend to have large territories; those of the Spruce Grouse may range from about 2–4 ha, the total home range not being much larger. Territories in the Blue Grouse are often smaller, especially when populations are rather dense. Territories of the Rock and Willow Ptarmigans range from about 1–100 ha in size, depending on habitat, while those of the White-tailed Ptarmigan are often less than a hectare. Far smaller yet are the territories of the socially displaying grouse, such as the Black Grouse, Sharp-tailed Grouse, Pinnated Grouse and Sage Grouse. In these species the males defend small, contiguous territories often less than 100 m^2 in total area, in which all display activity occurs and likewise mating takes place. These areas are known as LEKS, and the term has now been applied to social displaying grounds in general, although in North America they are more often referred to as 'strutting grounds' (Sage Grouse), 'dancing grounds' (Sharp-tailed Grouse), 'booming grounds' (Greater Prairie Chicken) or 'gobbling grounds' (Lesser Prairie Chicken). Whatever they are called, they are all rigidly structured male display areas, in which the size and especially relative location of the territory plays an important role in determining individual mating success among males. Older and more experienced males are more successful in establishing and holding central territorial positions, while younger and less experienced males arrange themselves in peripheral territories. Although females may be initially attracted to the entire displaying group, they invariably exhibit a high degree of selectivity in their mating, gathering around certain central 'master cocks' that perform the large majority of the actual matings. The same areas serve as leks from year to year, and individual males often defend nearly the identical territories in subsequent years, gradually moving toward the centre to replace older males as they disappear from the population. The displays performed on such leks are typically highly stereotyped sequences of postures, movements and calls, nearly all of which are probably derived from aggressive tendencies associated with inter-male competition, and very few of which are specifically associated with male-to-female 'courtship' tendencies.

The solitary displays of such species as the Ruffed Grouse and Blue Grouse differ little from those of the typical lek species with respect to their origins and functions, but are often modified for effective transmission of sound in a wooded environment. Most species produce low-frequency sounds that are transmitted well in wooded environments, and may be vocal or the result of mechanical scraping (of feathers against one another) or percussion (of wings beating the air or one another). One species, the Hazel Hen, is known to produce a weak, high-pitched whistling. This species is believed to be monogamous, retaining a permanent territory, and the male may also have a limited involvement in brood care. Similarly, among the true lek grouse individual males sometimes display and call solitarily some distance away from, but often within hearing distance of, an established lek. Thus there is a complete gradation between lek-forming and solitary species of grouse, with corresponding variations in territorial size and ecological correlates.

Breeding. All species of grouse are ground-nesting; the nests usually have little lining. Clutch-sizes range from about 6–12 eggs, and in all species the female incubates the eggs, although in a few monogamous or semi-monogamous species the male may show a limited degree of nest or brood defence. The incubation period ranges from 21 days in ptarmigan to 26 days in the Sage Grouse. Renesting is infrequent in most species, and only a single brood is raised each breeding season. The downy young develop surprisingly rapidly, and often are able to fly short distances within as little as 5–8 days after hatching. Family bonds are rather weak, and by winter the young birds are typically well scattered.

See photos COLORATION, ADAPTIVE; VOCALIZATION.

(F.H. & F.H.) P.A.J.

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GROUSE, SAND-: see SANDGROUSE.

GROWTH: the process of increase from conception to adult size, with concomitant development in morphology, physiology and behaviour. EMBRYONIC DEVELOPMENT takes place in the egg and post-natal growth spans hatching to adulthood.

Patterns of avian development. Two extreme modes of development are found in birds. Precocial species are those in which the young bird hatches from the egg in an advanced state, largely capable of leading an independent existence. In contrast, altricial species produce dependent young which remain in the nest for a long period, the young being born blind and with little or no down, and requiring some considerable period of post-natal growth in the care of their parents before they can become independent.

In practice there are many intermediates between these extremes, Fig. 1 indicates the major categories used in cataloguing growth patterns, together with the features used to this purpose. These features—the presence or absence of down, and the degree of parental care afforded—are, broadly speaking, restricted taxonomically. The Gruiformes and the Charadriiformes are the major exceptions to this rule, the two orders containing species with quite diverse development.

Altricial species produce small eggs with little yolk; the females can lay these readily, but the young subsequently require considerable investment of parental care. In contrast, precocial development is from large yolk-rich eggs which impose a strain on the female for egg production but require little further energy input from the parents. The different growth patterns are associated with different types of food used by the young. Consequently precocial growth is found predominantly amongst primary consumers (eaters of plant foods) such as waterfowl and galliforms, whilst altricial growth is the rule amongst species whose prey is difficult to catch and therefore not exploited well even by independent young. Precocial development is an energetically costly process, since the young have to metabolize food for their own maintenance during their continued

Mode		Down	Eyes	Mobility	Parental nourishment	Parental attendance	Examples
Precocial	1	○	○	○	○	○	megapodes
	2	○	○	○	○	●	ducks, shorebirds
	3	○	○	○	○	●	quail, grouse
	4	○	○	○	◒	●	grebes, rails
Semiprecocial		○	○	◒	●	●	gulls, terns
Semialtricial	1	○	○	●	●	●	herons, hawks
	2	○	●	●	●	●	owls
Altricial		●	●	●	●	●	passerines

○ precocial character ● altricial character

Fig. 1. Summary of the characteristics of the grades of altricial and precocial development according to Nice's classification. (After Ricklefs in press).

growth; in altricial species these costs are met in part by parental brooding. For these reasons precocial development is much commoner in temperate and subarctic regions where the seasonal food flush makes it relatively easy to support growth. In the Temperate Zone 35% of all young develop precocially whilst in the tropics fewer than 15% of the species are precocial.

Postnatal growth.

Weight versus age curves. Most studies of postnatal growth in birds have concentrated on recording the way in which nestling or chick weights alter with age. For most young such curves show an initial period of relatively slow weight accretion followed by a period of accelerating increase which eventually levels off toward some asymptotic weight. The form and size of such curves can in general be well approximated by one of three sorts of curves (Fig. 2). First is the logistic curve whose equation is

$$W = \frac{A}{1 + e^{-K(t-t_0)}}$$

which describes a pattern of an increasing rate of weight gain until nestling weight is half-way towards its asymptotic value; the rate of weight gain thereafter decreases. The second is the Gompertz equation

$$W = Ae^{-\exp[-K(t-t_0)]}$$

in which the rate of growth peaks rather earlier than would a logistic curve with the same numerical value of the growth constant K. The third equation is the von Bertalanffy equation

$$W = A(1 - e^{-K(t-t_0)})^3$$

in which the early growth is very rapid but later growth is relatively slow.

In each of these equations the parameter A describes the asymptotic weights towards which the nestling is growing and the parameter K describes the rate of growth of the young at the point of fastest growth. Because of the asymptotic nature of these weight curves, instantaneous growth rates vary continuously during growth. Growth rate constants from different growth equations are not strictly comparable but it is possible to derive approximate standardizing factors.

Weight recession. Although the majority of birds grow in logistic fashion there is significant variation in the relationship between nestling asymptotic and adult weights. Nearly half the species studied to date fledge with asymptotic weights below those of adults of the same species. Another 20% of all species grow as nestlings towards asymptotic weights significantly above the adult weight for their species. Most such species subsequently undergo a period of weight recession in which they lose weight and eventually fledge at weights closer to adult levels. For some species this period of weight recession appears to be due to a reduction in food consumption by the nestling and greater consumption of nestling fat reserves, possibly serving to reduce nestling wing loadings and to improve their flying capabilities at fledging, but in the majority of species it appears to be due to water losses from the developing tissues of the nestling. The proportion of water in muscle tissue, in particular, reduces as the tissue approaches mature function.

There are substantial differences in the incidence and amplitude of weight recession between passerines and non-passerines and amongst birds of different habitats and feeding behaviours. Some 78% of passerines with asymptotes more than 10% below adult weight are ground feeders such as finches, thrushes and icterids, whilst foliage feeders and perch feeders tend to have intermediate ratios; the more aerial species (swifts and hirundines, oceanic seabirds) tend to have high ratios of asymptote to adult weight. The correlation is thus with the degree of dependence upon flight ability at fledging, as would be expected if water loss from flight muscles is an important component. Hole-nesting species also have peak nestling weights substantially above adult values, presumably because in their secure nest sites they can afford the longer development time needed to fledge with fully mature muscles.

Amongst passerines, nearly two-thirds of all species fledge at below adult weight, but amongst non-passerines only 28% do this. Whether this taxonomic difference is associated with taxonomic differences in be-

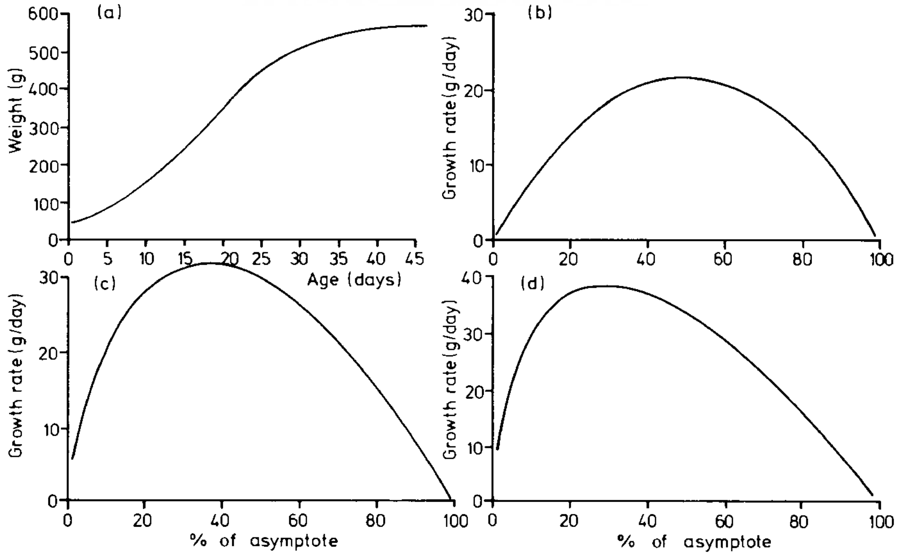

Fig. 2. Examples of different shapes of growth curve with fixed asymptote and rate constance: (a) logistic growth equation fitted to growth data for Barn Owl *Tyto alba* (asymptote 570 g, rate constant 0.152); (b) instantaneous growth rate (g/day) as a function of growth completed for this logistic equation; (c) the same parameters but with a Gompertz growth equation, showing the earlier peaking of growth rate; and (d) the same parameters in a von Bertalanffy growth equation, showing the still slower completion of body growth. (Data and growth equations from Ricklefs 1968).

haviour has not been studied.

Variation in growth rates. Explanations of inter-specific variation in growth rates are of two types, (1) theories based on internal physiological constraints within the growing bird, with each species growing as fast as it can within a body plan optimized with respect to its life history (Ricklefs 1973) and (2) the idea that growth is an independent channel of adaptation to selective forces such as mortality or food supply (D. Lack, T.J. Case).

A large proportion of the variation in growth rates in birds is associated with adult body weight, with larger species growing relatively more slowly than do smaller species (Fig. 3). This relationship is linear and has a slope of 0.722 when growth rate and body weight are plotted on logarithmic axes, and therefore shows that growth rate increases with weight according to a power function virtually parallelling the Aschof and Pohl equation for the relationship between standard metabolism and body weight

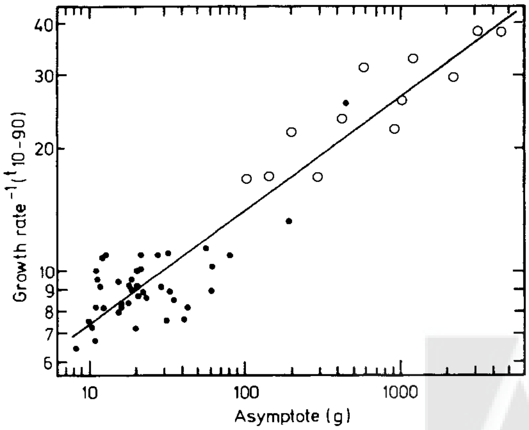

Fig. 3. Growth rate as a function of body size amongst passerines (solid dots) and raptorial birds (open dots). (From Ricklefs 1968).

$$m = 0.761\,A^{0.726}$$

where m is metabolic rate (Kcal/bird/day) and A is adult body weight (g). The parallelism suggests that growth rates may be functionally dependent on each species' weight-determined metabolic rate. Although this growth rate on adult size regression explains a large part of the variation in growth rate between species, there remains significant variation around the regression line, indicating that individual species tend to grow somewhat faster or somewhat slower than expected for their body weight. For example, precocial species lie significantly below the line, indicating that precocial development results in slower post-natal growth than does altricial development.

The time that a nestling spends in the nest is inversely related to the mortality rate for its species, birds in secure nest sites tending to remain longer than birds in sites more exposed to predation or other mortality. This was originally interpreted as reflecting clutch size adjustments, secure nest sites allowing slower development and therefore the production of more young for a given peak rate of energy expenditure in gathering food and caring for the young by the adults. But consideration of the rates at which the nestlings require energy shows that this explanation is not sufficient: species exposed to mortality whilst in the nest do not accumulate weight faster than the species not exposed to such mortality: they simply leave the nest at an earlier stage in development.

Ricklefs points out that this situation can come about because different species have different functional requirements as fledglings: cursorial species need to be able to walk and run efficiently but since even as adults most do not fly to a great extent, they have little need for efficient flight and large flight muscles during early development. In contrast, aerial insectivores must be able to fly efficiently from the moment of fledging if they are to lead an independent life but even as adults have only weak leg muscles. Different species thus achieve equivalent competence of mature function whilst developing morphologically in very different ways. Ricklefs found that growth rates are significantly related to the amount of mature function (measured in terms of relative muscle mass) that a fledgling is called upon to perform (Fig. 4). Species with a large proportion of their body mass given over to functional muscle during the fledging period grow more slowly than do species with a smaller proportion of mass as muscles; this applies irrespective of whether the principal use of muscle is in flight or on the ground.

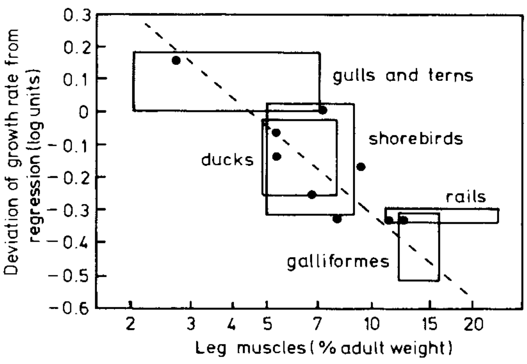

Fig. 4. The relationship between size corrected growth rate (deviation of growth rate from rate-body weight regression) in relation to their proportional leg muscle size in various groups of birds. (From Ricklefs).

Differential development. Young birds do not grow their organs and tissues at uniform rate throughout development. The organs most needed for nestling life develop first, those needed on independence at fledging develop late in the nestling period. Certain organs—the skeleton being an obvious example—need, however, to develop early in order to provide the necessary foundations for later tissues.

Development of sense organs. The timing of eye opening is probably a function of overall development. Most precocial species open their eyes either in the egg or shortly thereafter, whilst altricial species have their eyes closed for several days following hatching. In the Common Grackle *Quiscalus quiscula* eyelids first begin to part midway through the third day and are fully open by day 12. This slow development reflects incomplete development of the organs, for the ciliary muscles in House Sparrows *Passer domesticus* are not functional until day 6 and the optic nerve is incompletely myelinized in the Starling *Sturnus vulgaris* until day 8. The pupillary reflex and the optomotor response appear about half way through the period of eye opening in the Common Grackle.

Once the eyes are open, the behaviour of the nestlings is altered from a general responsiveness to mechanical stimuli (e.g., jarring associated with the arrival of the parents with food) and their begging is oriented towards the head of the parent. In addition, eye function is essential for the nestlings to balance adequately: small young have strong grasping reflexes prior to eye-opening but are unable to balance properly when tested on twigs until after their eyes have opened.

Hearing develops embryonically rather than post-natally. Embryos of precocial species are able to respond to 'bill-clicking' by other embryos from some days before hatching. In domestic chicks a cochlear response to low-frequency stimulation is first detected on day 12 and its sensitivity and frequency range improves with age until shortly before hatching. This is important for the development of postnatal chick recognition of the parents based on calls uttered by them as they arrive with food for the young.

Newly-hatched young have fewer taste buds (perhaps only one-third as many) than have adults and their tasting abilities are correspondingly poorer. Nevertheless, even newly hatched pigeons can discriminate bitter, sour and salty substances and young Bobwhite Quail *Colinus virginianus* can additionally discriminate sweet substances by 10 days of age.

Plumage. Although the main function of down is to provide insulation to precocial chicks, many altricial species have some down which becomes apparent once the amniotic fluids on the newly hatched bird have dried off. Only 11 families seem to have genuinely lost all down. A few species possess highly specialized down, often related to thermal considerations: in young Sandgrouse *Pterocles orientalis* the down barbules are coplanar and controlled by muscles allowing them to be elevated or depressed according to the heat of their desert nest site. In the Cape Barren Goose *Cereopsis novaehollandiae* down is extremely long, as befits a winter nester.

Young birds go through a sequence of plumages, varying in length according to species. For many the first coat of contour feathers forms a juvenile plumage which lasts until the first moult in autumn. Such plumages are often distinctively different in colour from those of the adult and are usually rather lighter and weaker in texture and structure. Where an autumn moult is present, the replacement feathers greatly improve the insulation afforded the nestling. Often the flight feathers are not renewed in this moult.

A variety of explanations has been advanced as to the significance of distinctive sub-adult plumages. Explanations include concealment, heat retention, protection from the sun, and signal functions. Amongst very young precocial birds a cryptic function is common, its value being increased by the chicks' behaviour in seeking appropriate cover and crouching extremely still whilst the predator is about. In young grebes and rails there appears to be a significant signal function to the plumage, used chiefly in feeding and appeasement until individual recognition of chicks by the parent develops.

Other body structures. In most nestlings the bill, especially the gape, is disproportionately large, presumably to serve as a feeding target for the parent. Its value in this respect is frequently enhanced by bright coloration and sometimes by the presence of specialized mouth spots. In young Red-winged Blackbirds *Agelaius phoeniceus* gape width and ramus length nearly double in size over the first 5 days, thus permitting the chick to take in larger meals as its age and energy requirements develop. In older chicks the shape of the beak moves steadily towards the adult structure which will be needed when it fledges. In precocial species bill structures also alter with age, the chicks in general having a short pecking-type beak initially and gradually developing more specialized structures.

In passerine nestlings the legs and their associated muscles increase in relative size over the first few days, thus improving their stability and ability to orientate during begging behaviour. In precocial species the legs are relatively better developed at hatching, in keeping with the greater motor needs of the chicks. In addition, however, the leg musculature provides a heat production capacity by shivering. For example, in the Willow Grouse *Lagopus lagopus* shivering heat production is almost exclusively by leg muscles until the pectoral muscles take over this role. This is shown even more strikingly in Leach's Storm Petrel *Oceanodroma leucorhoa* which does not move about as a chick but whose legs grow at 10% per day when first hatched; this provides the thermogenic capacity needed for thermo-regulation whilst its parents are away on long food searches.

The leg bones progressively calcify during the nestling period. In newly-hatched thrushes primary bone is largely absent and the femur contains only about 1.1% calcium but at fledging the young has a well-developed medullary cavity surrounded by cortical bone and the femur contains an average of 6.2% of calcium. Precocial species are rather better developed at hatching, averaging about 3% calcium. On the other hand, domestic chicks take about 17 days to bring their development to the stage reached by thrushes after only 12–13 days of nestling life.

The wings and their associated pectoral muscles develop relatively late. The bone structure develops rather earlier to provide the base for the growth of flight feathers, and pectoral muscles develop later still. In a few species a degree of flying is required at an early stage, as with young Guillemots *Uria aalge* which have to leave their nesting cliffs when only 25–30% of adult weight. Their secondaries develop earlier and, with the disproportionately large webbed feet, provide a degree of lift for the descent from the cliff. In many such species wing loading is maximal at this stage, declining as the body mass develops faster than does feather growth. Moreover, in adults a greater proportion of body mass is pectoral muscle, so overall flight ability further increases.

In most species the digestive organs (see ALIMENTARY SYSTEM) initially increase relative to the body as a whole and in altricial and semi-altricial species they (notably the gizzard, alimentary tract and liver) quickly peak in relative weight. Such organs are probably maximal at the time of most rapid growth and in some species the intestines may account for 33% of nestling weight. Precocial species do not develop quite so dramatically, though the liver may increase slightly in relative size. The gizzard, on the other hand, remains a relatively constant proportion of a precocial species' weight. Although the liver accounts for only about 5% of body weight over the first few weeks of life, its relative growth in neonatal young is correlated with overall growth rate, both in altricial and precocial species. This presumably reflects the food processing function of the liver.

Organs such as the HEART are required to pump blood about the body from an early embryonic stage, so vary little in relative size during postnatal growth.

In most species the growth of the PLUMAGE and its FEATHERS results in the integument increasing relative to body weight as a whole. However, the feathers generally remain in quill until the period of fastest weight increase is past. In young altricial species the plumage forms about 10% of the entire weight but in precocial species it accounts for 13–15% of dry weight, reflecting the greater relative weight of plumage required for insulation in the precocial group.

Body composition. In most species the amount of water in the body increases with age, but this is largely a function of individual weight curves: when water content is expressed as a ratio between dry weight and age expressed as a percentage of each species' nestling period, most of the variation is eliminated. Thus, water content is determined by the maturity of the tissues carried by the nestling. In altricial species the water index (water content/lean dry weight) has a value of around 7–9 at hatching but decreases steadily to values of 2–3 at fledging. In precocial species, on the other hand, water indices are generally rather lower at hatching, generally around a value of 4.0, and decrease to about half this level by fledging. Similar patterns apply to the water content of individual tissues. Consequently, water indices are probably a measure of tissue maturity, with the proportion of solid matter in individual cells increasing as they accumulate proteins and enzymes.

Fat reserves similarly vary between species and with age within species and a measure of standardization can be achieved by dividing fat content by lean dry weight to yield a lipid index. This index describes the amount of lipid available to support the continued functioning of each unit of tissue. Amongst young nestlings lipid indices are typically low, around 0.05, and only a few species with particular ecological problems, such as oceanic seabirds and aerial insectivores, have values much above this, e.g., 0.30 in the House Martin *Delichon urbica.* For most species lipid indices increase during nestling growth and again the increase is most pronounced in those species ecologically likely to need recourse to fat reserves.

As a result of the accumulation of fat and lean material during growth and a relative decrease in water content with age, the caloric density (Kcal/g wet weight) increases with nestling age (Fig. 5). Altricial species have generally a low intercept in such plots and precocial species have

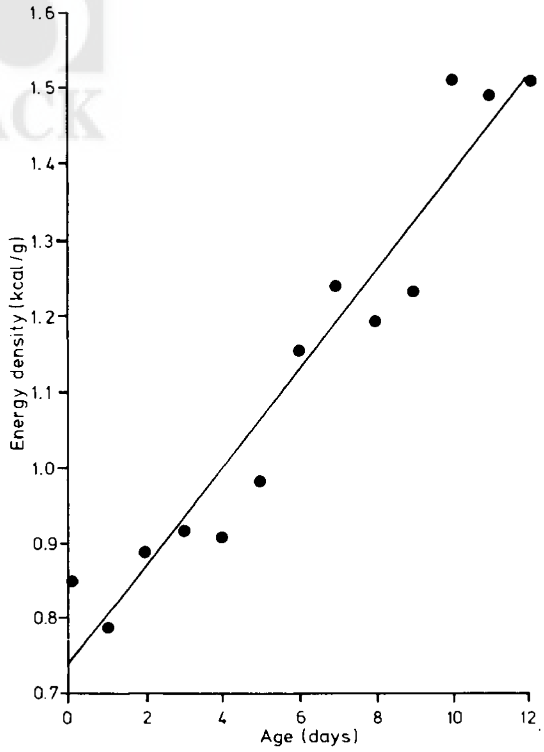

Fig. 5. Energy density (calories per gramme wet weight) in relation to age in House Sparrow *Passer domesticus* nestlings between hatching and 12 days.

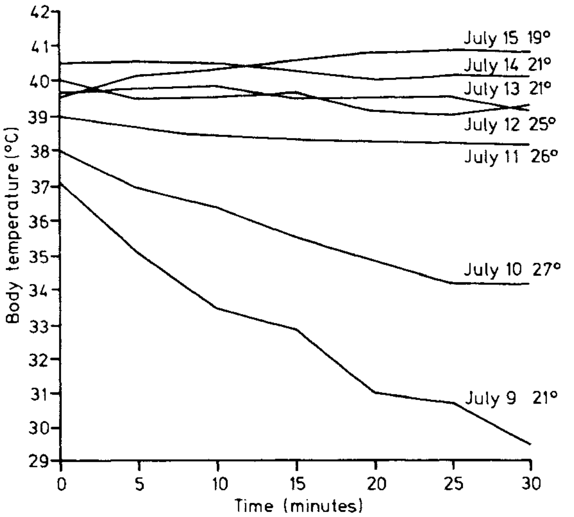

Fig. 6. Cooling curves of nestling Ovenbirds *Seiurus aurocapillus* exposed to ambient temperatures (shown on each curve) outside the nest on various days following birth on 9 July, showing how nestlings progressively improve temperature regulation with age. (After Hann 1937).

generally a high intercept, but adults of the two groups have rather similar final energy densities.

Fat deposits in nestlings are primarily around the abdomen, reflecting the absorption of the yolk sac lipids, but amongst older nestlings the other major depots—cervical and subscapular—are equally important.

Calcium is probably the mineral component of growth that is of most importance to birds. In young thrushes calcium concentration (mg/100 mg lean dry weight) more than trebles between hatching and fledging, its accumulation over this period being more or less sigmoid in time. This high intake of calcium (it has been estimated at 20–30 mg per gram of dietary protein) must underlie the frequently recorded habits of altricial species feeding their young fragments of shell and other sources of extraneous calcium.

Development of thermoregulation.

Body temperatures. Young nestlings are initially unable to regulate their body temperatures to a constant level and in the absence of parental brooding cool towards ambient temperatures (Fig. 6). Both nestling insulation and the abilities of the young birds to produce heat are involved here. Figure 6 shows that older nestlings were more able to resist heat loss than were younger birds and to do so more effectively at warmer temperatures than at colder. If such nestlings are tested experimentally at these temperatures for prolonged periods their abilities to maintain even this degree of temperature control are lost and they become torpid. Similar results are obtained when the nestlings are exposed to particularly low temperatures, so they are unable to compensate for the rate of heat loss from their bodies.

Much of the variation in the timing of thermoregulation is associated with the specific growth rate of the nestling, with fast-growing species becoming thermally independent sooner than slow-growing species. But amongst species with a given growth rate, those with the longer nestling period attain thermoregulation somewhat later.

Amongst precocial species the onset of thermoregulation is harder to define, given the independence of such young. However, there are a number of obvious gradients with ecological factors (Table). The diving ducks were the most resistant to cold stress, followed by dabbling ducks, then the gallinaceous species and semi-altricial gulls. This sequence basically reflects the normal exposure to cold. Amongst the auks young Guillemots show temperature control at 10–12°C from about 3 days of age and Puffins *Fratercula arctica* by 6–7 days of age. However, these are experimental findings and in the wild the chicks are in fact brooded at these temperatures until 5–6 days from hatching. Amongst young waders thermoregulatory abilities seem poorly developed, with various sandpiper chicks averaging 37.2°C when actively brooded but averaging 3° lower when actively feeding and becoming quite torpid when crouching in response to adult alarm calls (see also HEAT REGULATION).

Table of temperature regulation in recently-hatched young of various species when experimentally kept in ambient temperatures of 10°C for 20 minutes. (Data were estimated from the graphical presentation of Koskimies, J. & Lahti, L. (1964 Auk 81: 281–307).)

	Drop in body temp., °C
Goldeneye *Bucephala clangula*	0.2
Mallard *Anas platyrhynchos*	1.0
Teal *Anas crecca*	1.3
Blackcock *Tetrao tetrix*	3.8
Capercaillie *Tetrao urogallus*	4.0
Lesser Black-backed Gull *Larus fuscus*	4.0
Herring Gull *Larus argentatus*	4.2
Pheasant *Phasianus colchicus*	4.4
Black-headed Gull *Larus ridibundus*	5.8
Willow Ptarmigan *Lagopus lagopus*	8.0
Domestic Pigeon *Columba livia*	15.4

Metabolic rate and body weight. Metabolic output of young birds is a power function of their body weight at any age but the exponent is greater than amongst adults. There are significant differences between passerines and non-passerines in the speed with which they reach adult levels of metabolic intensity, the latter achieving this level sooner. There is a similar difference in passerine embryos, their weight-specific metabolism averaging about one-quarter to one-third the levels shown by adults of the same weight, whilst a non-passerine's metabolic intensity is nearly one-half of the adult level.

Body temperatures can be regulated either by controlling body conductance (the resistance offered by the body to the loss of heat produced internally) or by regulating heat production. Because their plumage is initially inadequate, young birds at first thermoregulate by producing excessive amounts of heat, only later reducing this rate of heat production with improvements in their body conductance.

Figure 7 shows the pattern of oxygen production in Blue Tit *Parus caeruleus* nestlings of different ages. In the youngest birds oxygen consumption is directly proportional to the prevailing temperatures, whilst in the oldest young the pattern of respiration approaches that of

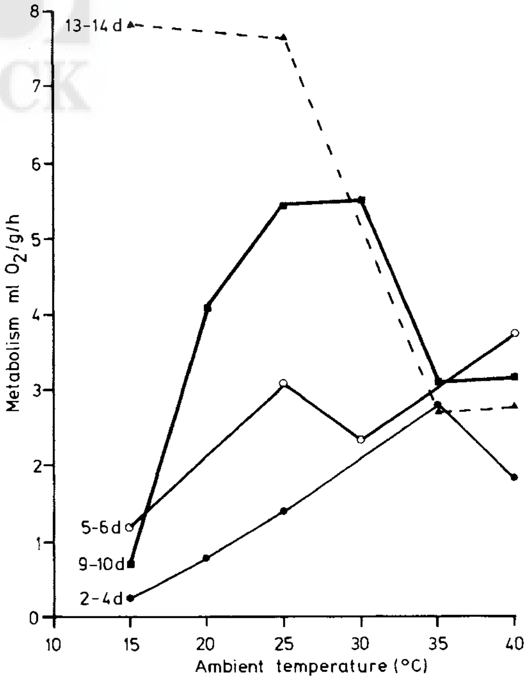

Fig. 7. Age changes in the metabolic rate of Blue Tit *Parus caeruleus* nestlings exposed to various ambient temperatures, showing the development of the nestlings' ability to produce heat. (After O'Connor, 1984).

the adult, with the inverse relationship between temperature and metabolic output. At intermediate ages the situation is more complex, the birds elevating their heat production in response to lower temperatures over a range of the warmer ambients but losing heat too rapidly and becoming torpid at the lower temperatures.

These patterns of thermoregulatory development in nestlings are associated with concomitant changes in the physiology and morphology of the young bird. As it increases in size its surface to volume ratio decreases, reducing the rate at which heat is lost from the body. Secondly, air sacs—functional in adult respiration—do not develop fully until some days into the nestling period and thus contribute increasingly to the metabolism of oxygen later. A third change involves the circulatory system, for the heart increases slightly in relative size and there are major increases in the erythrocyte concentration of the blood and in haemoglobin concentration. These changes contribute to the ability of the circulatory system to transport oxygen to the lungs. Carbohydrates form the main energy reserve for short-term responses to cold stress and their concentration in the body increases with age. Chemical thermoregulation by the young is also promoted (at least in domestic fowl) by injection with such hormones as noradrenalin, and thyroid hormones also contribute to cold stress responses. Thyroid activity peaks in altricial nestlings a day or so before the onset of full homeothermy. Finally, development in heat production by shivering under nervous system control contributes to heat production, appearing 3 or 4 days into the nestling period but increasing efficiency of heat production for sometime thereafter.

In precocial species very similar processes are apparent, though some of the responses, e.g., muscle tremor, begin shortly before the embryos hatch.

Another way in which young birds can regulate their heat loss to the environment operates by way of a lower body temperature than is shown by the adult bird. By doing this, the thermal gradient between bird and environment is reduced, with consequential reduction in the rate of cooling. Nestlings of several species have been shown to increase their equilibrium body temperature with age in this fashion.

Evaporative cooling and hyperthermia are the main defences available to nestlings subjected to heat stress. Hyperthermia operates to cool the nestling by elevating its body temperature above the ambient temperature, thus creating a temporary gradient down which heat can flow from the nestling to the now cooler environment. Conversely, in extremely hot conditions elevation of temperature reduces the rate at which further heat can flow into the nestling. Thermal ability of this type is more marked in very young birds than in older birds: 3-day-old House Wren *Troglodytes aedon* nestlings can safely withstand temperatures as high as 45.5°C but nestlings 11–16 days old can withstand high temperatures only to 42.1°C.

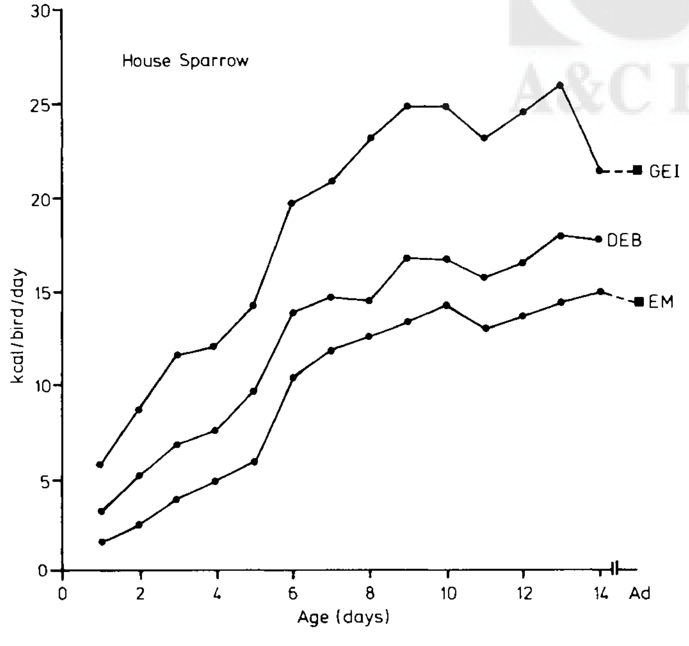

Fig. 8. Changes in energy budgets of House Sparrow *Passer domesticus* nestlings with age, showing changes in gross energy intake (GEI), in daily energy budget after assimilation (DEB), and in existence energy (EM). (From Myrcha, Pinowski & Tomek, 1972. *In* Kendeigh & Pinowski, (eds). Productivity, Population Dynamics and Systematics of Granivorous Birds. (PWN) Warsaw).

Evaporative cooling also serves nestlings faced with heat stress. Each millilitre of water evaporated carries with it 580 cal of latent heat. Consequently a nestling can work, e.g., by panting, to evaporate water and thereby lose more heat through evaporation than is produced by the extra effort of panting. Even quite young nestlings are able to pant when exposed to heat, and in tropical species regularly exposed to high temperatures this cooling can be enhanced by gular flutter.

Energetics of growth. The pattern of energy used during growth differs between altricial and precocial species (Fig. 8). Gross energy intake is higher in altricial species than in precocial species. In the House Sparrow the amount of energy spent on basic existence and maintenance costs rises to nearly twice the adult level before declining, thus implying that the young nestling is less efficient than an adult in its use of energy for maintenance costs. Precocial and altricial young alike have higher gross energy intakes than adults, but the excess is larger and increases virtually until fledging in precocial species. The energy expended in this way comes from the metabolization of food ingested and in the altricial House Sparrow food assimilation efficiency is at first below adult levels but reaches these after 4–5 days. In the precocial Black-bellied Tree Duck *Dendrocygna autumnalis* this efficiency varies little during the first part of postnatal life.

The daily energy requirements (Kcal/bird/day) of young birds increases with body weight according to the equation

$$\mathrm{DEB} = 1.353\,\mathrm{W}^{0.814}$$

(Kendeigh *et al* 1977), showing a faster increase with weight (exponent = 0.814) than would be the case amongst adults (exponent = 0.67). The young thus expend more energy per day than would an adult of the same weight, probably the result of the inferior insulation afforded by feathers whose shafts are vascularized until late in development. The different life-styles of altricial and precocial species result, however, in different proportions of their energy intake being devoted to maintenance costs. Despite these differences, though, there are no major differences in the proportion of energy consumed which is eventually converted into growth (see also ENERGETICS). R.J.O'C.

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GRUES; GRUIDAE: see GRUIFORMES; CRANE.

GRUIFORMES: an order comprising 7 suborders: Turnices, Grues, Heliornithes, Rhynocheti, Eurypygae, Cariamae, Otides; 11 families: Turnicidae (BUTTONQUAIL), Pedionomidae (PLAINS-WANDERER), Rallidae (RAIL), Aramidae (LIMPKIN), Psophiidae (TRUMPETER), Gruidae (CRANE), Heliornithidae (FINFOOT), Rhynochetidae (KAGU), Eurypygidae (SUNBITTERN), Cariamidae (SERIEMA), Otididae (BUSTARD).

Of the assemblage as a whole, it may be said that it consists essentially of ground-living birds—ground-feeding and mainly ground-nesting; many of them seldom fly, and a few never. The Heliornithidae and some of the Rallidae, e.g., coots (Fulicinae) and gallinules of various genera, are adapted to an aquatic life; many others frequent marshes or the margins of water. Of the families, the Rallidae include a large number of genera; 4 of the families are monotypic. Only the Gruidae and Rallidae are cosmopolitan, although the Turnicidae and Otididae are widespread in the Old World; the others have restricted distributions.

GUACHARO: alternative name of *Steatornis caripensis* (see OILBIRD).

GUAIABERO: substantive name of the Philippine species *Bolbopsittacus lunulatus* (Psittacinae) (see PARROT).

GUAN: substantive name of some species of Cracidae (see CURASSOW).

GUANO: the excreta of seabirds, dried to a crusty, rock-like or rough powdery consistency. Huanu is an Incan (Quechuan) word and its derivative is now widely used and applied, also, to other animal excreta such as 'bat guano' from caves (see also GUANO, CAVE). Guano, the Inca's 'secret' (see The Royal Commentaries of the Incas (1609) by Garcilaso de la Vega), introduced to the modern world by Alexander von Humboldt, has been extensively used as organic fertilizer, that from Peru giving rise to scandalous 19th-century commercial and political machinations. As Murphy wrote: 'Small though the Chinchas (Peruvian guano islands) are, their name is known in the farthest seaports of the world and their share in making fortunes and abetting calamities, in debauching men and demoralizing administrations, and in serving as the inanimate cause of greed, cruelty, extravagance, economic ruin and wars has given them a historic place quite out of proportion to their size.'

Guano is formed over many years where huge and densely packed colonies of seabirds breed on arid, flattish islands. Guanay Cormorants *Phalacrocorax bougainvillei* nest at a density of 3 pairs per m^2 whilst Cape Gannets *Sula capensis* have been recorded at 6.8 nests per m^2 though 3 or 4 is more usual. Many guano islands at times hold more than a million birds and some hold several millions (Central Chincha, maximum estimate 6 million). Necessarily, these colonies are situated in or near to enormously productive upwelling areas which support inconceivable numbers of fish (the catch of anchovies by Peru, 1969/70, contained more than 10 trillion). The Peruvian guano islands adjacent to the Humboldt current, those off SW Africa in the region of the Benguela and the seabird islands in the Gulf of California in the region of the California current are the best examples. Global wind and current systems are such that the cold and nutrient-laden upwellings are on the western seaboards of land masses (North America, South America, South Africa, India, Australia). These areas are also dry, the cold upwelling accentuating aridity by delivering cold moist air to a hot land mass, thus preventing precipitation (the moisture is retained in the warm air as mist).

Pelecaniforms, especially cormorants (*Phalacrocorax bougainvillei* in Peru; *P. capensis* in South Africa), sulids (*Sula variegata* and marginally *S. nebouxii* in Peru, *S. capensis* in South Africa) and pelicans (*Pelecanus occidentalis thagus*) produce most guano, partly because they are most numerous and also because some species tend to withhold their excreta until they are at the breeding site, where they deposit it to form the nest. Cape Gannets (average nest weight 1,770 gm) have been shown to reproduce more successfully where ample guano was artificially provided than in otherwise comparable areas. Guano can be used as nest material only in a dry climate; otherwise it would become sticky and coat the egg and chick. A Guanay Cormorant deposits on land, throughout its life, a minimum dry weight of 1 kg of guano per month. In addition to the 3 main guano-producing species, penguins (Peruvian Penguin *Spheniscus humboldti* in Peru and Jackass *Spheniscus demersus* in South Africa) and diving petrels (*Pelecanoides garnotii* in Peru) have been significant contributors, whilst the Gulf of California and islands off Mexico were seriously investigated as the potential basis for a guano industry, to which the Blue-footed Booby *Sula nebouxii* would have been the main contributor.

Seabird excreta leached by moisture lose nitrogen and leave calcium phosphate minerals, called phosphatic guano. This is less nutritious to plants than the original high-grade nitrogenous guano. The calcium phosphate from the Indian Ocean Christmas Island (apatite ore for conversion into superphosphate fertilizer in Australia and New Zealand) is said to be modified guano, but if this is so, vast changes in topography, climate and seabird population have occurred since its deposition. In some parts of the world, low-grade 'guano' is collected, consisting of annual increments of excreta scraped up together with much substrate and nest material.

Peruvian guano contains approximately 21% water, 53% organic material capable of being burnt off, 1.7% insoluble materials (silicon dioxide, etc.), 3.5% sodium oxide, 2.5% potassium oxide, between 3 and 11% calcium oxide, 0.5% magnesium oxide, between 7 and 11% phosphorus pentoxide, 2% chlorine, 0.3% sulphur trioxide and 0.9% of a complex of aluminium and ferric phosphate (Hutchinson 1950).

Although the guano caps of the islands were up to 90 m thick, this represented the deposits of no more than 2–3,000 years. However, C^{14} dating has indicated a much greater age for at least one deposit. Earlier guano caps may have been washed away by periods (measured in scores or hundreds of years) during which a wetter climate prevailed. Indeed, the distribution of guano-birds has changed within (relatively) recent times. There are extensive and old (fossil) guano deposits in Peru/Chile well south of the present concentrations of guano birds and the 'modern' deposits of guano. This southern area evidently became uninhabitable whilst the northern one became attractive, having presumably been climatically unsuitable previously. The factors which led to the decline of guano birds in the south may have been oceanographic (change in currents and distribution of food fish and in sea level, submerging many islands off Chile).

Between 1848 and 1875 more than 20 million tons of guano were shipped from Peru, mainly to Europe, USA and Britain. This was the era of total exploitation, both of the resource (including the seabirds) and the labour force. In 1909, the Guano Administration instituted protection for guano birds, the single most effective measure being the stationing of official wardens at the main breeding stations to control human and other animal predators (foxes, gulls, Condors *Vultur gryphus* and Turkey Vultures *Cathartes aura*). Since 1945 extra nesting areas have been provided on Peruvian coastal headlands. Peninsulas have been isolated by high concrete walls, nesting areas enlarged and sites created. Up until 1956 these measures dramatically increased the mainland population and in 1962 headlands held some 4,500,000 guano birds. Other regulations, though rarely enforced, oblige boats to remain at least 3 km away from the islands holding breeding colonies, fishing boats to refrain from operations within a 5-km belt around all stations (8 km around some) and planes to fly over stations at a height no lower than 500 m. Harvesting of guano takes place every second or third year on a rotating basis; the maximum yield per year is in the region of 300,000 tons.

Harvesting inevitably disrupts breeding cycles and may be partly responsible for the considerable movements of birds between nesting islands, although shifts in the distribution of anchovies may also be involved.

The populations of Peruvian guano birds (mainly *Phalacrocorax bougainvillei*, *Sula variegata* and *Pelecanus thagus*), and also the proportions of each, fluctuate massively. Little can be inferred about changes prior to the 20th century though Vogt (1942) suggested that there had been a massive decline due to climatic changes and/or disease. However, this century the population has fluctuated between less than 3 and more than 20 millions of individuals. When estimated from the amount of guano deposited (a surprisingly accurate method), the highest figure is 28 million. The population crashes periodically. The cold upwelling fails, anchovies *Anchoveta engraulis* avoid the warm surface layers and become inaccessible and guano birds starve en masse. Until recently recovery was rapid but overfishing by the Peruvians, for example an official catch of 11 million metric tons in 1969/70, largely for the manufacture of fish meal, has apparently reduced stocks and/or altered the age composition of the anchovy population. Presumably as a result of this, recovery from the most recent crashes (1965, 1972/3, and 1983/4) has been greatly retarded. In addition, in the 1960s, many thousands of breeding guano birds were killed by fishermen. At the present time, after a period during which anchovy stocks remained low, some recovery in them and the seafowl has taken place, the boobies having fared better than the cormorants and pelicans.

In South Africa declining catches by fishermen has led, as in Peru, to requests for an official policy of killing off seabirds. Apart from the fact that the seabirds catch fish and interfere with the nets, it has been argued that man can convert fish into meal more efficiently (at 5 : 1) than birds can convert it into guano (at 9.7 : 1). But birds not only produce a better and cheaper product, they also remain in a stable relationship with their ecosystem. Man should learn to do the same. And a colony of guano birds is more beautiful than a stinking fishmeal factory.

(R.C.M.) J.B.N.

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GUANO, CAVE: of avian origin, occurs in limestone caves in South-east Asia occupied by swiftlets of the genera *Collocalia* and *Aerodramus* (see EDIBLE NESTS). Droppings gathering below nest sites are quickly reduced, by a rich fauna of coprophagic arthropods, to a dark brown material with the consistency of damp sawdust. This is composed chiefly of organic matter and normally contains 6–10% phosphate and 3–9% nitrogen. In undisturbed dry caves this fresh guano is underlain by deposits, which can be several metres thick, of a compact, powdery 'fossil' guano containing 10–45% phosphate by weight (characteristically as collophanite, $3CaOP_2O_5H_2O$), often with other minerals, and 10–30% organic matter. Despite low nitrogen and unpredictable phosphate yield, both types of guano are locally popular as fertilizer. Most accessible caves in the region have already been stripped down to bedrock. C.

GUIDING LINE: less appropriate alternative term (translating 'Leitlinie') for LEADING LINE (see MIGRATION).

GUILLEMOT: substantive name of *Uria* spp. ('murre' in American usage) and *Cepphus* spp. (also called 'tystie')—see AUK. Although originally a French word, it is now pronounced in English with the final syllable as in 'hot'.

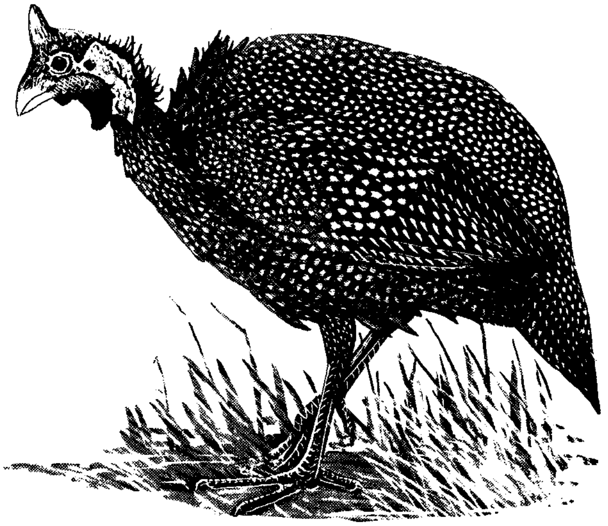
GUINEAFOWL: substantive name of species of Numidinae (Galliformes, family Phasianidae); a group of sedentary terrestrial gamebirds. There are 6–7 species, assigned to 4 genera, 2 of which are superspecies.

Characteristics. The major external feature of guineafowl is a largely unfeathered head and neck, which is adorned with cartilaginous gape wattles and areas of richly pigmented, sometimes folded skin. Some species have a well-developed casque or feathered crest surmounting the crown, and cartilaginous bristles or warts at the cere. These structures provide some of the most useful specific and subspecific taxonomic characters, and presumably play important roles in species and individual recognition, and possibly in thermoregulation. Patterns of geographic variation in these and other morphological features of guineafowl correlate well with, and may be adaptively related to, variation in the thermal and moisture environments.

All guineafowl species show little sexual dimorphism, with males averaging slightly larger than females, range 45–60 cm. Size among the various species appears to be inversely related to the density of the vegetation in which they live. The smallest guineafowl are *Agelastes* spp. (mean wing length 20.4 cm), which inhabit dense, virgin, tropical rain-forest. Among the guineafowl with feathery crests (*Guttera* spp.) *G. plumifera*, which inhabits dense forest, is smaller (mean wing length 22.5 cm) than *G. pucherani* (range of mean wing length among subspecies 24.5–26.0 cm), which lives in secondary and riparian forest, and along the forest edge. Larger still is the Helmeted Guineafowl *Numida meleagris* (range of mean wing length among subspecies 25–28 cm), which lives in relatively open savanna vegetation and mixed savanna-bush. The Vulturine Guineafowl *Acryllium vulturinum* is the largest of the guineafowl (mean wing length 29.5 cm), and frequents the semi-desert steppe of the Horn of Africa.

Distribution and habitat. The ancestral guineafowl is thought to have arisen from an Asian, savanna-living, francolin-like phasianid which colonized Africa during the mid to late Miocene, and radiated into terrestrial biotopes which were relatively unexploited. With the exception of an isolated population in Morocco, guineafowl now occur naturally only in sub-Saharan Africa. Distribution patterns of species and subspecies correlate well with the present-day distribution of vegetation, so that nearly every African biome and biotope has an associated guineafowl species or subspecies. However, guineafowl evolution at all taxonomic levels has been influenced by past changes in the distribution of forest, savanna and desert during geological time (see AFROTROPICAL REGION). One species, *Numida meleagris*, has been domesticated (probably several times independently), and/or captured and introduced widely throughout the world (see DOMESTICATION). This accounts for its presence in south-western Arabia, the Malagasy Republic and on offshore African islands.

Food. They consume varying amounts of grit, and appear to be opportunistic omnivores, probably favouring insects when they are abundant. The bill of the Helmeted Guineafowl *Numida meleagris* is arched, and therefore well-suited to digging for underground bulbs, which are a favoured food item during dry periods and may be an important supplementary source of water.



Helmeted Guineafowl *Numida meleagris*. (*M.W.*).

Social behaviour. With the exception of *Agelastes* spp., which appear to associate in small (family?) parties, all guineafowl species are highly gregarious in the non-breeding season, and flocks of 50 birds or more are not uncommon sightings. All species roost in trees at night. At least 3 species (*N. meleagris*, *G. pucherani* and *A. vulturinum*) exhibit courtship feeding, and this behaviour is highly ritualized in *A. vulturinum*. These 3 species are monogamous in their breeding habits, although males may attempt to copulate with unattended females.

Voice. As with size, the pitch of the rattling alarm calls given by guineafowl species is inversely related to habitat vegetation density. Thus the desert-living *Acryllium* has the highest pitched, while *Guttera* spp. and *Agelastes* spp. have the lowest-pitched calls. *Numida meleagris* and *Acryllium vulturinum* females, especially when separated from their mates during the breeding season, emit a characteristic two-noted buck-wheat call, to which their cocks respond antiphonally with a single note.

Breeding. The nests of *Agelastes* spp. have not been described, but those of all other guineafowl are well-concealed shallow scrapes in the ground, which may be thinly lined with grass. The eggs of all species are pitted, creamy or buff in colour, remarkably thick shelled, blunt at one end and pointed at the other. Nests with 12 or more eggs are not uncommon. Sometimes several hens may lay in the same nest. The incubation period for the various species ranges from 23 days (for *Guttera* spp. and *Acryllium*) to 27–28 days (for *Numida*). At 15–20 days old, *Numida* chicks can fly up to roosts 2 m above ground.

Specific distribution. The most widely distributed and well-studied member of the family is the Helmeted Guineafowl *Numida meleagris*. This open-country, polytypic species has a virtually unfeathered head and neck, with the exception of the hindneck, which is covered by a concentration of short, downy, or long, hair-like feathers. The bill is heavy, a bony helmet (see CASQUE) with a horny sheath surmounts the crown, and a pair of long wattles hangs from the gape. The nostrils are exposed, and are rimmed with cartilaginous bristles or warts in subspecies which live in hot, arid biotopes. The blood vessels which supply the wattles, cere and upper hindneck are finally interwoven into *retia*, which may promote counter-current heat exchange, and thereby assist in the regulation of brain temperature through convective cooling of warm arterial blood coming from the heart. The iris of the chick is grey, but changes to brown by the age of 20 weeks. The tarsus is unspurred, and the legs are long and powerful, as befits a species which relies on running as its primary means of escape, and on scratching in the soil for much of its food. The ground colour of the plumage is black, with white spots intermeshed with a network of similarly-coloured vermiculation. The spots on the outer margins of the secondaries merge to form bars (perpendicular to the rachis), which also have intervening vermiculation. The degree of vermiculation is most intense in subspecies which live in hot and arid biotopes, and may afford some degree of camouflage.

There are 9 well-marked subspecies of *N. meleagris*, which fall into 3 groups: the West African, East African and Central–Southern African subspecies groups. These groups are separated by relatively narrow zones of intergradation, and hence have been regarded as semispecies. The West African subspecies group (*N. m. galeata* and *N. m. sabyi*) consists of small- to medium-sized birds, with very short helmets (i.e., less than 1 cm tall), a naked cere, a grey to blue-grey mantle, rounded red wattles, very pale blue facial skin, and long hair-like feathers confined to the mid-dorsal line of the hindneck. Since *N. m. sabyi*, the isolated Moroccan subspecies, differs relatively little from *N. m. galeata*, the hundreds of kilometres of desert which presently separate the 2 subspecies are likely to be a relatively recent development on a geological time scale.

The domesticated guineafowl is derived from *N. m. galeata*, and artificial selection has significantly modified its external morphology. Since domesticated guineafowl have been bred to be broilers, they are 20–25% heavier than their wild counterparts, which weigh about 1,300 g. They have thicker tarsi, which are orange and not black as in wild stock. The colour of the face, and that of the plumage of some breeds, is entirely white, and the wattles and helmet are 30–50% larger. There are no qualitative differences in displays, social and maintenance behaviour between wild and domesticated guineafowl. Even wild populations of this species can be more or less commensals of man, since the distribution and numbers of Helmeted Guineafowl have increased markedly when critical resources, e.g., water (bore holes and dams), roosts (telephone poles, exotic trees), and food (maize, wheat, lucerne, etc.) have been provided.

The East African subspecies group (*N. m. meleagris* and *N. m. somaliensis*) are medium-sized guineafowl (mean wing length 26.5 cm) with short helmets (mean height 1.2 cm), a cere with long bristles (up to 2.5 cm), a finely barred mantle, rounded blue (or with small red tips) wattles, cobalt blue facial skin, and a blanket of short downy feathers covering the hindneck.

The Central–Southern African subspecies group (*N. m. reichenowi*, *N. m. mitrata*, *N. m. marungensis*, *N. m. papillosa*, and *N. m. coronata*) consists of relatively large birds, with tall helmets (i.e., greater than 1.8 cm), a naked cere (except *N. m. papillosa* which has its cere rimmed by warts), a finely barred mantle, triangular-shaped blue wattles with red tips (except *N. m. reichenowi* which has rounded red wattles), cobalt blue facial skin, and varying amounts of long hair-like feathers confined to the mid-dorsal line of the hindneck.

Although *N. meleagris* is virtually sexually monomorphic, the sex of live birds can be determined accurately by cloacal examination, and through study of individual behaviour. During the breeding season, males develop a cloacal protuberance, which is easily discovered by gently everting the cloaca. Males, again mainly during the breeding season, display laterally to each other, and to hens, in a 'hump-backed' posture (i.e., with the wings raised and laterally compressed against their bodies), and run on the tips of their toes. In this 'hump-backed' posture all important taxonomic characters of this species are displayed to their fullest.

Closely allied to *Numida* is the Vulturine Guineafowl *Acryllium vulturinum*. In captivity the 2 species will hybridize to produce sterile offspring. However, encounters between these 2 guineafowl in the wild are rare, since they segregate according to habitat where they are sympatric. The bare skin of the head and neck of *Acryllium* is blue-grey, and the only plumage thereon is a band of short, downy chestnut feathers which stretches across the occiput from ear to ear. The wattles are rudimentary, and the iris a brilliant crimson. The most striking field characters for this species are well-developed hackles, and a pair of long central tail feathers. The former consist of long, narrow, pointed feathers striped longitudinally with black and white, and margined with cobalt blue. The breast and abdomen are also extensively covered by cobalt blue plumage. The remainder of the plumage resembles that of *Numida* except that the outer margins of the secondaries are lilac, and the inter-spot vermiculation is much denser. The only external feature which shows obvious inter-individual variation is the tarsal adornment, which is a series of degenerate, rounded spurs or 'bumps'. No two individuals have both the same number (up to 6) and size of 'bumps', and there is even variation in 'bump' arrangement between legs. As with important characters in *Numida*, this species' characteristic features are displayed to their fullest in aggressive and courtship postures.

The first guineafowl encountered as one enters forest biome is the Crested Guineafowl *Guttera pucherani*. Most taxonomic treatments recognize 2 species of these 'forest-edge' birds, but breeding experiments with captive individuals have demonstrated complete interfertility between 'species', and morphological intermediates have been identified among museum specimens collected in zones of contact. Nevertheless, all subspecies attributed to *G. pucherani* are much more well-marked than are those for *N. meleagris*, which supports the idea that forest-dwelling guineafowl have been more effectively isolated in refugia during the geological past than have savanna species.

The body plumage of *G. pucherani* is similar to that of *Numida* and *Acryllium* except that the spots are tinged with blue, and there is no vermiculation between them. The outer margin of the secondaries is white, and the tarsus is unspurred. The crown is surmounted by a crest of curly, downy feathers; gape wattles are rudimentary; there is a well-developed fold of skin at the occiput and, in all but one subspecies, at the base of the neck; and the skin of most of the head and neck is dull blue-grey. A striking feature of the internal anatomy of this species is the hollow furcula of the clavicle through which passes the trachea. This feature may act as a resonant organ which allows the broadcasting of calls over relatively long distances.

The 5 subspecies attributed to *G. pucherani* can be divided into 3 groups: the West–Central, East and Southern African subspecies groups. These groups can be distinguished through differences in the morphology of the head, neck and mantle. Subspecies of the West–Central African group (*G. p. verreauxi* and *G. p. sclateri*) have red throats and brown irides. Those of the Southern African group (*G. p. edouardi* and *G. p. barbata*) have dull blue-grey throats and red irides. The Kenyan Crested Guineafowl *G. p. pucherani* has a red throat and red irides, and differs further from other subspecies in having virtually no black feathers in the mantle (all other subspecies have a distinct black 'collar'), and a ring of red skin around the eye.

Moving deeper into forest biome, the next guineafowl which may be encountered is the Plumed Guineafowl *Guttera plumifera*. This species and *G. pucherani* form a superspecies. The body plumage of *G. plumifera* is similar to that of *G. pucherani*, except that there is little or no tinge of blue to the spots, and the entire mantle is spotted (i.e., lacks a 'collar' of black feathers). Other characteristic features of *G. plumifera* are: a tall crest of straight bristly feathers, brown eyes, long gape wattles, and a rudimentary occipital skin fold. Like *G. pucherani*, *G. plumifera* has a hollow furcula, but it is much less well-developed. Although the Congo forest (to which this species is confined) stretches relatively uninterrupted from the Atlantic coast to Uganda, there are 2 subspecies of *G. plumifera*. One subspecies (*G. p. plumifera*) is confined to the western reaches, the other (*G. p. schubotzi*) to the eastern portion of the forest. The major difference between the 2 subspecies is that *G. p. schubotzi* has patches of orange-yellow skin at the base of the nape and just anterior to the ear, while the head of *G. p. plumifera* is entirely dull blue-grey. The fact that this relatively uninterrupted forest can harbour more than one subspecies of forest-dwelling bird suggests that it was formerly fragmented into island-like refugia.

Deeper still in virgin tropical rain-forest live the Turkey Guineafowl *Agelastes meleagrides* and the Black Guineafowl *A. niger*. There is only fragmentary or anecdotal information on the natural history of these forest guineafowl, and this has already been summarized above. These species differ conspicuously from other guineafowl in having a wholly unspotted body plumage. That of *A. niger* is uniformly blackish-brown, and that of *A. meleagrides* blackish-brown with fine grey vermiculation. The bare skin of the heads of both species is red, brighter in *A. meleagrides*. The head of *A. meleagrides* is unfeathered, and that of *A. niger* is surmounted by a crest of short feathers which extends from the base of the bill to the occiput. The mantle and breast of *A. meleagrides* are snowy white. Both species have brown irides and well-developed spurs on their tarsi.

T.M.C.

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GUIRA: *Guira guira* (see CUCKOO).

GULAR: pertaining to the throat (see TOPOGRAPHY).

GULAR FLUTTER: rapid oscillation of the thin floor of the mouth and upper throat (see HEAT REGULATION).

GULL: substantive name of nearly all the species of the family Laridae (Charadriiformes, suborder Lari); in the plural, general term for the family. The other families of the suborder are the Sternidae (see TERN), Rynchopidae (see SKIMMER), and Stercorariidae (see SKUA).

Characteristics. All species are medium to large (length 31–76 cm) and have relatively long and narrow wings (span 64–165 cm), with 10 functional primaries and one vestigial. The tail of 12 rectrices is usually almost square and of moderate length, generally 35–45% of the length of the closed wing. The bill is usually stout, sometimes slightly hooked, with a tapering nail, and a marked gonydeal angle. The tarsus is rather long and slender, the 3 front toes webbed, the hind toe very small or in a few species vestigial. The plumage of adults is basically white and grey. Head, underparts, rump, tail and underwings are white, sometimes washed grey to a variable degree, the head often covered for part of the year by a dark brown or black hood, leaving contrasting white marks above and below the eye, the tail adorned in a few species by a subterminal black band. Mantle and upper wing-coverts are grey, white in one species, black in a few. The tips of the primaries are usually patterned with black or black and white. Irides are usually brownish-black, sometimes white or pale yellow. The fleshy eye-ring is usually red or deep red tending to black, but yellow or purple in a few species. The bill is usually red, reddish-black or black, sometimes yellow with black or red distal marks or entirely yellow. Legs and feet are red to black, but yellow, bluish, greenish or flesh-coloured in a few groups of species.

Adults have an annual complete moult, starting during or immediately after the breeding season, but, in a few species, after the autumn migration, and in the Ivory Gull *Pagophila eburnea* before the breeding season. A second moult, not involving, except in a very few species, the wings and tail, takes place before the breeding season. Breeding and non-breeding plumages differ in most species.

Downy chicks are usually grey or buff, variously patterned with dark brown stripes and spots. Juveniles of almost all species are brown and buff with strongly patterned mantle and upper wing-coverts, dark remiges and rectrices. This plumage is replaced after a few weeks to a few months by a usually distinct first-winter dress. Adult plumage is acquired after as long as 4 or more years in some large species, through a succession of plumage stages reached by moults which generally take place earlier in the year than those of adults.

Systematics. The morphological uniformity of the family has made the construction of phylogenies difficult. The principal revisions are those of Dwight (1925), based entirely on structure and plumage, and Moynihan (1959), based partly on behaviour. The present arrangement is derived from these but more recent information on behaviour, morphology and distribution is taken into account.

Pelagic gulls. A small number of species, pelagic or semi-pelagic when not breeding, differs sharply from the core of typical gulls in voice, behaviour, proportions, tail-shape (either forked or wedge-shaped) and several adult and juvenile plumage characters. When hooded, they lack the white eye marks characteristic of gulls. Many of their characters are primitive within larids and they probably represent early offshoots near the common ancestors of typical gulls and terns. Their originality is best expressed by placing them in several small genera. The Swallow-tailed Gull *Creagrus furcatus* is a large species with long forked tail, slaty breeding hood and prominent wing pattern. Three small species, Sabine's Gull *Xema sabini*, Ross's Gull *X. rosea* and the Little Gull *X. minuta* have similar juvenile plumage. *X. sabini* and *X. minuta* have dark breeding hoods, without white eye marks, while *X. sabini* and *X. rosea* share unique black neck rings, bordering the slaty hood in *sabini*. The 2 kittiwakes, Black-legged *Rissa tridactyla* and Red-legged *R. brevirostris*, have juvenile plumages, which are reduced versions of those of *Creagrus* and *Xema*, and a shallowly forked tail. They are white-hooded in summer. It is unclear whether the peculiar Ivory Gull, white when adult, spotted brown in juvenile plumage, belongs near these primitive species.

All other gulls may be placed in a single genus *Larus*, subdivided into 5 main groups.

Central Eurasian gulls. The Great Black-headed Gull *Larus ichthyaetus*, Mediterranean Gull *L. melanocephalus* and Relict Gull *L. relictus*, breeding on the inland seas and lakes of Eurasian steppes are much alike in downy and juvenile plumages and, when adult, differ mostly in size and mantle shade. They are hooded in breeding plumage and have a characteristic auricular bridle in non-breeding dress. The agonistic behaviour of the Mediterranean Gull is very un-*Larus*-like, while that of the Relict Gull seems to have similarities with those of possibly primitive species in other groups such as Audouin's Gull *L. audouinii* or the Slender-billed Gull *L. genei*, so that the central Eurasian gulls may well occupy a position near the centre of evolution of the *Larus* gulls.

Masked gulls. The relatives of the Black-headed Gull *L. ridibundus* form a successful homogeneous group, best characterized by the presence of a conspicuous white triangle along the leading edge of the wing, dark underside to the primaries, and the development of the Forward Display in the Long-Call performance. They are hooded or not in breeding plumage, differ in wing-tip pattern, but generally have a characteristic double band across the top of the head in non-breeding or immature plumage. The core species are the Black-headed Gull, the Grey-headed *L. cirrocephalus*, the Brown-headed *L. maculipennis*, the Andean *L. serranus*, the Silver *L. novaehollandiae*, Buller's Gull *L. bulleri*, and Hartlaub's Gull *L. hartlaubii*. Somewhat more distantly related seem to be Bonaparte's Gull *L. philadelphia* which lacks the dark underwing, the Slender-billed which lacks the Forward Display, the Indian Black-headed Gull *L. brunnicephalus* and Saunders' Gull *L. saundersi*. The masked gulls seem to represent the top of one evolutionary line among *Larus* gulls, perhaps derived from the previous group.

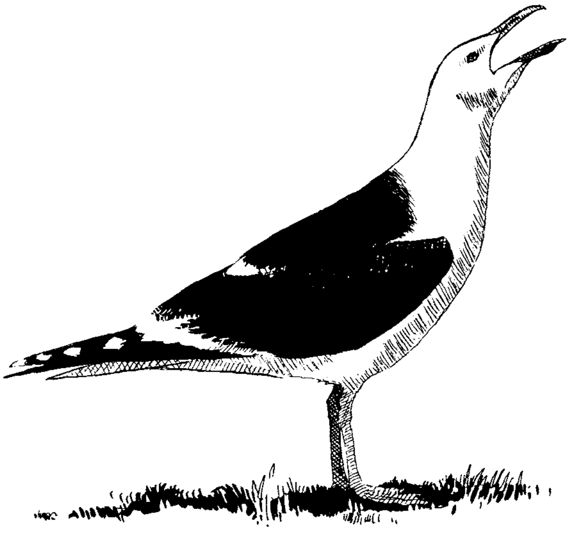
Herring gulls. This is also a large, homogeneous, successful group, probably at the summit of another evolutionary line; all species are large, with patterned or white wing tips, a white head in breeding dress, and usually a streaked hood in winter. Their legs are yellow or flesh-coloured, their bills usually with a red gonydeal patch, a unique pattern in *Larus*. The group comprises many closely related species, of almost identical behaviour, e.g., Glaucous *L. hyperboreus*, Iceland *L. glaucoides*, Thayer's *L. thayeri*, Glaucous-winged *L. glaucescens*, Western *L. occidentalis*, Yellow-footed *L. livens*, Dominican *L. dominicanus*, Slaty-backed *L. schistisagus*, Vega *L. vegae*, Great Black-backed *L. marinus*, Herring *L. argentatus*, Yellow-legged *L. cachinnans*, Lesser Black-backed *L. fuscus*, Armenian *L. armenicus* and California Gull *L. californicus*.

American hooded gulls. The Laughing Gull *L. atricilla* and Franklin's Gull *L. pipixcan* are very similar in adult breeding plumage and almost identical in voice and behaviour. They are unquestionably closely related. The Lava Gull *L. fuliginosus*, endemic to the Galapagos, is an obvious dark derivative of the Laughing Gull. The affinities of the group with other gulls are not entirely clear but may be with the central Eurasian gulls on the one hand, the 'black-tails' (see below) and their allies on the other.

Black-tailed gulls and allies. The Pacific Gull *L. pacificus*, Olrog's *L. atlanticus*, Belcher's *L. belcheri* and Japanese Gull *L. crassirostris* have a black band in the tail of the adult plumage, plain black wing-tips, a white head in breeding plumage; they approach the herring gulls in their ritualized behaviour, their juvenile and downy plumages, the yellow bill with a red or black and red tip, and the yellow legs; they may constitute an early offshoot of the line that leads to the *argentatus* group. A few fairly isolated species, the Grey *L. modestus*, Scoresby's *L. scoresbii*, Sooty *L. hemprichii*, White-eyed *L. leucophthalmus*, Audouin's and Heermann's Gull *L. heermanni* may all be related, more or less distantly, to the black-tailed gulls.

Common and Ring-billed gulls. These 2 species are difficult to place and have usually been considered related. The Ring-billed *L. delawarensis* closely resembles the herring gulls in plumage but its behaviour seems to differ more from them than it does from some members of the black-tailed group. The Common Gull *L. canus* differs more from the herring gulls in downy and juvenile plumages, recalling the Laughing Gull or some 'black-tails', and is behaviourally isolated.

Habitat. Most gulls are coastal throughout their life cycle. A few (the kittiwakes, Swallow-tailed and Sabine's Gulls) are truly pelagic during the non-breeding season, others (Ivory, Ross's Gull) frequent the edge of ice, or (Little Gull, Mediterranean Gull) offshore waters. A few feed inland in open terrain, away from water. For breeding most species resort to flat or fairly flat open ground near water, often on islands. A few (the kittiwakes, Swallow-tailed, Ivory and Thayer's Gulls) breed on cliffs and have developed a series of adaptations to minimize the risk of eggs or young falling (Cullen 1957, Hailman 1964). Others breed in coastal or inland marshes (e.g., the Black-headed, Grey-headed and Franklin's Gulls) where they may build floating platforms (Burger 1974). Bona-



Great Black-backed Gull *Larus marinus*. (*B.P.*).

parte's Gull breeds in trees in wooded tundra, the Grey Gull in total desert far from the sea (Howell *et al* 1974). A few species (e.g., Black-legged Kittiwake, Herring, Yellow-legged and Dominican Gulls) have adapted in some areas to nesting on man-made structures.

Distribution. Worldwide, but with a scarcity of species in the tropics. Main centres of differentiation, with several original and isolated species, seem to exist in South America and in central Eurasia, while a more recent radiation of the herring gulls has given the northern shores a wealth of closely related forms.

Populations. Many species are numerous and some, in association with man, are increasing at remarkable rates. These belong mostly to the herring and masked groups. A few species, however, are uncommon with a restricted range and thus vulnerable. Examples are the solitary Lava Gull of the Galápagos, the very local Olrog's Gull of the coast of Argentina and the Mediterranean Audouin's Gull.

Movements. No gull is completely sedentary, and most species undertake migratory movements of at least restricted amplitudes, often along the coasts they frequent. These generally take the form of a post-breeding movement to lower latitudes, but a few species disperse to higher latitudes (Heermann's Gull and the Yellow-footed in western North America, the Yellow-legged Gull in Europe) and some populations shift longitudinally (the Mediterranean Gull from the Black Sea to the Mediterranean and the Atlantic, Ross's Gull from Siberia east in the Arctic Ocean). Three species regularly perform trans-tropical or trans-equatorial movements, the Lesser Black-backed Gull from northern Europe and western Siberia to Africa and India, Franklin's Gull from the northern American prairie to South America, reaching Tierra del Fuego, Sabine's Gull from the Arctic as far as the open seas off South Africa and South America.

Food. Many species feed on marine invertebrates in the intertidal zone. A few, such as the Slender-billed or Grey Gulls (when feeding young) are specialized fish predators; pelagic gulls take fish and invertebrates. Many species feed for at least part of the year on freshwater or even terrestrial invertebrates. Some (e.g., Great Black-backed, Glaucous and Dominican Gulls) are predators of mammals and birds. Fishing and hunting techniques include probing and prying, actively chasing on foot (e.g., Grey Gull), pecking at the surface of the water, up-tilting, quartering, hovering and snatching, plunging. Many species are scavengers, some specializing in robbing eggs, young or spilled food at sea-bird colonies, or in associating with marine mammals (Scoresby's Gull). Piracy on terns or smaller gulls is widespread, as is association with flocks of fishing mergansers *Mergus*, cormorants *Phalacrocorax* or divers *Gavia*. Many species, notably of the herring and masked gull groups, also Franklin's Gull, exploit human refuse and fishing activities.

Behaviour and voice. Gulls are almost completely diurnal, though some migrate at night; the Grey Gull undertakes at night the long flights between the sea and the desert where it feeds its young and the Swallow-tailed Gull is mostly nocturnal, at least on the breeding grounds. Almost all species are highly gregarious, often breeding in large, dense colonies, roosting in vast multispecific roosts, and feeding socially. They have thus developed a rich repertoire of both visual and auditory social signals, the significance of which has been best described by Howell *et al.* The form taken by the expression of self-advertisement, anxiety, threat, intention to flee or attack, dominance, and submissiveness differs somewhat from species to species, though along consistent lines. It has been studied in detail for several species, representing most groups, and comparative, partial summaries have been made, for example by Tinbergen (1959a) and Moynihan (1962). Among the most important, widespread, and conspicuous displays are the silent Upright, indicating anxiety or aggression, the aggressive Choking, the begging Head-toss, and the Long Call, a usually ringing and far-carrying vocal utterance, accompanied by a complex posture and proclaiming a readiness to interact either aggressively or amicably. Besides the Long Call and Long Call notes, the most often heard vocalizations are the guttural alarm notes, the cat-like mewing, and the whining soliciting calls of females and juveniles. The Swallow-tailed Gull has a peculiar 'rattle and whistle' alarm call, which has been correlated with the threat from frigate-birds (Fregatidae) (Snow and Snow 1968).

Breeding. Most gulls breed upon assuming adult plumage, at 1–5 years old. The pair-bond is normally monogamous, and fidelity to colony, nest-site and partner is high in established breeders. Pair formation may occur at the nest-site or in 'clubs' of non-breeders, which are characteristic of some species. The breeding cycle of most species is annual but 2 broods a year are known in some populations of the Silver Gull (Nicholls 1964) and Hartlaub's Gull. The Swallow-tailed Gull breeds throughout the year. Gulls' nests are sometimes extremely rudimentary, sometimes bulky and sometimes untidy. One to 4, mostly 2 to 3 brown, olive, blue or grey, heavily mottled eggs are laid. The incubation period is from 3–4 weeks; both parents incubate and care for the young. The chicks are alert at birth and are fed in or near the nest for 2–3 weeks, usually until fledging at 4–5 weeks and, in the herring gulls, sometimes for several weeks thereafter.

See photos: COLORATION ADAPTIVE; CONSERVATION; DRINKING; FEEDING HABITS; MOBBING; NOCTURNAL HABITS; PARENTAL CARE; PIRACY; RITUALIZATION. P.D.

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GULLET: the anterior part of the oesophagus (see ALIMENTARY SYSTEM).

GUT: the alimentary tract, from mouth to cloaca (see ALIMENTARY SYSTEM).

GYMNORHINAL: see NARIS.

GYNANDROMORPHISM: see PLUMAGE, ABNORMAL.

GYPAETINAE: see VULTURE (1).

GYRFALCON: *Falco rusticolus* (see FALCON).

H

HABITAT: the particular environment inhabited by a particular living organism. The environment thus described comprises the whole complex of flora, fauna, soil and climatic factors to which the organism is adapted.

The term has been extended to cover the particular environment inhabited by a community of organisms. When it is used like this, the emphasis moves from the relationship with an organism to the biological nature of an area, and hence the term becomes virtually synonymous with BIOTOPE. The meaning of the word 'habitat' is further confused because at one time it could also mean the geographical distribution or range of a species.

The habitat of a bird species can only be determined by field studies in which the full range of opportunities and constraints in nature is related to the adaptive characteristics of the bird. Much is known about the general requirements of different species and their general adaptations, but very little about the exact constraints, and so it is not yet possible to describe the habitat requirements of most birds definitively. For example, the distribution of many species can be fitted to isotherms, but it is not usually known whether temperature is operating directly or through food supply or some other component of the environment. In some cases limited food or nesting site requirements clearly limit the species' habitat. For example, the Snail or the Everglades Kite *Rostrhamus sociabilis* is restricted by the distribution of the freshwater Apple Snail *Pomacea* on which it is almost entirely dependent for food. The Golden-shouldered Parrot *Psephotus chrysopterygius* is dependent for nesting on the large termite mounds found in parts of the Cape York Peninsula of Australia. Nest sanitation of this species depends upon its symbiotic relationship with larvae of the moth *Neossiosynoeca scatophaga*. The timing of nesting of a particular bird species may indicate its dependence on a particular food species, for example, the nesting of the White-cheeked Honeyeater *Phylidonyris niger* coincides with the peak flowering of *Banksia ericifolia*, the beak of the Honeyeater being adapted to obtain the nectar from the Banksia flowers. In general the more specialized species are found in stable tropical habitats (see ECOLOGY). At the other extreme, highly adaptable opportunist species (the 'r' species) such as House Sparrows *Passer domesticus* and Starlings *Sturnus vulgaris* can live in numerous kinds of biotopes throughout the world. Most species appear to be intermediate in their habitat requirements: they are confined to major botanical formations, e.g. temperate broad-leaved woodland, but not restricted by the distribution of particular plant or animal species.

In some birds the breeding habitat is very different from the wintering one. For example, in Europe the Chiffchaff *Phylloscopus collybita* breeds in light broadleaved woodland and coniferous forests but winters in dry savanna in Northern Africa. The Little Auk *Plautus alle* breeds on Arctic sea cliffs and mountains, but is largely pelagic in winter, and the Black Tern *Chlidonias niger* breeds in freshwater marshes and lagoons but spends the winter on tropical sea coasts.

In some species the habitat differs in different parts of its range. For example in Britain the Dartford Warbler *Sylvia undata* is confined to areas dominated by tall heather *Calluna*, thick gorse *Ulex* or mixtures of the two, but in North Spain it also occurs in open pinewoods.

Sudden changes in habitat requirements have been observed from time to time. These have enabled the species concerned to enlarge its range, as when the Little Ringed Plover *Charadrius dubius*, whose principal original habitat was sand banks in large rivers, extended its range by colonizing gravel pits.

The habitats of birds (and mammals) tend to be much wider than those of insects. This reflects their more catholic feeding habits and more plastic behaviour. Structure of habitat is usually more important to birds than the plant species which form it. Therefore it is possible to devise quite simple classifications of bird habitats, for example that of J.F. Reynolds, which has 16 basic categories consisting of easily identified structural types of vegetation (e.g. grassland, bushed grassland, wooded grassland etc.).

The relatively simple habitat requirements of birds have an important bearing on their conservation. It is possible to create suitable habitats for many species of birds simply by digging ponds, flooding fields or planting trees and bushes, whereas many plant and invertebrate species, with their more exacting requirements, are unable to colonize these places for many years and so can only be conserved by retaining their existing habitats.

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HACK: term used in FALCONRY.

HACKLE: a long slender feather on the neck; such feathers are found, especially, in various species of Galliformes.

HADADA: *Hagedashia hagedash* (see IBIS).

HAEMATOPODIDAE: see under CHARADRIIFORMES; OYSTERCATCHER.

HAEMOGLOBIN: see BLOOD.

HAGGARD: term for a hawk caught as an adult and trained (one caught as full-grown but in its first plumage is a 'passage hawk')—see FALCONRY.

HALCYON: poetic name for KINGFISHER.

HALLUX: the first toe, usually 'opposed' (i.e. directed backwards) in birds and often much reduced (sometimes absent)—see LEG; SKELETON, POST-CRANIAL.

HAMERKOP: name, alternatively 'Hammer-headed Stork' or 'Anvilhead', of *Scopus umbretta*, sole genus and species of the Scopidae (Ciconiiformes, suborder Ciconiae). In the past a relationship to the Charadriiformes has been proposed for *Scopus* as it shares with them 2 genera of Mallophaga and only one with the Ciconiidae, but its egg-white protein suggests it may be related to the storks. However, Kahl (1967) found its behaviour quite different from either the storks or herons and concluded that it has no 'particularly close relationship with any other living bird so far studied'.

Many legends are centred about the bird and they receive some protection from the taboos that have developed. One common native legend is that other birds bring nesting material to their remarkably structured nest (see below).

Characteristics. The Hamerkop is a rather heavy-looking bird (*c.* 56 cm long), with short legs, a moderately long bill that is laterally compressed and slightly hooked, and rather long wings and tail. The conspicuous feature is a long backward-pointing crest which, together with its bill, produces an anvil shaped head from which it gets its common names. The plumage, which is the same for both sexes, is dark chocolate-brown, and the bill and legs are black, giving it a sombre appearance. Powder-down patches are lacking, but the middle toe is pectinated as in herons, and the 3 forward toes are connected by a partial web. Hamerkops are very agile fliers and their relatively large, rounded wings give them an owl-like shape when in flight. During normal flapping flight the head is only partially retracted on the shoulders but, when soaring or gliding, both less frequent than in storks, it usually extends its neck fully.

Habitat and distribution. It is found throughout the Afrotropical region and its range extends also to Madagascar and south-western Arabia. The birds inhabiting the coast of West Africa belong to a dwarf race. Hamerkops may be found in a wide variety of wetlands including estuaries, mangrove creeks, swamps, rice fields and ponds provided these are bordered generously with trees and/or cliffs. Because of taboos the birds are often tame and found in villages.

Food. A variety of small fish, shrimps and insects may be taken, but the principal food is frogs of the genus *Xenopus* and their tadpoles, which also form a major part of the nestling diet. When foraging, the bird usually walks along the edge of a pool or stream or wades in shallow water. In muddy water the Hamerkop probes repeatedly for prey, whereas in clear water the prey are snatched from the water surface. In both cases, it uses its feet to disturb prey from the substrate. Hamerkops pick tadpoles from off the surface by flapping low over the water and flying at low speed into the wind with very deep wing strokes.

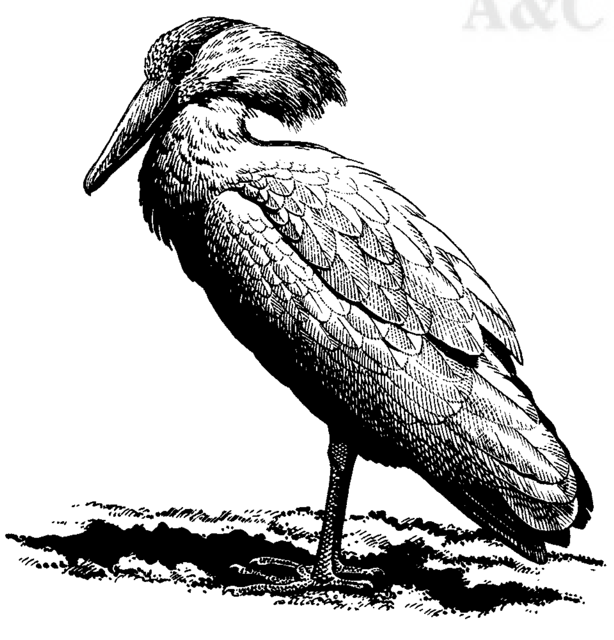
Behaviour. Social gatherings, sometimes involving up to 20 birds, are common away from nesting areas; the most demonstrative displays take place in groups when they feed. Several displays have been described by Kahl (1967), one of the more bizarre being the false mounting display. This may occur outside the breeding season and consists of one bird jumping on to the back of another as if intending to copulate, and standing there while beating its wings and giving a specific series of calls. Either sex may assume the top position and often the birds may alternate positions a number of times. This behaviour often occurs between mates but is not confined to mated pairs, and may occur on a tree, on the ground or on top of a nest. There are some preliminary displays that precede the false-mounting display and also precede true copulation. Paired birds indulge in a wing-flapping and bowing display while uttering braying calls. Hamerkops are apparently monogamous and birds may remain paired for several years, but co-operative nest building has been observed (Gentis 1976).

Although active during the day, Hamerkops become more active at dusk and are semi-nocturnal in their habits. They often use the backs of hippopotamuses as perches.

Voice. When 3 or more birds are together they generally join in mutual calling displays; the calls start with a series of loud, high pitched *yips*, becoming more rapid until they run together into a trilling note. These notes also accompany the false-mounting and other displays. Sometimes when a pair is flying together the birds keep in mutual contact by means of a few soft *kep* notes.

Breeding. The Hamerkop, a non-colonial nester, builds a remarkable enclosed nest of sticks, grass and mud placed 5–12 m up in the fork of a tree (often over water) or, less commonly, on the ground or on a cliff face. It may take a few months to build and measures about 1 m in diameter. Inside is a carefully shaped internal chamber, which is about 30–50 cm in diameter and height. The entrance tunnel (*c.* 13–18 cm in diameter and *c.* 40–60 cm long) is heavily plastered with mud to give it a smooth surface.

The 3–6 eggs are chalky white; the incubation period is about 21 days, and the nidicolous young, fed by both parents, spend about 7 weeks in the nest before fledging. The initial plumage of the young is brown apart from white on the head, neck, back and wings, but by the time they leave the nest they are brown all over. W.R.S. and L.G.G.



Hamerkop *Scopus umbretta*. (*R.G.*).

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HAMMERHEAD: see HAMERKOP.

HAMULUS: a hooked barbicel (see FEATHER).

HANDBOOK: see regional articles.

HANDEDNESS: see FOOTEDNESS.

HANDSAW: see HERNSHAW.

HANGNEST: name sometimes applied, in North America, to *Icterus* spp. (for family see ORIOLE (2)).

HAPLOOPHONAE: see under PASSERIFORMES.

HARDY–WEINBERG LAW: a law of population genetics, established in 1908 by G.H. Hardy and W. Weinberg, which relates mathematically the frequency of alleles in a population at a particular genetic locus to the frequency of genotypes at that locus. In its simplest form the law states that if at a particular locus there are 2 alleles A and A^1, and if the frequency of $A = p$ and the frequency of $A^1 = q$ (such that $p + q = 1$), then the frequency of the 3 genotypes AA, AA^1 and A^1A^1 will be $p^2 : 2pq : q^2$. This is the binomial expansion of the expression $(p + q)^2$. Thus if a population is in Hardy–Weinberg equilibrium, it means that there is a predictable and defined ratio between the 3 genotypes. The law is only true if a number of stringent conditions apply. These are (1) that the population must be large enough for sampling errors to be ignored, (2) that there is no mutation, migration or differential selection, and (3) that mating among individuals of the different genotypes be random. The law is valuable to population biologists in two ways. Firstly, if a polymorphism is suspected to have a genetic basis, then it defines the expected relative frequencies of the distinct phenotypes. For instance, if it is suspected that the 3 morphs of the Arctic Skua *Stercorarius parasiticus*, dark, intermediate and light, are determined respectively by 3 genotypes AA, AA^1 and A^1A^1, then at equilibrium the 3 morphs will occur in a predictable ratio dependent only upon the frequencies of the 2 alleles A and A^1. If as an example 36% of the population (p^2) were dark, 48% (2 pq) should be intermediate and 16% (q^2) light. The law is also useful when the genetic basis for the polymorphism is already known. If then the genotypes are not in the predicted frequencies, it may be suspected that one or more of the conditions stated above are not holding. Deviations from the Hardy–Weinberg equilibrium have been used as a crude first indication that selection is occurring or that a population is not mating at random (see also GENETICS.) F.C.

HAREM POLYGAMY: see POLYGAMY.

HARLEQUIN: sometimes used by itself for the Harlequin Duck *Histrionicus histrionicus* (see DUCK).

HARPY: sometimes, at least formerly, used alone for the Harpy Eagle *Harpia harpyja* (see under HAWK). See also FABULOUS BIRDS.

HARRIER: substantive name of *Circus* spp.; in the plural, general term for the subfamily Circinae of the Accipitridae.

HARRIER EAGLE: substantive name, alternatively 'serpent eagle', of species of Circaetinae (Accipitridae); in the plural, general term for the subfamily (see HAWK).

HARRIER-HAWK (1): substantive name of species of Polyboroidinae (Accipitridae); in the plural, general term for the subfamily (see HAWK).

HARRIER-HAWK (2): sometimes used as the substantive name, alternatively 'forest falcon' (Brown and Amadon), of *Micrastur* spp.; in the plural, serves as a general term for the Herpetotherinae (see FALCON).

Whimbrel *Numenius phaeopus* chicks hatching. (*Photo: E.J. Hosking*).

HATCHING: emergence of the developed chick from the egg after incubation; the term is applied both to the egg and the chick, e.g. the eggs 'hatch', the young 'are hatched' or 'hatch out'. Eggs showing the first cracks in the shell are 'pipped', 'chipping' or 'starred'.

Hatching is prepared for by several synchronized processes. It often takes some hours, but may be reduced to about half an hour in small birds. The young bird has to change from breathing in the amniotic fluid to respiration in air, and it must break the hard eggshell by its own means. The time of hatching is fixed for each species by an innately determined series of events.

Some days before it breaks the shell, the embryo starts swallowing the amniotic liquid. The tissues, particularly the muscles, thus acquire a very high water content at birth, but this diminishes rapidly. The contents of the albumen-sac go the same way. The yolk-sac is driven into the body cavity by movements of the abdominal musculature. The new-born bird always has an internal yolk-sac, of which the mass varies from 25% of the birth weight in the Ostrich *Struthio camelus* to *c.* 5% in small passerines. The yolk mass vanishes rapidly in the first 6 days after hatching.

During incubation a constant water loss by evaporation produces an air chamber between the two shell-membranes (at the blunt pole of the egg). An aerated space is thus formed, into which the embryo penetrates. This moment marks the beginning of air respiration and is often announced by the cheeping of the baby bird, 2 or even 3 days before hatching. The blood supply of the allantois is still functioning and provides the necessary oxygen, the air-chamber being rich in carbon dioxide and insufficient for the needs of the young bird.

Very soon partial respiration by the lungs is started, the eggshell is opened, and the rapid drying up of the allantois begins. The vessels of the allantois are functional until the last moment before the navel is closed. At the moment of hatching the adult type of breathing is firmly established.

Immediately before the bill enters the air-chamber, the embryo changes from a transverse position into a longitudinal one, thus directing its bill towards the air space. This movement permits the use of a special tool for hatching, the egg-tooth on the tip of the maxilla. The formation of this structure, present in the great majority of birds, begins about the sixth day of incubation (domestic fowl, duck). It is horny, without any mineral substance. In some birds a corresponding thickening is produced also at the tip of the lower mandible.

The egg-tooth produces the first openings; stretching of the head and movements of the legs help to burst the shell. Sooner or later after hatching the shell-breaking tool is lost, in some groups, such as the penguins, not for some weeks.

No egg tooth is formed in the Ostrich and the megapodes, but it is not known whether this condition is primitive or secondary; the young of these birds are very far developed and strong enough to break the eggshell by movements alone. The shell is always weaker after incubation through the loss of mineral substances dissolved out of it, transported by the blood and used to prepare the first ossification of the skeleton.

The hatching of different eggs in a clutch may be almost synchronous or there may be a considerable interval between first and last. In many species the parents remove the fragments of eggshell from the nest; but those with nidifugous young tend to leave them *in situ*. See also BEHAVIOUR, DEVELOPMENT OF; DEVELOPMENT, EMBRYONIC; EGG; GROWTH; INCUBATION; PARENTAL CARE; YOUNG BIRD. See photo PARENTAL CARE. A.P. and W.S.

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HATCHLING: term sometimes applied to a newly hatched bird (see YOUNG BIRD).

HAWAIIAN HONEYCREEPER: substantive name for species of the family Drepanididae (Passeriformes, suborder Oscines). This family, treated by some as the subfamily Drepanidinae of the family Fringillidae, is endemic to the Hawaiian Archipelago including 63 ha Nihoa Island and Laysan Atoll in the North-western Hawaiian Islands. The recent discovery of the Poo-uli *Melamprosops phaeosoma* on Maui (Casey and Jacobi 1974) brings the total number of described species to 23. To this at least 15 recently discovered fossil species, as yet undescribed, must be added (Olson and James 1982). Geographic isolation within the archipelago has produced impressive variation—40 taxa are currently recognized.

Evolution, morphology and characteristics. The Hawaiian honeycreepers are supposed to have been derived recently from cardueline finches: *Telespyza c. cantans* on Laysan and *T. c. ultima* on Nihoa are most similar to the founder species (Raikow 1977). The subfamily is best known for its remarkable adaptive radiation. Bill shapes (Fig. 1) range from powerful seed-cracking cones (Grosbeak Finch *Psittirostra kona*) to attenuate, decurved probes 6.6 cm long, one third the bird's length (Kauai Akialoa *Hemignathus procerus*). Between these extremes are found bills shaped like those of parrots (Maui Parrotbill *Pseudonestor xanthophrys*) and warblers (*Loxops parva*, *Paroreomyza maculata*), and the unique bill of the Akiapolaau *Hemignathus wilsoni*, whose upper mandible, long and decurved, is nearly twice the length of the stout, straight lower mandible. Despite this diversity in bill structure, the Drepanididae have very similar appendicular myology, much like that of cardueline finches. The similarity of the tubular tongues of the nectarivores to New World 9-primaried oscines is due to convergence. Plumage colours include black, brown, white, green, yellow, red, and dazzling orange. Sexes are alike in colour in some species, unlike in others. Overall lengths

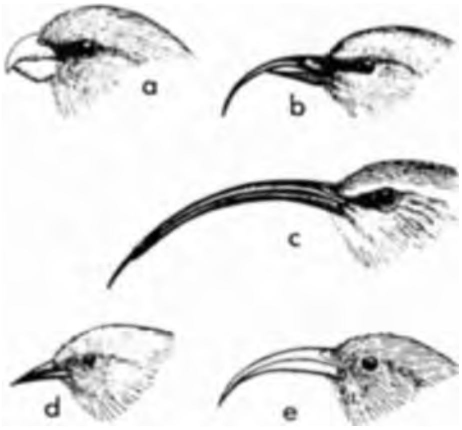

Fig. 1. Bills of some Hawaiian honeycreepers: (a) *Psittirostra bailleui*; (b) *Hemignathus wilsoni*; (c) *Hemignathus procerus*; (d) *Loxops coccinea*; (e) *Vestiaria coccinea*.

range from 10 cm (Anianiau *Loxops parva*) to nearly 20 cm (Greater Koa Finch *Psittirostra palmeri* and Hawaii Mamo *Drepanis pacifica*).

Habitat. The majority of the extant drepanidids are presently confined to wet (rainfall up to 1,164 cm per year) montane forests dominated by Ohia *Metrosideros collina* or Koa *Acacia koa*. On the island of Hawaii several species inhabit the much drier Mamane *Sophora chrysophylla*—Naio *Myoporum sandwichense* forests up to 3,000 m elevation. The family was formerly widespread in dry lowland forests, but these habitats, and their fauna, have been largely destroyed in the islands.

Food. The Hawaiian honeycreepers feed upon a diversity of foods. Some, like the Apapane *Himatione sanguinea*, Iiwi *Vestiaria coccinea*, and Crested Honeycreeper *Palmeria dolei* are primarily nectarivorous, while others feed upon fruit (Ou *Psittirostra psittacea*) or green seeds (Palila *Psittirostra bailleui*). Most species, however, are primarily insectivorous. The omnivorous Nihoa Finch includes seabird eggs in its varied diet. The Apapane and Iiwi undertake daily migrations, often of many kilometres, in search of patchily distributed but locally abundant Ohia flowers, their primary source of nectar. Perhaps as a result of this mobility, they are monomorphic in the main islands (one other widespread species, the Ou, is undifferentiated between islands), and the Apapane reached Laysan Island, about 1,125 km north-west of Kauai, where it was represented by a local race that is now, unfortunately, extinct.

Voice. Song is highly variable within the family, ranging from disconnected squeaky notes to melodic trills. The Apapane sings a bewildering variety of songs that vary within, and between, islands.

Breeding. The breeding season extends from February to June for most species. Chasing is an important part of courtship, and often directly precedes copulation. Nests of only half the family have been described (Scott *et al* 1980). Most are open cups composed of twigs and lined with fine materials, such as mosses, tree fern scales, and other fibres (Berger 1972). They are generally placed within the canopy and are well hidden within terminal leaf clusters. Clutch size ranges from 1–4 eggs; 2 or 3 is the usual complement. Normally only the female incubates; she is fed away from the nest by the male. Nests of 3 species have been found in tree cavities; 2 species are known to use rock cavities, the Nihoa Finch preferentially so. The Laysan Finch nests in grass tussocks.

Current status. It is tragic that of 40 described taxa, 16 are recently extinct and an additional 17 endangered. Their demise has resulted from a number of interrelated stresses that began with the first Polynesian settlement. Habitats have been vastly altered by man, and introduced mammals, notably pigs, goats, cattle, sheep, and Axis Deer *Axis axis* have devastated additional thousands of hectares. The Hawaiian honeycreepers proved highly susceptible to introduced diseases, especially avian malaria and pox, which were transmitted to them by an introduced mosquito *Culex quinquefasciatus* (Warner 1968). Predation by cats and rats may have also been important (Atkinson 1977), and competition with introduced forest birds, many now quite common, may have produced additional stress. Many of these factors remain uncontrolled, and more species may be lost unless vigorous corrective action is taken. A programme that successfully eradicated feral sheep from Mauna Kea in 1982 should help restore the essential habitat of the Palila. Similar programmes in prime rain-forest sites throughout the state could do much to improve the outlook for these fascinating birds. C.B.K.

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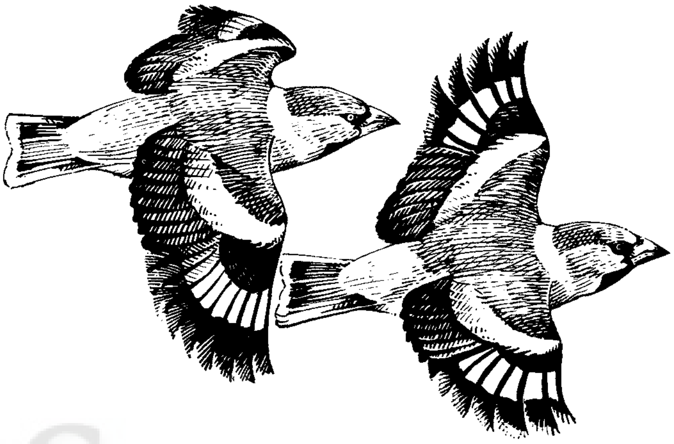
HAWAIIAN ISLANDS: a mid-oceanic archipelago having an avifauna largely related to the Nearctic Region but with elements of Australasian affinities (see AUSTRALASIAN REGION; DISTRIBUTION, GEOGRAPHICAL; HAWAIIAN HONEYCREEPER).

Peterson, R.T. 1961. A Field Guide to Western Birds. 2nd ed. Boston, Mass.

HAWFINCH: substantive name of *Coccothraustes coccothraustes* and of *Eophona* spp.; used without qualification for the first mentioned (see FINCH).



Hawfinch *Coccothraustes coccothraustes*. (*D.A.T.*).

HAWK: substantive name, or part of the substantive name, of many members of the Accipitridae (Accipitriformes, suborder Accipitres)—in North America the name is given to species of Accipitridae that in British usage have special substantive names (e.g. 'buzzard', 'harrier'), and is even applied to some species of Falconidae (see FALCON); in the plural, general term for the Accipitridae, the subject of this article except that the several genera of Old World vultures are separately treated (see VULTURE (1)). Apart from the vultures, the family is often divided into subfamilies: the Accipitrinae (true hawks, including accipiters, buzzards, and eagles), Circaetinae (harrier eagles or serpent eagles), Circinae (harriers), Polyboroidinae (harrier-hawks in one sense), Milvinae (true kites and fish eagles), Perninae (honey-buzzard etc.), Elaninae (white-tailed kites), and the monotypic Machaerhamphinae (Bat-hawk). For convenience this grouping is followed here, but K.H. Voous regards all but one of these suggested subfamilies as united in a single group constituting the Accipitridae; and the monotypic Pandionidae as a separate family.

Characteristics. The birds in this large and varied assemblage range from small sparrowhawks *Accipiter* spp. to huge and powerful eagles, those of the genera *Harpia*, *Pithecophaga*, and *Haliaeetus* being among the largest and strongest birds of prey in the world and among the largest of flying birds. Several of these large eagles exceed 6 kg in weight, 1 m in body length and 2 m in wingspan. In almost all birds-of-prey the female of the species is larger than the male; she is often duller and browner in colour, and immature birds may be quite different in appearance from the adults. The degree of size dimorphism between the sexes is correlated with feeding habits, as species which specialize on snails, insects, reptiles, mammals or birds respectively show progressively greater dimorphism (Newton 1979). In some extreme bird-feeders, such as the European Sparrowhawk *Accipiter nisus*, the female weighs almost twice as much as the male.

The family has the characteristics of the order, of which the most obvious are the decurved and pointed bill, with base covered by a cere in which the external nares are situated, and the powerful gripping feet with strong sharp claws. Leaving aside the carrion-eating Old World vultures, they are—with some exceptions—hunters of live prey; the latter ranges from birds in flight to fish, and from sizeable mammals to insects. Unlike many of the owls, which have similar adaptations of bill and foot by convergence, they are diurnal in their habits—occasionally crepuscular (*Machaerhamphus*).

Habitat and distribution. The Accipitridae are represented on all continents except Antarctica and in all kinds of habitat from thick forest to open grassland and desert. As expected of predators, these birds live at relatively low densities, and mostly in individual territories or home ranges, which include feeding areas. Under natural conditions, small species occur at densities up to about 1 pair/km^2, but larger ones are very much sparser. The large African Martial Eagle *Polemaetus bellicosus* occurs at one pair per 125–300 km^2, with 30–40 km between pairs, and is thus one of the most thinly-spread birds in the world. However, in 'developed' regions, most species have been much reduced in numbers by human activities, especially habitat destruction, direct persecution and pesticide use. In consequence, many species which were numerous a century ago are now quite scarce, and some are among the most endangered of all birds.

Where undisturbed, some species show extreme stability in breeding population, with the numbers over large areas changing by no more than 10% of the mean over long periods of years (e.g. Golden Eagle *Aquila chrysaetos*). Such species usually feed on a wide spectrum of prey species, and thus have fairly stable food-supplies. Other species, which have restricted diets based on cyclic prey, fluctuate greatly in numbers from year to year, depending on their prey (e.g. Rough-legged Buzzard *Buteo lagopus* which feeds on lemmings and other rodents).

Movements. From northern regions many species migrate south for the winter. The broad-winged types, such as buzzards and eagles, travel by soaring and gliding, and are thus dependent on updraughts or thermals. They form narrow migration streams along routes where conditions are favourable, such as north to south mountain chains or narrow sea crossings. In Europe, many thousands of individuals en route to Africa circumvent the Mediterranean each year via the Straits of Gibraltar in the west and the Bosphorus or Dardanelles in the east. In North America similar concentrations occur along mountain ranges, of which the most famous for observation is Hawk Mountain in Pennsylvania.

Voice. Different species of the Accipitridae have screaming, yelping, mewing or cackling cries, which are heard mainly in the breeding season. Such vocalization is used primarily for communication between the sexes, but also in some species for territorial advertisement. Many call loudly when the nest area is invaded by a human or other predator.

Behaviour and breeding. These raptors have mainly aerial displays, involving soaring over the nesting area, diving or undulating flights, which probably serve to advertise possession of the territory. Other displays, early in the breeding cycle, are centred on nest-sites. Most species breed in trees, either making their own nests or sometimes adopting the nests of others; some eagles and buzzards breed on crags. The nests are built of sticks and are often lined with green leaves, sometimes with grass, rags, and oddments. The larger species build huge structures to which they return year after year. The main trends in breeding within the group are related to body-size. The larger the species: (1) the later the age at which breeding begins, (2) the longer each successful attempt takes, and (3) the fewer the young produced with each attempt (Newton 1979). Small clutches of 1–2 eggs are typical of large eagles, but the smaller species may lay 3–5 or even more. Incubation times vary from about 28 days in small sparrowhawks to 49 days in large eagles, and fledging periods from 28 days to 120 days. After leaving the nest, the young continue to be fed by their parents for another 21 days in small accipiters to several months in large eagles. In one or two eagle species, breeding cycles may be so long as to prevent breeding in successive years: the largest species are long-lived, slow-breeding birds.

While breeding, there is a clear division of labour between the sexes, the male providing the food and the female incubating the eggs and tending the young. Only when the young are large enough to be left does the female help with the hunting. The young themselves could be described as 'semi-precocial' in that they hatch with a full covering of down and with their eyes open, in contrast to most other nidicolous birds. Initially the mother tears up small pieces of meat for them, which they take from her bill, but before fledging they learn to tear up prey for themselves.

True hawks and eagles. The Accipitrinae are the largest and most varied subfamily, containing most of the world's hawks (in the strict sense), buzzards, and eagles. They may conveniently be divided into several smaller groupings. First, the genera *Accipiter, Melierax*, and *Urotriorchis* are small to medium-sized hawks of swift flight, generally inhabiting woodlands or forests, and preying upon birds, small mammals, and reptiles. Of these only *Accipiter* occurs in the New World, while the others (*Urotriorchis* being monotypic) are confined to the Ethiopian Region. Three other genera, to be mentioned later, also belong to this group.

The genus *Accipiter* contains the true sparrowhawks and is the largest of all the genera of the birds-of-prey, cosmopolitan in distribution, and with representative members in any woodland ecotype, from the pine forests of the far north to the most luxuriant tropical rain-forests and the thorn-scrub of Africa. All are broad-winged, long-tailed hawks, with rather long thin legs; they fly from tree to tree in the forest, and when hunting adopt methods of stealthy approach behind cover, culminating in a short, fast attack. Few of them can fly down birds in the open, but they are adept at catching them in thick vegetation. The largest member of the genus, the Goshawk *Accipiter gentilis*, is about 48–62 cm long, grey above and white barred grey below, with a fierce yellow eye; it has been trained for falconry, as have several others of the genus, and is capable of killing birds as large as a Pheasant *Phasianus colchicus* and mammals up to the size of a hare (see FALCONRY). At the other extreme is the tiny African Little Sparrowhawk *Accipiter minullus*, about the size of a thrush, and living to a considerable extent on insects; these it catches in a short sortie after the manner of a flycatcher (Muscicapinae). Between these two extremes are hawks of every intermediate size, but all bold and aggressive, all inhabiting woodlands, and all living mainly on birds, with mammals and reptiles as side-lines. Close to the genus *Accipiter* is *Melierax* (including '*Micronisus*'); these are birds of the open African thorn-bush, grey above, with white undersides barred with grey. The two chanting goshawks *Melierax* spp. are large birds (length 35–50 cm) capable of killing guineafowl, but living chiefly on insects and lizards, which they often catch on the ground, running about like small editions of the Secretary-bird *Sagittarius serpentarius*. The Gabar Goshawk *Melierax gabar* is like a sparrowhawk in its habits. Finally there are the Long-tailed Hawk *Urotriorchis macrourus*, a strange dark-coloured hawk, black above with chestnut below and a long tail ornamented with white dots, which inhabits dense forests in West Africa and lives chiefly on arboreal squirrels and birds; 2 Australasian genera, *Erythrotriorchis* and *Megatriorchis*, of large and powerful hawks; and the Lizard Buzzard *Kaupifalco monogrammicus*, which preys chiefly on lizards and is found in east and southern Africa.

The next subdivision of the Accipitrinae comprises large hawks with soaring flight, inhabiting woodlands or open country, and preying upon mammals and reptiles caught on the ground, with birds forming a minor part of the diet. The genus *Buteo* (including '*Rupornis*' and '*Asturina*'), containing the true buzzards, is the largest of this group, and is cosmopolitan in distribution save for Australasia and Malaysia. The genera *Heterospizias, Leucopternis, Parabuteo, Buteogallus*, and *Busarellus* are confined to Central and South America, and *Butastur* to Africa, India, and the East. *Butastur* spp. (e.g. the Grasshopper Buzzard *B. rufipennis* of Africa) are the least like buzzards of the whole group, having more the habits of harriers (Circinae). All these birds are large, with a body length of 50–65 cm, and a wing-spread of 1–1.5 m. They all can soar, but they perch a great deal on trees, telegraph posts, or rocks, and catch their prey on the ground. Some frequent lowland swamps, others mountainous country; the Augur Buzzard *Buteo rufofuscus* occurs in Africa up to 5,500 m, and the Mexican Black Hawk *Buteogallus anthracinus* is found in swampy areas or tropical forest regions at low altitudes. They are mainly brown in colour when immature, but as adults often develop handsome plumages of brown, white, and red-brown, or black and white. Females are generally only slightly larger than males. Some are migratory, e.g. the Rough-legged Buzzard *Buteo lagopus*, which is also one of the few members of the group with the tarsus feathered to the toes. Others remain in their haunts all the year round, the tendency being for those that live in the far north to migrate, while most tropical and subtropical species do not.

The third subdivision of the Accipitrinae consists of large or very large birds-of-prey, with wing-spread of up to 2.5 m and weight of 1–7 kg, generally called eagles. They include the following American genera: *Harpyhaliaetus, Spizastur, Oroaetus, Morphnus*, and *Harpia*. *Stephanoaetus* and *Polemaetus* inhabit Africa, and *Ictinaetus, Harpyopsis*, and *Pithecophaga* occur only in India and the Far East. The genera *Aquila, Spizaetus*, and *Hieraaetus* are of wider distribution. *Aquila* in particular is found in all regions of the world except South America and the Malaysian area, being represented in Australia by *Aquila audax*. All these birds are both large and aggressive, preying on large and small mammals, birds, and reptiles. Some eagles, especially *Aquila* spp., eat carrion; the Tawny Eagle *A. rapax* (length 65–77 cm) pursues and robs other raptors of their prey. Although some are hardly bigger than buzzards, they are in general fiercer and more active than the birds of that group. They vary in size from small, active hawk-eagles of the genera *Spizaetus* and *Hieraaetus* to huge and powerful birds-of-prey (*Stephanoaetus, Polemaetus, Aquila, Harpyopsis, Pithecophaga,* and *Harpia*). *Aquila, Spizaetus, Spizastur, Hieraaetus, Stephanoaetus, Polemaetus, Oroaetus,* and *Ictinaetus* have feathered tarsi, the rest bare tarsi. The largest and most powerful of all is the Harpy Eagle *Harpia harpyja*, inhabiting tropical South America; and scarcely smaller is the Philippine Monkey-eating Eagle *Pithecophaga jefferyi*, which has unusual blue eyes. The smaller members of the group include Ayres' Hawk-eagle *Hieraaetus ayresi*, a rare bird of Africa which is like a sparrowhawk in its habits, living on birds of the tree-tops, and the very handsome *Hieraaetus kieneri* of India. Those that live in open country (*Aquila, Polemaetus*) tend to live principally on mammals and gallinaceous birds, caught upon the ground but often seized in spectacular fashion. All these birds are capable of beautiful soaring flight, and some of them are probably as fast as or, faster than, any other birds-of-prey, although they may appear, by reason of their large size, to move more slowly than some falcons. Their plumage varies from dull brown (*Aquila*) through various patterns of grey and white and black and white to very rich and beautiful combinations of black, buff, chestnut, and white (*Stephanoaetus* and *Spizaetus ornatus*). Two, Verreaux's Eagle *Aquila verreauxi* and the Black Eagle *Ictinaetus malayensis*, are mainly black, with white on the rump; the former lives almost entirely on hyraxes *Procavia* and *Dendrohyrax*; the latter species has the peculiar habit of feeding upon the eggs of other birds, taken in the nest.

Snake eagles. The snake eagles, serpent eagles and harrier eagles are sometimes placed in a subfamily Circaetinae; they live principally on snakes and other reptiles and have feet specially adapted, with short rough toes of immense power, for grasping and holding this prey. *Circaetus, Terathopius,* and *Dryotriorchis* are African genera, the latter two monotypic and the first with one of its species, the Short-toed Eagle *C. gallicus* (length 62–68 cm) extending over the warmer parts of Europe, Asia, and Africa. The crested serpent eagles *Spilornis* spp. occur from India to the Philippines, and *Eutriorchis astur* inhabits Madagascar. The habits of these birds in the field are much like those of other large eagles. They are given to soaring for long periods, or to perching on outstanding trees and rocks whence they can see their prey; the Short-toed Eagle can hover like a Kestrel *Falco tinnunculus*, although relatively large (see FALCON). They drop on their prey and either snatch it in the air or kill it on the ground. When eating snakes, they crush the head first, afterwards swallowing the rest of the body whole. They inhabit open country, forests, and bushland. The most remarkable of the whole group is the Bateleur *Terathopius ecaudatus* (length 80–85 cm) of Africa, which has exceptionally long wings (wing span 170–180 cm) and a very short tail (8–10 cm). Birds of this species fly perhaps 300 km on most days of their lives, canting from side to side and occasionally performing astonishing aerobatics. They eat carrion and mammals as well as reptiles, and will pursue and attack other carrion birds in the hope of making them disgorge. The Serpent Eagle *Dryotriorchis spectabilis* of West Africa is a strange bird of dense tropical forests and has large eyes that perhaps help it to see in poor light.

Harriers. The subfamily Circinae, cosmopolitan in distribution, contains the harriers *Circus* spp., a very characteristic genus inhabiting open country, cultivations, or swampy land. They are either mainly brown in colour or, in some species, the males are grey and the females and juveniles brown; two species, *Circus maurus* of South Africa and *C. melanoleucus* breeding in north-eastern Asia, are black and white. All harriers are slender, long-winged, long-tailed birds with long legs, and rather owlish heads, ranging between 40–56 cm in body length. They spend most of the day on the wing but also perch on posts and hillocks. Their habits are similar all over the world: they fly low over the ground, systematically quartering to and fro, and dropping on prey in the grass. Unlike most birds-of-prey, they both roost and breed on the ground; and the male, when bringing prey, characteristically passes it to the female in flight, a little way from the nest. One species, the Spotted Harrier *C. assimilis* of Australia, nests in trees. Some of the species are migratory, the Palearctic Pallid Harrier *C. macrourus* being one of the commonest birds-of-prey in the plains of Africa and India in winter. On migration they tend to be gregarious, and they roost in company in 'forms' in the grass (Pallid Harrier and Marsh Harrier *C. aeruginosus*). Some tend to concentrate in swampy localities and others in dry open plains or steppe, but they never frequent woodland country for long. They live on small mammals, frogs, and some insects and reptiles, but occasionally also take birds on the ground.

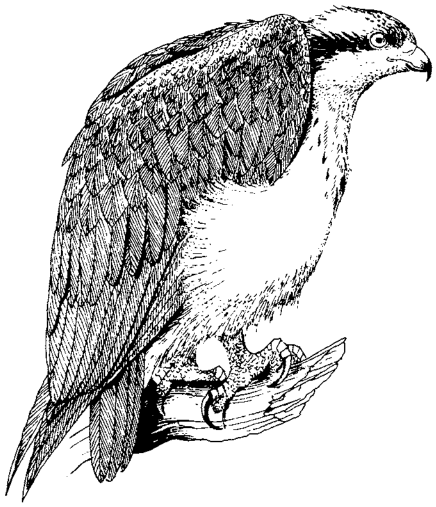
Harrier-hawks. The subfamily Polyboroidinae contains the harrier-hawks, curious long-tailed, long-legged birds the size of a buzzard, grey and black in plumage with yellow legs and bare skin on the face; they inhabit Africa and Madagascar, usually in wooded country. The South American genus *Geranospiza* is probably closely related. The African continental species is the Harrier-hawk *Polyboroides typicus*. They are unable to kill any large prey, and have buoyant, rather erratic flight. They feed largely on the young of other birds, and in attacking weaver-bird (Ploceidae) broods, they often hang head downwards with flapping wings. The double-jointedness of their legs enables them more easily to extract nestlings from tree-holes and other enclosed nests. They are also fond of the fruits of the Oil Palm *Elaeis guineensis*. The term 'harrier-hawks' is also applied to certain Neotropical Falconidae (see FALCON).

True kites and fish eagles. The Milvinae are a large and varied subfamily of cosmopolitan distribution, containing the genera *Milvus, Lophoictinia, Hamirostra, Haliaeetus, Ichthyophaga, Haliastur, Rostrhamus, Harpagus,* and *Ictinia*. The Black Kite *Milvus migrans* (length 55–60 cm), in its many races, is one of the commonest and most obvious birds-of-prey in the warmer parts of the Old World, scavenging in hundreds in towns and villages of the East. It is migratory throughout its range to a greater or lesser extent, and decidedly gregarious on migration. However, it was apparently the Red Kite *M. milvus* (length 60–66 cm) that was formerly a common scavenger in London.

Haliaeetus and *Ichthyophaga* are 2 genera of large or very large birds-of-prey living mostly on fish. *Haliaeetus*, comprising the fish eagles and sea eagles, is nearly cosmopolitan in distribution and contains some of the largest and finest of all birds-of-prey, among them the European Sea Eagle *H. albicilla* (length 70–90 cm), the American Bald Eagle *H. leucocephalus* (length 70–90 cm), Steller's Sea Eagle *H. pelagicus* (length 80–100 cm) of north-eastern Asia and the Fish Eagle *Haliaeetus vocifer* (length 74–84 cm) of tropical Africa. The smaller fishing eagles *Ichthyophaga* spp. inhabit inland lakes, rivers, and ponds in southern Asia and live on fish amongst other food. *Haliastur* is a genus of 2 species, inhabiting India, the Far East, and Australia, and in places very common; the Brahminy Kite *H. indus*, regarded as sacred in India, inhabits swampy areas, and lives on frogs and offal.

The American genera *Rostrhamus, Harpagus,* and *Ictinia* are rather unlike the Old World kites in their general habits, and their members are considerably smaller. The Snail or Everglade Kite *R. sociabilis* breeds in colonies and feeds exclusively on snails, which it extracts from the shell with the long point of its upper mandible. *Rostrhamus hamatus* also has a remarkably long and sickle-shaped bill. The genus *Ictinia* contains small grey kites, in appearance very unlike the typical *Milvus* spp. of Europe and Asia; they live in open country, feed largely on insects, spend a great deal of time on the wing, and are capable of remarkable aerial evolutions; they are migratory and tend to be gregarious on migration.

Honey-buzzards. The subfamily Perninae contains a variety of genera difficult to relate to others—*Leptodon, Chondrohierax,* and *Elanoides* in America, *Pernis* and *Aviceda* in Europe, Asia, and Africa, and *Henicopernis* in New Guinea and nearby islands. The Honey-buzzard *Pernis apivorus* (length 52–60 cm) of Europe and Asia is a medium-sized buzzard-like bird which feeds chiefly on the grubs in bees' and wasps' nests. It is a migrant, moving south from Europe in numbers to Africa, and from northern Asia to India and farther east. The Swallow-tailed Kite *Elanoides forficatus* of America (not to be confused with the African bird of the same English name, mentioned below) is a very beautiful bird, with black back, tail, and wings, the rest of the plumage being white; it has remarkable powers of flight, and on account of its beauty has been much persecuted. The so-called cuckoo-falcons *Aviceda* spp. are widespread in Africa, India, and the Far East, one reaching Australia. Superficially rather like sparrowhawks, but distinguished by having two notches on the upper mandible, they are crested and generally conspicuously patterned in plumage; the Black Baza *A. leuphotes* of north-eastern India and Malaysia is a very striking black-and-white bird, while other members of the genus are grey or brown above and often handsomely barred below. They are generally insectivorous, and in most parts of their range rather rare. They were formerly placed close to *Harpagus*, to which they have certain similarities.



Osprey *Pandion haliaetus*. (*K.J.W.*).

White-tailed kites. The Elaninae are a nearly cosmopolitan subfamily of small or very small birds-of-prey (length 30–35 cm), inhabiting open country. *Elanus* spp. occur in America and the warmer parts of Europe, southern Asia, Africa, and Australia; examples are the White-tailed Kite *E. leucurus* of America and the Black-shouldered Kite *E. caeruleus* widespread in the Old World. All members of the genus are small grey-and-white hawks, superficially like falcons, with black markings at the fore edge of the wing. They are attractive birds, perching constantly on telegraph posts or tall trees, dropping on insects and small mammals in the grass. They can hover very gracefully, like the Kestrel.

The other two members of the subfamily are very small and beautiful birds-of-prey in monotypic genera, the Pearl Kite *Gampsonyx swainsoni* of America and the Swallow-tailed Kite *Chelictinia riocourii* of northern tropical Africa. The Pearl Kite is one of the smallest birds-of-prey, and is blackish above, with rufous on head and back, and white below; it has well developed powder-down tracts. *Chelictinia* is an exquisitely graceful little bird with swallow-like forked tail, grey and white plumage, and a flight so buoyant that it resembles a tern rather than a bird-of-prey. It is gregarious, migratory, and breeds in small colonies, sometimes associated with larger birds-of-prey; it feeds on insects.

Bat-hawk. The subfamily Machaerhamphinae contains a single species, the Bat-hawk *Machaerhamphus alcinus*, which inhabits Africa and parts of the Far East and has the remarkable habit of catching bats as they emerge from caves or buildings at dusk; this prey is commonly swallowed in flight. In general appearance like a large falcon, the Bat-hawk has a wide gape and very large eyes adapted to its habits; it flies extremely swiftly, looking up, down, and sideways when hunting. It requires an open space such as a large pool in a river, a station platform, or an open lawn to be successful, and in addition to bats it eats swallows and martins (Hirundinidae); it spends the day in shady trees, and it is a rare bird, solitary in habit, throughout its range.

Osprey. The Pandionidae comprise only the Osprey *Pandion haliaetus* (length 55–58 cm) a bird of almost cosmopolitan distribution, absent only from South America as a breeding species but occurring even there on migration. It feeds exclusively on fish, catching them with a tremendous headlong dive in which it often completely submerges, throwing its feet forward at the last moment before entering the water so as to grasp the prey. The feet are specially adapted, with a spiny rough surface, for holding such prey. Where it is common it breeds in colonies, notably on the coasts of North America and on islands in the Red Sea. It is commoner on sea coasts but occurs also on inland lakes. It is frequently robbed of its prey by eagles of the genus *Haliaeetus*. In parts of the range it declined in the 1960s through pesticide poisoning.

See photos AGGRESSION; FLIGHT. (L.H.B.) I.N.

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HAWK-EAGLE: substantive name of species of *Spizaetus*, *Hieraaetus*, and allied genera (Accipitrinae)—see HAWK.

HAWKING: synonymous with FALCONRY; also used to describe the behaviour of a bird of any kind flying in search or pursuit of prey.

HEAD: see TOPOGRAPHY; also BILL.

HEADING: the direction in which a bird is flying through the air, as distinct (in a wind) from its 'track' relative to the earth's surface (see MIGRATION; TRACK).

HEARING AND BALANCE: senses here treated together because in both cases the sensory apparatus is in the ear.

Ear. As with other vertebrates, the ear may be functionally divided into outer, middle, and inner parts. The outer ear of birds usually includes specialized feathers covering the opening of a short auditory canal. An enlarged ear funnel has developed in some species, especially the owls, and in some instances these ear funnels are movable. The ear funnels in owls are asymmetrical, aiding in sound localizations. The ear canal in some diving birds can be closed by muscle contraction.

The middle ear cavity is composed of several cranial bones and this air filled cavity communicates with other air filled cavities of the skull. Thus, the middle ear cavities are not acoustically isolated from one another and sound impinging on the external surface of one typanic membrane is transmitted through the skull and affects the interior surface of the opposite tympanic membrane (Rosowski and Saunders 1980). This may provide a special mechanism by which birds with small heads can localize sounds in the frequency region of 1–8 kHz. Impedance matching from the tympanic membrane to the oval window is accomplished by the columella, extracolumellar cartilage, supporting ligaments, and middle ear muscle. The movements of the columella during sound stimulation are probably more complex than was earlier thought and may involve rotational forces.

The inner ear of birds is a short, slightly curved tube consisting of three fluid filled cavities similar to mammals. The receptor surface, the basilar papilla, was first thought to contain a homogeneous cell population (Retzius 1884). Now it appears that a complex scheme exists consisting of tall, intermediate, and short hair cells which also differ on the basis of shape, cuticular plate dimensions, and innervation. Efferent nerve fibres form extensive networks from which many branches are given off to the hair cells. The basilar papilla is shorter and wider than the mammalian basilar membrane. There are no rods or tunnels of Corti and thus no division between inner and outer hair cells. As many as 40 hair cells can be seen across the width of the basilar papilla and it appears that the cilia may be more firmly inserted into the tectorial membrane than is the case in the mammalian cochlea. The scala vestibuli is not well-developed in birds and there is some question whether the two perilymphatic canals communicate by means of a helicotrema, as is seen in mammals. The size of the helicotrema influences low frequency sensitivity in mammals and the lack of a similar structure in birds may provide a mechanism for enhanced sensitivity to low frequency sounds.

Hearing. Birds as a group hear best in the frequency rage of 1–5 kHz. Within this range, absolute sensitivity approaches the levels reported for man. Sensitivity declines dramatically for frequencies above this range and most birds show a high frequency hearing limit of about 10 kHz. Owls show slightly better high frequency sensitivity with a hearing limit around 12 kHz. Even those birds which are known to echolocate utilize signals in the frequency region of 2–8 kHz (Konishi and Knudsen 1979). Below 1 kHz sensitivity decreases gradually but there is evidence in some birds (Rock Dove *Columba livia*) of a special sensitivity to infra-sound. Since infra-sound travels great distances, it is hypothesized that sensitivity to these sounds may aid in navigation.

Discrimination of acoustic signals by birds is of considerable interest due to their use of complex vocal signals. Within the frequency region of 1–5 kHz, birds are almost as sensitive as man to changes in the frequency, duration, or intensity of simple pure tones (R. Dooling 1982). On more sophisticated measures of frequency resolving power such as masking, at least one species (Budgerigar *Melopsittacus undulatus*) consistently out-performs man. It may be that the auditory system is especially tuned to complex acoustic signals in this frequency region. On several measures of temporal resolving power, birds have shown levels of sensitivity similar to those reported for other mammals, suggesting that the bird ear may not be specialized for a high speed of response as once thought.

Sound localization abilities in owls and other avian predators are extremely well-developed both in azimuth and elevation (Knudsen 1980). The cues for sound localization in these species are interaural arrival time and interaural spectrum. For common bonds with unspecialized auditory systems both the cues and the mechanisms for sound localization are less clear. Behavioural studies indicate that birds localize high and low frequencies better than mid-range frequencies and broad band noise better than pure tones. The complexity of avian vocalizations probably provides a rich source of potential cues for sound localization and it is clear that birds can and do localize the sounds of conspecifics. But the existence of an interaural pathway in birds suggests that the mechanism for sound localization in birds is considerably different from that used by man and other mammals.

Balance. As with other vertebrates, the three semi-circular canals lie in nearly orthogonal planes and function to indicate the angular motion of the head. The receptors of the superior division of the labyrinth consist of the ampullary crests, utricular macula, and the papilla neglecta. The inferior division, in addition to the basilar papilla, consists of the saccular macula and the lagenar macula. No data are available on the function of this complex system but common observation of the flying skills of most birds would suggest a highly developed system with a short time constant. Differences in labyrinth structures across species do indeed show a correlation with flying ability. (R.J.P.) R.J.D.

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HEART: in its pericardial sac the heart occupies the cranial part of the thoracic cavity, its apex pointing caudoventrally. Its pulmonary surface (or base) lies below the lungs, trachea, and proventriculus. The dorsal ventricular portion of the heart lies against the liver. Nearly its entire ventral aspect rests on the body of the sternum.

Surface features (Fig. 1). The heart consists of cardiac muscle (myocardium) invested with the shiny layer of epicardium; its lining of endocardium is continuous with endothelium of vessels entering and leaving the heart. The grooves between the heart chambers are often obscured by subepicardial fat (Fig. 1A). The cone-shaped heart is truncated in some species, elongated in others. The wide cranial end of the heart is formed by the two atria and their ear-shaped appendages, the auricles. The pulmonary trunk and the ascending aorta intervene between the atria. The coronary sulcus separates atria and ventricles. The shallow ventral interventricular (I–V) sulcus extends obliquely between the short right ventricle and the longer left ventricle, and is continuous with the dorsal I–V sulcus of the hepatic surface of the heart.

Skeleton and musculature. The skeleton of the heart is composed of rings (annuli) of fibrous connective tissue that surround the atrioventricular (A–V) openings (ostia) and the openings of the aorta and pulmonary trunk. The annuli support the cusps of the valves of these ostia and prevent collapse of the ostia during valve closure. The annuli serve as origin and insertion of atrial and ventricular myocardium. The smooth-walled parts of the atria are thin; the thicker rib-like pectinate muscles of the auricles stand out in relief. Certain pectinate muscles coalesce into prominent median and transverse arches. The bundles of ventricular myocardium sweep spirally from the annuli toward the apex then back toward the bases of the ventricles. This arrangement causes the wringing of the ventricles during their contraction. Ventricular walls are much thicker than those of the atria.

Heart chambers. The adult heart of some birds (ratites) retains the foetal heart chamber, the sinus venosus. The three caval veins empty into

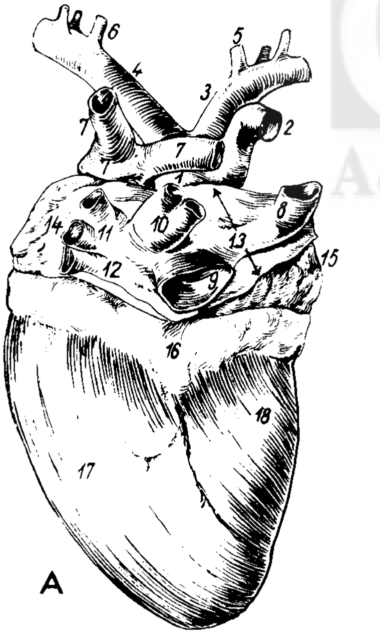
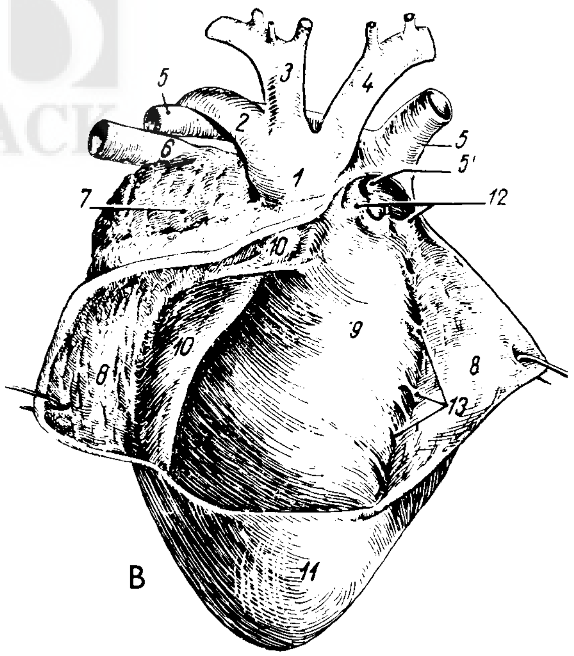


Fig. 1. Heart of the goose, *Anser*. (From Ghetie *et al* 1976).
(A) Dorsal aspect of heart and great vessels. Upper half of figure is the base or pulmonary surface. Note that the right cranial vena cava has a greater calibre than the left, reflecting the greater dimensions of the right jugular vein prevailing in most birds.
1 ascending aorta; 2 aortic arch; 3,4 brachiocephalic aa.; 5,6 common carotid aa.; 7 pulmonary trunk and aa.; 8 right cranial vena cava; 9 caudal vena cava; 10,11 pulmonary aa.; 12 left cranial vena cava; 13 right atrium; 14,15 left and right auricles; 16 coronary (atrioventricular) sulcus covered with fat; 17,18 left and right ventricles.



(B) Sternal surface of heart and great vessels, right ventricle opened.
1 ascending aorta; 2 aortic arch; 3,4 brachiocephalic aa.; 5 pulmonary aa.; 5′ ostium of pulmonary trunk; 6 right cranial vena cava; 7 right auricle; 8 right ventricle; 9 interventricular septum; 10 right atrioventricular valve (muscular); 11 left ventricle; 12 valve of pulmonary trunk; 13 trabeculae carneae.

this chamber which communicates with the right atrium via the slit-like sinu-atrial (S–A) opening. In other birds (e.g. *Gallus*) the sinus receives only two caval veins, the left cranial vena cava emptying directly into the right atrium. In most birds that have been studied the three caval veins open individually into the right atrium (Fig. 1A); no definitive sinus venosus is present. Most of the foetal sinus becomes incorporated into the right atrium; remnants of the S–A valve persist.

The right atrium receives venous blood from all parts of the body and the heart wall itself. The inflow ostia of the right atrium are those of the huge caval veins (or sinus venosus) and the cardiac veins; the single outflow opening is the right A–V ostium. The main part of the interior of the right atrium, including the interatrial septum, is smooth-walled and communicates with the subchamber of the auricle. Another feature of the interior is a cul-de-sac, the left recess of the right atrium.

The right ventricle is short and wide. The entrance of the right ventricle is equipped with the right A–V valve, a crescent-shaped muscular fold with its free edge projecting into the ventricle. During ventricular contraction (systole) the valve clasps the interventricular septum, preventing regurgitation of blood into the atrium. Blood entering the ventricle passes apically, then flows into the conus arteriosus, the funnel-shaped subchamber of the right ventricle. Its outflow opening is the pulmonary trunk, where the pulmonary valve is located. Blood then travels via the pulmonary arteries to the lungs for aeration.

The avian I–V septum is a curved partition between the ventricles; almost two-thirds of the circumference of the left ventricle is enveloped by the free wall of the right ventricle (Fig. 1).

The left heart receives blood from the lungs and propels it throughout the arterial tree to all parts of the body. The paired pulmonary veins (Fig. 1A) enter the left atrium independently or become confluent (Fig. 1). The cavity of the left atrium is partitioned by a transverse fold known as the valve of the pulmonary vein, which directs blood into the left A–V ostium.

The left ventricle forms the apical one-third of the heart. Its wall is 2–3 times thicker than that of the right ventricle, reflecting its function as a high pressure pump. One or more papillary muscles project from the wall of the left ventricle. The left A–V ostium is rounded in contrast to the semilunar one of the right A–V ostium. The left A–V valve differs from the right one in that its two or three cusps are membranous. The cusps are restrained by tendinous cords from the papillary muscles or ventricular wall. The vestibule of the aorta lies between the septal cusp of the valve and the interventricular septum and leads to the outflow channel, the aorta.

Blood supply and drainage. The right and left coronary arteries originate from the aortic sinuses, enlargements at the base of the aorta, just distal to the aortic valve. Ordinarily each coronary artery divides into superficial and deep rami. Unlike the mammalian heart, most of the blood to the myocardium of the avian heart is distributed via deep rather than surface arteries. The superficial rami course in the coronary sulcus, supplying atria and ventricles. The deep rami course within the I–V septum, gradually inclining toward the surface.

The major venous trunks course just beneath the epicardium; generally the veins do not accompany coronary artery branches. The smallest cardiac (luminal) veins carry some of the myocardial blood directly into the heart chambers.

Conducting system. The cardiac conducting system initiates and carries the impulses that bring about the co-ordinated contraction sequence of the heart muscle required for pumping blood through the pulmonary and systemic circuits. This impulse-conducting system is derived from transformed cardiac muscle cells (or fibres), and forms impulse-conducting chains. The terminal network is partly subendocardial and partly periarterial around branches of the coronary arteries. The terminal rami branch further, ultimately becoming contiguous end-to-end or side-to-side with contractile myocardial cells. The cardiac impulse is automatically generated in the nodal tissue, then transmitted over the bundles, branches, and terminal rami. The rami excite the myocardial fibres, bring about their contraction, the wave of excitation passing to adjacent myocardial fibres. Cell-to-cell transmission is electrical, conducted from one cell to the next over nexuses (gap junctions), low resistance zones of continuity between adjacent cells.

The compact S–A node ('pace-maker') is located in the right atrial wall somewhere near the apical end of the right S–A valvule or its vestige. The A–V node is embedded in the caudodorsal part of the interatrial septum. The A–V node continues apically as the A–V bundle of His which enters the I–V septum and divides into its right and left crura that travel on each side of the septum. From the region of its bifurcation the A–V bundle gives off its Ramus recurrens (truncobulbar fasciculus). The ramus then joins the ventral extremity of the right A–V annulus. Here the truncobulbar node is reported to be present in adult heart of *Gallus*. The right A–V annulus courses in the right A–V valve; its dorsal extremity arises directly from the A–V node.

Atrial musculature is not continuous with ventricular musculature. Both are 'insulated' from one another by attachment to the non-conducting skeleton of the heart. The only direct connections between the two muscle groups are by way of the bundles of conducting tissue.

Heart innervation. The innervation to the heart modulates the activity of the conducting tissue. The most densely innervated regions of the avian heart are the S–A node, right atrium, and the A–V node. The periarterial and subendocardial conducting tissue of the ventricles also receives a double innervation of interacting (autonomic) nerves. In general the cholinergic vagal efferent nerves produce effects that slow the heart beat. On the other hand, the thoracolumbar (sympathetic) adrenergic nerves from the lowest of the cervical paravertebral ganglia accelerate the beat. The vagal afferent fibres are involved in cardiac reflexes. The direct innervation of the heart muscles probably modifies their response to stimulation from the conducting system, adrenergic innervation enhancing the force of their contraction and cholinergic innervation the reverse. Coronary arteries also receive a double innervation of noradrenergic and cholinergic fibres for regulation of coronary blood flow.

Heart size. The weights of avian hearts, as a percentage of body weight (B.W.), range from 1.4–2 times larger than mammals of comparable size. Species living at high altitudes have larger hearts than the same species at lower altitudes.

The ratio of heart size to body weight is significant for flight, i.e. birds with large hearts but only modestly developed flight muscles can fly for long periods. Thus, although the tinamous (Tinamiformes) have powerful limb muscles and extremely large flight muscles, they are capable only of explosive flight over short distances. Their hearts are relatively the smallest of all birds (0.19–0.25% of B.W.), which appears to limit prolonged flight effort. Compare this with flying abilities of pigeons (Columbidae) whose flight muscle weights are equivalent to those of tinamous while the heart ratio is greater (0.93–1.29% of B.W.).

Since the avian heart rate is so high (see below) the relatively large heart in birds may provide the means for quickly increasing heart output by utilizing the reserve portion of the blood not ejected from the ventricles at each beat during moderate activity. Large hearts requiring a relatively reduced degree of muscle shortening may facilitate adequate filling of the chambers at the high rate prevailing in birds.

Heart rate. Normal heart rates for resting birds (e.g. pigeon, chicken, duck) range from 150–350 beats per min. The resting rate in the ostrich (*Struthio*) is 60–70 per min, in a small passerine (Black-capped Chickadee *Parus atricapillus*) 500 per min, in hummingbirds (Trochilidae) up to 1,000 per min. During excitement, stress, or sustained flight the above rates more than double. For example, during flight the heart rate of small birds (10–20 g) is 2.4 times that at rest; in large birds (500–1,000 g), the flight rate is 3 times resting rate. In diving birds the heart rate is slowed reflexly about 50% during the dive.

Some coupling of heart rate to wing beat frequency in flight has been observed: in some forms 1 : 1, in others 1 : 2. It has been suggested that the pectoral muscles of small birds in flight may operate as a venous pump in order to maintain adequate venous return to the heart, compensating for high cardiac output. (E.T.B.F.) J.J.B.

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HEATH FOWL: antique term (in British game laws) for Black Grouse *Tetrao tetrix*—contrasted with 'Moor Fowl' for Red Grouse *Lagopus*

Ostrich *Struthio camelus* showing exposed bare skin to reduce heat, sexual dimorphism and male giving distraction display. (*Photo: J.F. Reynolds*).

lagopus scoticus (see GROUSE).

HEATH HEN: name of the now extinct nominate race of the Greater Prairie Chicken *Tympanuchus cupido* (see GROUSE; EXTINCT BIRDS).

HEAT REGULATION: also called thermoregulation; the process by which a bird maintains a stable body temperature, irrespective of variations in the surrounding temperature.

Birds are endothermic animals (= warm-blooded or homoiothermic), that maintain a high body temperature of 40 ± 2°C. Their body heat is generated metabolically by the oxidation of absorbed nutrients (see METABOLISM) and accounts for a large proportion of the total energy metabolized by the body. Apart from species that can go torpid (see TORPIDITY) body temperature shows only a small daily variation; in diurnal birds the daytime core temperature may be 42°C, dropping to 39°C at night; in nocturnal birds the cycle is reversed.

In an inactive bird metabolic heat production is normally never less than the Basal Metabolic Rate (see ENERGETICS) and when the bird is active it may be much more. To maintain a stable body temperature it is necessary that heat production is balanced by heat loss. At low to moderate ambient temperatures this is achieved mainly by conduction and radiation and at high temperatures by the evaporation of water. The rate at which heat is lost by conduction and radiation is proportional to the temperature difference between the body core and the outside, thus

$$\text{Rate of heat loss} = C(T_{\text{body}} - T_{\text{ambient}}),$$

where C represents the heat conductance ($\text{Joules} \cdot \text{sec}^{-1} \cdot \text{cm}^{-2} \cdot {}^{\circ}\text{C}^{-1}$) of the body and plumage (its reciprocal is the insulation). Over a range of ambient temperatures known as the *thermoneutral zone* the heat production of an inactive bird is able to remain constant at the Basal Metabolic Rate, because changes in ambient temperature, which would alter the rate of heat loss, are compensated by changes in the thermal conductance (or insulation) of the body. By a complex neuromuscular arrangement connecting adjacent feather follicles, the ptilomotor system, a bird can fluff out its feathers to their maximum extent, so trapping a greater amount of still air between them and greatly increasing the insulation value of the plumage. Conversely, the feathers can be sleeked back to increase the conductance. Birds may also make postural changes to alter heat loss; to reduce heat loss the face may be hidden under the scapulars and the feet withdrawn up into the feathers, or (especially on ice or in water) the bird may stand on one leg. Heat loss through the feet may be reduced by an arrangement of the blood vessels in the upper leg that acts as a counter-current heat exchanger. Warm arterial blood from the body passes through fine arteries in close contact with the veins returning cold blood from the feet. The venous blood is thus warmed before it can return and cool the body, while the arterial blood is cooled before it can lose its heat to the exterior. A gull with its feet in ice water may lose only 1.5% of its metabolic heat through its feet because of the efficiency of the heat exchange. Even so the feet cannot be allowed to freeze; below freezing point additional heat is supplied to the feet to prevent freezing and heat loss is therefore increased.

If the insulation is already maximized, but the ambient temperature drops still further, heat loss increases in proportion to the increasing temperature difference ($T_b - T_a$). A stable body temperature can then be maintained only by increased heat production in the body core. The ambient temperature at which this occurs is the *lower critical temperature* and marks the lower end of the thermoneutral zone. It is generally much lower in well-insulated Antarctic and Arctic species (and hence the thermoneutral zone is wider) than in temperate or tropical birds. The lower critical temperature may vary seasonally in some species, being lower in winter than in summer. The lower winter value may be due to a better insulating plumage, or a higher basal heat production, or both (see ENERGETICS). As ambient temperature decreases, metabolic heat production increases more rapidly in poorly insulated tropical species than in well-insulated Arctic ones. Small birds are doubly disadvantaged because their size prevents them from carrying as thick a plumage as large birds, as well as requiring them to increase their heat production more rapidly with falling temperature, since the area of the body surface, through which the heat is lost, is proportionately greater than the volume of the body core, where heat is produced. All species, however, are eventually limited by the maximum additional metabolic heat that they can produce. The maximum heat production determines the minimum ambient temperature below which hypothermia and death result.

At high ambient temperatures heat may be lost by increased blood circulation to the periphery, particularly to the legs and to any bare, well-vascularized patches of skin. The wings may be partly spread, e.g. in coursers, allowing radiation from the sparsely-feathered under surface of the wing. Incubating birds, e.g. plovers, may sit with their backs to the wind and raise the mantle feathers, allowing the wind to break the insulating boundary layer of air trapped in the plumage. However, as ambient temperature approaches that of the body, conduction and radiation become less effective at dissipating heat and cooling by the evaporation of water becomes increasingly important. Since birds do not possess sweat glands, water is usually evaporated through the respiratory tract, where the rate of evaporation is greatly increased by panting or, in some non-passerines, by gular flutter, a rapid oscillation of the thin floor of the mouth and upper throat. Nevertheless among birds, unlike mammals, evaporative water loss at high ambient temperatures rarely dissipates more than half the total heat production. Some species, e.g. incubating Fairy Terns *Gygis alba*, reduce heat production by slowing the heart rate and reducing the basal metabolic rate. Others, particularly some desert birds, e.g. the American Mourning Dove *Zenaidura macroura*, allow the body temperature to rise above normal to 45°C, thus re-establishing a temperature gradient to their surroundings so that heat loss by conduction and radiation can continue. The temperature at which this occurs is the *upper critical temperature* and marks the upper limit of the thermoneutral zone.

Where the environment is hotter than body temperature, the bird absorbs heat. Small birds are again at a disadvantage compared with large ones; they already have a high basal metabolic heat production and their surface area being large relative to body volume causes them to gain heat faster from their surroundings. Small birds seek shade to lessen the heat intake from solar radiation and large soaring birds take to the wing to reach cool air at high altitude; but birds can cope with heat stress only for as long as they have an adequate supply of water that they can evaporate fast enough. Some large birds may even excrete down their legs to provide an additional site for evaporative cooling. The capacity for evaporative cooling determines the ambient temperature at which body temperature begins to rise (the upper critical temperature). As hyperthermia proceeds, the metabolic heat production, which is temperature dependent, also increases, resulting in an explosive heat rise and death at body temperatures of 46–48°C.

See photos BELLY SOAKING; ENERGETICS; INCUBATION. P.J.J.

HEDGESPARROW: name (misnomer), alternatively 'Dunnock', of *Prunella modularis* (see ACCENTOR).

HEEL PAD: a callosity behind the intertarsal joint in nestlings of some piciform and other birds (see LEG).

HELIGOLAND TRAP: see BIRD OBSERVATORY; TRAPPING.

HELIORNITHES; HELIORNITHIDAE: see under GRUIFORMES; FINFOOT.

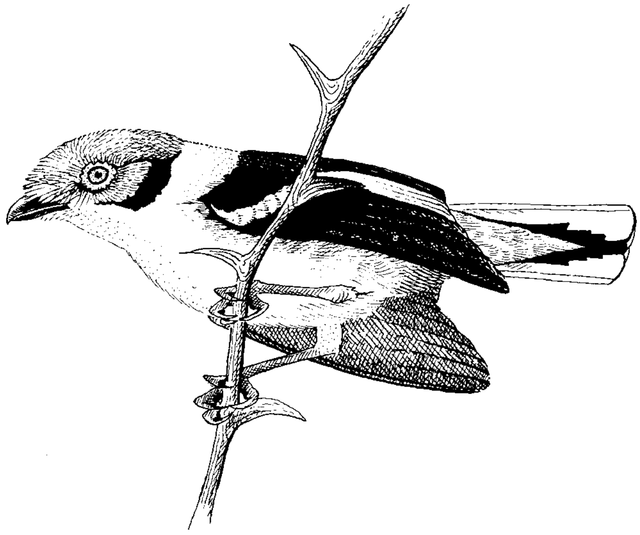
HELL-DIVER: popular American name for the Pied-billed Grebe *Podilymbus podiceps* (see GREBE).

HELMET: an ornament, usually composed of feathers, on the top of the head, as in helmet-shrikes (Prionopinae)—compare CASQUE.

HELMETBIRD: *Euryceras prevostii* (see VANGA).

HELMETCREST: *Oxypogon guerinii* (for family see HUMMINGBIRD).

HELMET-SHRIKE: substantive name of most species of Prionopidae (Passeriformes, suborder Oscines); in the plural general term for the family; formerly considered a subfamily of the shrikes (Laniidae) by Rand (1960). The helmet-shrikes, all endemic to the Afrotropical region, have bills that are hooked and notched near the tip, similar to the true shrikes (Laniidae). The wing has 10 primaries and the tail 12 rectrices. Legs and feet are strong and claws sharp for catching prey. Lengths range from 18–25 cm. They are unusual in having a tarsus scutellated on both side and front, and most species have specialized head feathering and eye-wattles that are distinctively coloured. The feathers on the forehead are stiff and project forward, covering the nostrils. Two genera are recognized, following Hall and Moreau (1970), *Prionops* (7 species) and *Eurocephalus* (2 species); others place some species of *Prionops* in a separate genus *Sigmodus*, and place *Eurocephalus* in the Laniidae. The sexes are alike.



Common Helmet-shrike *Prionops plumata*. (*M.W.*).

Field characteristics, habitat and distribution. The species of *Prionops* fall into two groups, 3 black-billed species and 4 red-billed. Of the black-billed species the Common Helmet-shrike *Prionops plumata* has the widest distribution in savanna and light woodland throughout the Afrotropical region; 5 races are recognized by Hall and Moreau. It is a black, grey and white bird, with orange eye-wattles. The Grey-crested Helmet-shrike *P. poliolopha* differs from it in having no eye-wattles and replaces it in the Kenya highlands and in drier areas further south. The Yellow-crested Helmet-shrike *P. alberti*, closely related to *poliolopha*, is confined to land above 1,400 m in the eastern Congo and is wholly black with a yellow crest and orange eye-wattle.

Of the red-billed species one, the Red-billed Shrike *P. caniceps*, is restricted to the West African and Congo forest block. It has a black back, throat and tail, whitish head and white and chestnut underparts, but no eye-wattle. Another, the smallest of the family, is the Chestnut-fronted Helmet-shrike *P. scopifrons* (length 18 cm) which has a blue eye-wattle and is confined to a narrow forest belt along the eastern sea-board of Africa.

The White-crowned Shrikes, *Eurocephalus anguitimens* and *E. rueppelli*, sometimes considered conspecific, are brown and white and inhabit acacia steppe in southern Africa and north-eastern Africa respectively. Their white heads and rumps are conspicuous in flight which resembles that of a large butterfly.

Movements. There are no ringing data to confirm the presence or absence of movements; observations suggest that local movements may occur in some populations of the Common Helmet-shrike.

Food. Helmet-shrikes search trunks, branches and leaves mainly for insects, each species foraging systematically in a group much like tits.

Behaviour. All species are intensely sociable, occurring in groups numbering 6–12 birds or more, throughout the year. Nothing is known about the permanency of the pair bond. Only the Common Helmet-shrike has been studied using colour-ringed birds. All group members co-operate in nest-building, incubation and feeding young; in addition, clumping and allopreening occur. A group normally has only one active nest used by one female but occasionally (8 cases in 225 recorded in Zimbabwe) 2 females may lay complete clutches in the same nest; pairs sometimes nest close to each other in neighbouring trees. In Retz's Red-billed Shrike *P. retzii* some pairs (1 in 36 recorded in Zimbabwe) breed alone. The 2 *Eurocephalus* species appear to breed only in pairs, although outside the breeding season they are found in groups of up to 10 birds. Group territorial defence and predator attack have been recorded in the Curly-crested Helmet-shrike *P. cristata* and may be common to the genus. Helmet-shrikes are often accompanied by other bird species when feeding. Their flight is buoyant, much like jays, and they are usually silent on the wing.

Voice. Although helmet-shrikes have a variety of calls, of which the most frequently listed are repeated whistles or flute-like notes, they are usually located in the field through the noisy chattering of a mobile flock. In addition, bill snapping is characteristic of the group.

Breeding. The nests of the helmet-shrikes are inconspicuous but neatly formed shallow cups, either secured to a horizontal branch or placed in a fork of a tree or thicket from 2–7 m above the ground. Materials used include tendrils, spider webs, lichen, rootlets, grass and bark fibre.

The normal clutch is 3 or 4; eggs have a range of ground colours, variously described as white, greyish-white, pale blue grey, blue, greenish blue, and pale pinkish. The eggs are either streaked, speckled or blotched with various shades of brown, purple-brown and chestnut-brown, the markings being concentrated usually at the large end. Incubation periods are in the range 12–14 days, nestling periods in the range 16–20 days. The breeding seasons are prolonged and overlap both the dry and wet seasons. L.G.G.

Hall, B.P. & Moreau, R.E. 1970. An Atlas of Speciation in African Passerine Birds. London.

Rand, A.L. 1960. Family Laniidae. *In* Mayr, E. & Greenway, J.C. Jr (eds.). Check-list of Birds of the World, vol. 9.

HELPERS AT THE NEST: see CO-OPERATIVE BREEDING.

HEMIPODE: alternative substantive name of species of Turnicidae and Pedionomidae, and also used as a general term for the suborder Turnices (see BUTTONQUAIL; PLAINS-WANDERER).

HEMIPROCNIDAE: see APODIFORMES; SWIFT.

HEMISPINGUS: substantive name of South American TANAGERS of the genus *Hemispingus*.

HEN: a female bird; applied without qualification to the female of the domestic fowl (compare COCK). Special terms apply to the females of some species, e.g. PEN, GREYHEN, PEAHEN, REEVE. The names of certain species have also a special use as terms for the female, e.g. DUCK, GOOSE, FALCON; but note that in North America the female of any duck species is the 'hen'.

HERALDIC BIRDS: avian symbols used as charges in armorial bearings. In heraldry the animals fall into roughly the same classes as in zoology, but with the addition of heraldic monsters. The four main classes are beasts, monsters, fishes, and birds. Most books on heraldry deal fairly fully with beasts; monsters can be studied in the many excellent beastiaries and books of monsters; Thomas Moule's *Heraldry of Fish* (1842) is the last word on that subject; but birds have been neglected. It is, therefore, particularly pleasant to be able to remedy here, if only in some slight measure, this deficiency.

Heraldry is a form of hereditary personal symbolism in which the basic medium for the display of the devices used is the shield. It is European in conception and application, just post-Conquest in time of origin and, to a great extent, dependent for much of its early symbolism and many of its conventions on the Crusades, jousts, and tournaments. Two symbols are used, the arms borne upon the shield and the crest. The crest is a device which was originally modelled on top of the helmet and which, together with the mantling which flows from it, is often shown in pictorial representations of arms. That heraldry was from its inception at once utilitarian and also pictorial and decorative accounts for the fact that crests are often absurdly impracticable and could never have been in actual use, but only engraved upon seals and otherwise used pictorially.

It is not surprising that birds are to be found in early heraldic symbolism, when it is considered how frequently they appear in more ancient symbolisms. The eagle on the standard of a Roman legion is well known; perhaps less familiar in this regard is the owl, which in a most heraldic form graced the reverse of an Athenian tetradrachmon minted about the time of the Persian Wars.

In Christian symbolism the dove holds pride of place as a symbol of the Holy Spirit and His attributes of peace (see also ART, BIRDS IN). If only for this reason, it has always been a favourite heraldic charge, whilst the pelican as a type of Christ is popular in the heraldry of ecclesiastics. In early heraldry she is often drawn more like an eagle, and is almost invariably depicted 'in her piety', i.e. on a nest and pecking her breast to feed her young with her own blood. The origin of this fable of self-wounding may lie in the habit of resting the pouched bill upon the breast. A well-known example of the pelican in heraldry occurs in the arms of Richard Foxe, Bishop of Winchester, *Azure a Pelican wings elevated and addorsed Or vulning herself proper*. Foxe, who died in 1528, founded Corpus Christi College, Oxford, in 1515, and his arms still form part of the cumbersome coat borne by his foundation.

An early arrival in the heraldic aviary was the martlet. This bird has always been shown *sans* legs and looking perhaps rather more like a fat swallow than anything else. Indeed, to preserve the obvious pun, it is described as an *hirondelle* (swallow) in the arms of Arundell (*Sable six hirondelles 3, 2, and 1 Argent*): variants of these arms are used by both the East Sussex and West Sussex County Councils. Most heraldic writers state that 'martlet' is a synonym for 'martin', a bird which has such short legs that it relies upon them but little, and is therefore always depicted heraldically without legs, albeit it is almost invariably shown 'close' and not in flight. Other writers assert that it represents a swift, for these birds are found in great numbers in the Holy Land and crusaders may have come to associate these elegant yet sturdy (and apparently legless) creatures with their own exploits in the Near East and adopted them as symbols of speed and endurance, as well as a reminder to others that the bearers had fought for the Faith. It is amusing to note that the martlet is used to denote a fourth son in heraldry. The story is that the first son inherited, the second became a soldier, and the third entered the church; but for the fourth there was nothing, so he flew away to seek his fortune. That the martlet is of great antiquity in heraldry is borne out by its presence in a great many of the coats depicted in 'Glover's Roll' (*c.* 1255).

It was a common mediaeval practice to show in arms not only military but also sporting symbols. Thus one finds hunting horns, greyhounds, and, of course, hawks. These last are usually shown belled and jessed, and sometimes hooded. The hawk is drawn in a somewhat stylized way and indifferently called a 'hawk' or 'falcon', except where a pun is required or where for some special reason a particular species was chosen for a charge. Then the hawks may be found looking much like any other, but blazoned a 'goss-hawk', 'sparrowhawk', 'gerfalcon', 'marlion', or 'hobbey'. See also FALCONRY.

The birds so far mentioned are to be found in heraldry principally owing to the qualities which they symbolize. Very many other kinds of bird grace armorial bearings, but principally because they pun on the name of the bearer of the arms. There is no need to mention what birds are to be found in the arms of Larkins, Bustard, Sparrow, Hancock, Cobbe, and Storke, to mention but a few.

Whilst it is often apparent why a certain bird appears in a certain coat of arms, as the pheasant which is found in the crest of the Worshipful Company of Cooks, this is not always the case. In 1550 one William Strickland, of Yorkshire, was granted arms and a crest, the latter consisting of *A Turkey Cock Argent beaked and legged Sable combed and wattled Gules*. The reason for this grant is that William Strickland was said to have introduced turkeys into England from North America; the sketch which is part of the docquet of this grant must therefore be one of

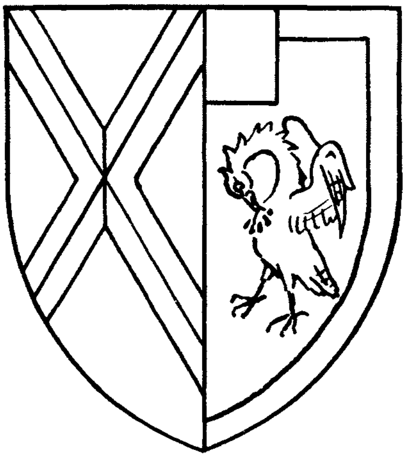


Fig. 1. Pelican; in the arms of Richard Foxe (as Bishop of Bath and Wells), from College of Arms Ms. L. 10.

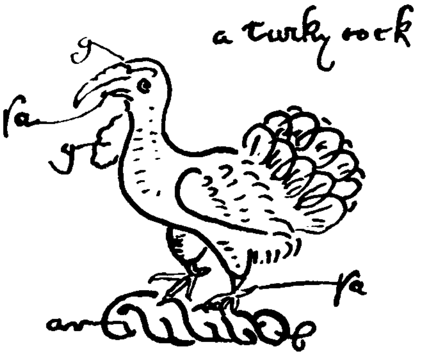


Fig. 2. Turkey; an early drawing in the records of the College of Arms.

the first ever made of a turkey in Britain—indeed, one look at the sketch lends support to this view! The arms of the Worshipful Company of Musicians are full of royal emblems, and this might suggest that the swan in the arms is a royal swan; however, the reason for its appearance is almost certainly an allusion to the legend that the soul of Apollo, the god of music, passed into a swan when it was at the point of death, thus enabling the bird to sing a beautiful song before it died.

The swan deserves particular mention as it was the famous badge of the powerful family of Bohun, Earls of Hereford and Essex, and the crest of the Beauchamps, Earls of Warwick, and from these families it percolated through to many others. Why these and other families adopted the swan is uncertain. It has been suggested that the reason is to be found in the fact that they can all trace descent from the house of Boulogne, connected in legend with the Knight of the Swan. This theory is carefully examined by A.R. Wagner in his essay 'The Swan Badge and the Swan Knight' (*Archaeologia* 97: 127). It is interesting to consider how legend and romance were mirrored in an heraldic charge which, because it was adopted by one or two powerful families, soon found its way into the heraldry of smaller families, as representing either consanguinity with, or feudal dependence upon, these early magnates.

Although birds are seen to best advantage as crests and charges in arms they are also used as supporters. It is a privilege of peers and certain grades of knight to have supporters on either side of the shield. Although a bird is a rather unsteady supporter, compared with a beast or a human being, it is becoming increasingly popular.

Birds have become increasingly popular as heraldic charges and particularly as crests during the present century. Although unspectacular birds frequently appear, they are not so popular as the more exotic breeds; unornithological Kings of Arms tend not to distinguish between, say, a blackbird, thrush and starling. Thus if a starling is granted as a crest, someone wanting a thrush will be unlucky as it will be dubbed 'the same sort of bird'. A glance through the recent grant books at the College of Arms has revealed hummingbirds, albatrosses, many cormorants, a rockhopper penguin, a Canada goose, many red cardinals, moas and sedge warblers.

When the Zoological Society of London was granted arms in 1959, it was desired to represent different classes of creature. Therefore, to the principal charge of a lion were added two zebra as supporters (Lord Zuckerman's idea) and a crest consisting of an osprey with a fish in its talons, as suggested by Sir Landsborough Thomson, and effected by the writer of this article. J.P.B-L.

HERBST'S CORPUSCLES: see TOUCH.

HERD: see ASSEMBLY, NOUN OF.

HEREDITY: see GENETICS.

HERITABILITY: the proportion of total variation in a population which is due to genetic causes (see GENETICS).

HERMIT: substantive name of species of HUMMINGBIRDS of the genera *Ramphodon, Glaucis, Phaethornis* and sometimes of *Threnetes*, so-called because of their generally sombre plumage colours.

HERMIT THRUSH: *Catharus guttatus*, a North American THRUSH, noted for its outstandingly beautiful song.

HERN; HERNSHAW: obsolete or dialect names, in Britain, for the Heron *Ardea cinerea*—the latter variously spelt, including 'handsaw' in Shakespeare.

HERODIONES: see CICONIIFORMES.

HERON: substantive name for most species of the Ardeinae (typical herons), one of 2 subfamilies of Ardeidae (Ciconiiformes); in Britain commonly used without qualification for the sole native species, the Grey Heron *Ardea cinerea*; in the plural, a general term for the Ardeinae and the Ardeidae. The substantive name 'egret' is used for several species. The other subfamily is the Botaurinae (see BITTERN). The Boat-billed Heron *Cochlearius cochlearius* was previously placed in a separate family.

Characteristics. Herons are medium to large birds, ranging from the Zigzag Heron *Zebrilus undulatus*, 30 cm long, to the Goliath Heron *Ardea goliath*, 140 cm long. Particularly in the day herons, the body is slender and neck and legs relatively long. Night herons are stouter with shorter necks. Long-necked herons keep their heads retracted in prolonged flight. A kink in the neck is caused by the structure of the relatively long sixth cervical vertebra. Toes are long and slender; the inner toe is shorter than the outer and is attached to the middle toe by a short basal web; the hind toe is lengthened and level with the inner toe; a pectinated middle toe nail is used for grooming. Bill structure ranges from very long and thin in the Chestnut-bellied Heron *Agamia agami*, to broad and thickened in the Boat-billed Heron. The tail is short, usually with 12 rectrices. Wings are long, broad, with 10 primaries, 9 in the Boat-billed Heron. Flight is slow but strong. Herons assume an erect or semi-crouched posture when active and retract their neck when resting.

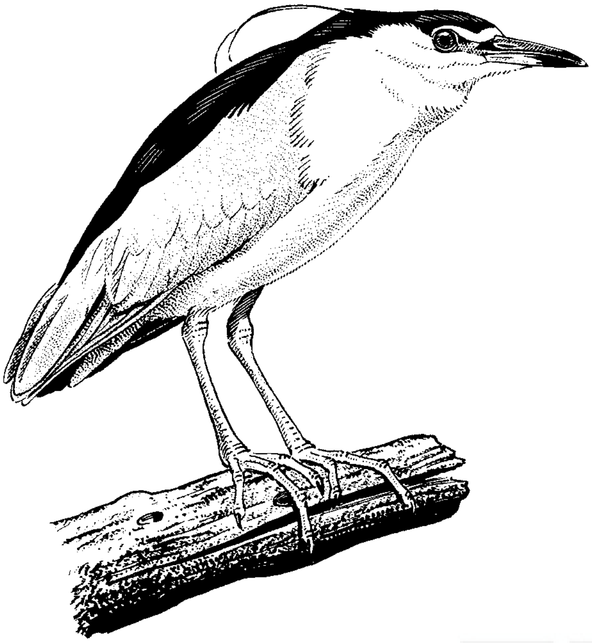
The plumage of herons is loose, the basic colours emphasizing black, brown, blue, grey, and white. Colour patterns may be complex, especially in cryptic species. The head is completely feathered except the lores. Some species, especially day herons, have lanceolate or filamentous display plumes on their head, neck, breast, or back. Sexes of most species are alike in plumage, but polymorphism occurs in several. Down is confined to apteria; feather tracts are extremely narrow (see PTERYLOSIS). Powder-down patches, characteristic of herons, occur in pairs on the breast and rump. Additional pairs are located on the back and thighs of some species. Powder down is used during preening (see COMFORT BEHAVIOUR). Moult and plumage development patterns are complex and variable, seasonally and with age. Juvenile may differ from adult plumage, the night herons being cryptically barred and the Little Blue Heron *Egretta caerulea* white.

Habitat. Herons are adapted for walking about in water and are with ibises and storks often referred to by the descriptive name of wading birds. They characteristically inhabit shallow marshes and swamps, the shores of rivers and lakes. Small herons tend to frequent dense marshes; larger species tend to forage in the open. The amount of wetland habitat available directly influences population size. Terrestrial habitats are frequented by many typically aquatic species and used extensively by Cattle Egrets *Bubulcus ibis* and the Black-headed Heron *Ardea melanocephala*. Many species use shallow marine habitats, but several are marine specialists.

Taxonomy and distribution. The Ardeinae are divided into 3 tribes, the tiger herons Tigriornithini, night herons Nycticoracini, and day or typical herons Ardeini. Herons as a group are cosmopolitan, but most species are tropical.

The Tigrionithini are considered to be the most primitive group (but see Payne and Risley (1976)). The secretive and solitary tiger herons, including 6 species in 4 genera, 3 of which are monotypic, have a discontinuous apparently relict distribution. The New Guinea Tiger Heron *Zonerodius heliosylus* is confined to Papua-New Guinea. Its nearest relative, the White-crested Tiger Heron *Tigriornis leucolophus* inhabits the equatorial rain forest of West Africa. The Zigzag Heron, the least known ardeid, occurs in South America in forest pools and streams. The 3 *Tigrisoma* herons are Neotropical, occurring in swamps and along streams from Mexico to Argentina, with the Bare-throated Tiger Heron *T. mexicanum* confined to Central America.

The Nycticoracini are medium-sized herons that typically, but not universally, feed at night. In general they are stockier, shorter-legged, and heavier-billed than day herons. The 8 species in 3 genera have



Black-crowned Night Heron *Nycticorax nycticorax*. (*R.G.*).

distinctive skeletal differences from the day herons. The 4 oriental night herons *Gorsachius* are Palaeotropical. The Black-crowned Night Heron *Nycticorax nycticorax* is found on all continents but Australia and on many islands. It is replaced in Australia by the closely related Nankeen Night Heron *N. caledonicus*.

The Neotropical Boat-billed Heron is distinguished by its peculiarly widened bill, 7.5 cm long by 5 cm wide, and by its exceptionally large eyes. It has diverged from other herons in its display repertoire and has 3 rather than 4 powder-down patches. It resembles night herons in plumage and frequently feeds at night. Some believe that the unusual bill primarily serves a display function. It seems more likely to be a feeding adaptation.

The Ardeini include the well known, typically day-feeding herons and egrets. Many species nest colonially and forage in aggregations. The day heron group of 35 species is cosmopolitan.

The little known Capped Heron *Pilherodius pileatus* has a distribution centred in the Amazon basin of South America. Considered in the past to be a night heron, taxonomic and field studies indicate it to be a typical heron, characteristic of forested stream edges. The Whistling Heron *Syrigma sibilatrix* has a disjunct distribution in northern and southern South America. Its whistling calls, duck-like flight, and complex social behaviour are distinctive. It is a bird of the tropical savannas.

The pond herons *Ardeola* include 6 diminutive, short-legged Old World herons of shallow, reedy marshes. In several species breeding and non-breeding plumage differ markedly. The Cattle Egret is primarily a terrestrial heron that forages in commensal association with African buffalo, domestic cattle, other large animals, and even agricultural equipment. In Africa this mostly white bird favours seasonally-flooded plains. Both Indian and African races have expanded their ranges markedly within historic times, probably taking advantage of changing agricultural practices. The Cattle Egret had become established in South America by the late 1800s, in Australia by the early 1900s, and in North America and Europe by the early 1950s.

The Green Heron *Butorides striatus* includes 3 small, dark herons previously considered to be separate species. The most distinctive population, on the Galapagos, includes individuals that are almost entirely dark grey. Green Herons are secretive, often foraging under the cover of trees along the shores of rivers and lagoons. The Galapagos form typically feeds on rocky shores.

The genus *Egretta* includes 13 species, the medium sized white Little Egret *E. garzetta* of Europe, Africa, and Australia being typical. The Little Egret has a mainly inland distribution and breeds in mixed-species colonies. The Snowy Egret *E. thula* of North and South America is similar but has different breeding plumes. Two polymorphic reef herons *E. gularis* and *E. sacra* tend to replace the Little Egret along the coast in Africa and in Asia to Australia, respectively. But see a recent discussion in *The Herons Handbook* (p. 132). Another similar heron, Swinhoe's Egret *E. eulophotes*, is now confined to China and Korea. Three New World forms are similar in habitats to the Old World reef herons. The Pied Heron *E. picata* has a patchy distribution in Australia to New Guinea. Two more occur in Africa, and the Intermediate Egret *E. intermedia*, larger than the Little Egret, has a discontinuous distribution from Africa and Asia to Australia. The Great White Egret *E. alba* is cosmopolitan, occurring in many habitats on all continents.

The genus *Ardea* includes 11 species of medium to very large dark-plumaged herons. The Grey Heron and Purple Heron *A. purpurea* are widely distributed in Eurasia and Africa. The Grey Heron forms a natural, mutually allopatric, group with the North American Great Blue Heron *A. herodias* and the South American Cocoi Heron *A. cocoi*. The White-necked Heron *A. pacifica* replaces these species in Australia. The White-faced Heron *A. novaehollandiae* is a medium-sized species of Australia, which has been introduced and has spread in New Zealand. The African Black-headed Heron is characteristically terrestrial, feeding in cultivated areas and open grassland. Finally, there are 4 very large herons of allopatric distribution: the Malagasy Heron *A. humbloti* of the Malagasy Republic, the Goliath Heron of Africa and Asia, the Imperial Heron *A. imperialis* of South Asia, and the Sumatran Heron *A. sumatrana* from Malaya to Australia.

The Agami or Chestnut-bellied Heron is a peculiarly attractive neotropical species of uncertain affinity. It has a long neck and bill and brilliant dark green, chestnut, and pale blue plumage. It occurs along stream banks in deep forests.

Populations. Over their known history many populations have been reduced by hunting and by habitat loss. Extensive surveys in North America have assembled information on nesting colonies in recent years. The Grey Heron is the best known species, colonies in the United Kingdom being tallied as early as 1872 and the nesting population of England and Wales being censused annually since 1928. The population decreases markedly after hard winters.

Movements. Herons demonstrate several types of population movements. In temperate latitudes, regular seasonal migrations are undertaken by many species. Herons of the eastern Palearctic move toward Malaysia and Indonesia; western Palearctic herons migrate on a broad front to central Africa and also to India; Nearctic herons move to southern North America with eastern birds moving through Florida and western birds moving through Central America; southern African herons and southern South American herons undoubtedly migrate northward but their routes require additional study; Australasian herons appear to migrate as far north as New Guinea. Nearly all herons show post-breeding dispersals of juveniles, and of adults after nesting failure. Such dispersing birds may be moving from areas where food is scarce. Dispersals before migration bring many birds as late summer visitors to localities well away from their breeding range. Intra-regional movements, nomadic responses to seasonally variable food resources, have also been documented for various species.

Food. Herons are almost entirely carnivorous, depending heavily on aquatic prey. Diets are broad and variable in time and place and reflect seasonal flushes of prey. Exploiting seasonal prey abundances is of critical importance to many populations, affecting nesting success, movements, migration, and food choice.

The foraging behaviour of herons can be as simple as standing motionless in the shallows or at the water's edge until a potential prey approaches, as is typical of the largest and smallest species. Food is commonly sought by walking stealthily in the water or on dry ground, or by more active behaviours. A bird may combine walking with running or hopping in a repetitive sequence, as is characteristic of Reddish Egrets *E. rufescens*. Use of the feet is common, particularly in species with distinctively coloured toes. Aerial feeding methods are used by several species. Special wing actions characterize actively foraging species. The Black Heron *E. ardesiaca*, stands with its wings extended completely over its head forming a canopy that appears to attract prey and may increase their visibility.

Prey are grasped or, less frequently, impaled by a quick thrust. Dead or slow-moving prey are grabbed or picked up. When bill thrusts are directed into the water, herons must compensate for refraction. Herons may tilt or cock their heads to improve visibility. Captured prey are mandibulated by bites or stabbing if they are large or possess counter-adaptations such as spines, hard bodies, or violent post-capture behaviour. Pellets of undigested material are disgorged. Smaller herons take longer to handle large prey, which may affect their choices. The New World Yellow-crowned Night Heron *Nycticorax violaceus* specializes in feeding on crustaceans. Most herons feed diurnally, but some species, e.g. the night herons, characteristically feed nocturnally or crepuscularly, while others, e.g. Great Blue Heron, may do so at times.

Behaviour. Some herons, such as the tiger herons, are typically solitary; others forage in isolation but nest colonially. Some species, such as the Cattle Egret, feed in flocks and nest in large colonies. Others are socially flexible, and individuals may alternately feed alone or in an aggregation. Social foraging provides opportunities for complex interactions, including aggression, commensalism, competition, and prey robbing. Territorial behaviour on the feeding grounds is common, and individual territories may be occupied over long periods. Individual distances are always maintained.

Many herons form mixed-species communal roosts in protected sites, often after assembling at staging locations. Nesting in groups on isolated sites confers some degree of protection. Herons may also use colony associates to obtain information on the direction of available food resources.

Pair formation behaviours are varied and elaborate, including aerial and non-aerial elements. Pair-bonding begins at the colony, with intensive displays by males. Three types of pair formation are distinguishable. A succession of females may visit a displaying male at his future nest site (Grey Herons). Several females may visit a male on one or more temporary display sites (Cattle Egrets). Both males and females may move as a group around the colony (Little Egrets). A male typically initiates courtship by advertising calls, defends his site, and attracts a female with various displays.

In many species lores, irides, bill, legs, or feet change colour during courtship. Often the colour remains for only a few days. Coloration may vary among populations, such as in the Great White Egret. The irides and feet of the Green Heron turn from yellow to orange; bills of the European Great White Egret turn yellow; and bills of the Squacco Heron *Ardeola ralloides* turn blue. Colour changes appear to be partly a result of the deposition of pigments (see COLOUR) and partly of increased vascularization.

Voice. Herons have a limited repertoire of guttural honks, frarnks, coos, and growls. Tiger herons and oriental night herons have booming bittern-like calls. The Whistling Heron has high-pitched calls. Calls are most frequent during agonistic encounters and early in pair formation. Bill-snapping also produces sounds. Acoustic signals are emphasized by species such as the Boat-billed Heron which occur in dense vegetation.

Breeding. Nesting generally occurs during the local spring and summer or when the rainfall cycle produces optimal foraging conditions. Some tropical herons nest year-round. Nests typically are stick platforms in trees, reeds, or on the ground. They are built by the female from sticks brought by the male. The 3–7 eggs are usually unmarked white, buff, or pale blue. Both the parents incubate the eggs for 16–30 days. The altricial, nidicolous young are fed regurgitated food. Young may leave the nest in as little as a week, returning to be fed. At this time both parents forage simultaneously. Young become progressively more independent and are seldom fed away from the nest site.

See photos CREST; DISPLAY; FEEDING HABITS; RITUALIZATION; SUNNING.

J.A.K.

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Mock, D.W. 1976. Pair formation displays of the Great Blue Heron. Wilson Bull. 88: 185–230.

Payne, R.B. & Risley, C.J. 1976. Systematics and evolutionary relationships among the herons (Ardeidae). Misc. Publ. Mus. Zool. Univ. Michigan, no. 150.

HERPETOTHERINAE: see FALCON.

HESPERORNITHIFORMES: an order erected to include such fossil forms as *Hesperornis*, *Hargeria*, *Enaliornis* (provisional placing) and *Baptornis* (see FOSSIL BIRDS).

HESSE'S RULE: that among warm-blooded animals the forms living in cold regions have relatively higher heart weights than those living in warm regions.

Hartman, F.A. 1955. Heart weight in birds. Condor 57: 221–238.

Hesse, R. 1921. Das Herzgewicht der Wirbeltiere. Zool. Jahrb. (Allg. Zool.) 38: 243–264.

HETEROCHROISM: see PLUMAGE, ABNORMAL.

HETEROCOELOUS: term for a type of vertebra (see SKELETON, POST-CRANIAL).

HETERODACTYL: see under ZYGODACTYL.

HETEROGYNISM: term introduced by Hellmayr for a situation in which the taxonomic characters distinguishing closely related species (often geographically replacing each other) are more strongly marked in the females than in the males (see SEXUAL DIMORPHISM).

HETEROSIS: 'hybrid vigour'; see under HYBRID.

HETEROZYGOUS: see GENETICS.

HIBERNATION: spending the winter in a state of reduced animation. It is common in some classes of animals; but it is scarcely known to occur in birds, although formerly fabled to do so as a regular event. (see ENERGETICS; TORPIDITY).

HILL: special term for the display ground (court) of the Ruff *Philomachus pugnax* (see LEK).

HILL-PARTRIDGE: substantive name of some species of *Arborophila* (for family see PHEASANT).

HILLSTAR: substantive name of *Oreotrochilus* spp. and *Urochroa bougueri* (for family see HUMMINGBIRD).

HINDNECK: see TOPOGRAPHY.

HIND TOE: see LEG.

HIPPOBOSCID: see ECTOPARASITE.

HIRUNDINIDAE: a family of the Passeriformes, suborder Oscines; SWALLOW.

HISTOGRAM: see BIOSTATISTICS.

HOARDING: see FEEDING HABITS.

HOATZIN: *Opisthocomus hoatzin*, sole member of the Opisthocomidae (Galliformes, suborder Opisthocomi). It is an inhabitant of the flooded forested borders of quiet streams in Amazonia, one of the most peculiar birds evolved in this greatest river system in the world. Local names are 'Cigana' (gypsy, because of its extravagant dress) and 'Catingueiro' (musk-smelling).

Characteristics. The Hoatzin resembles in general appearance the guans and chachalacas (Cracidae, see CURASSOW). Its total length is some 60 cm but it weighs little more than 810 g as the body is quite small. The sexes are almost alike. The remarkably small head on its long, thin neck bears a long, erect and bristly crest. The short but heavy bill is operated by strong muscles and the upper mandible is articulated with the skull and so is moveable, a feature found in the parrots (Psittacidae) and some other groups (see BILL). The wings are very large in relation to the body but are weak owing to the reduced flight muscles (see below). The tail is both long and broad, the legs and toes are stout. The plumage of the upper parts is dark brown, spotted with white in places; the crest is reddish brown, and the bare facial skin is brilliant blue. The under parts are reddish yellow, the belly rust-coloured.

Systematically the Hoatzin poses a still unsolved problem. Since 1837 it has been tentatively linked with 8 different orders, usually with the Galliformes, but also with the Cuculiformes (Musophagidae), Columbiformes, Gruiformes (Rallidae) and others. Primitive characteristics occur alongside specializations (crop, nasal fossa, wing-claws of the chick, syrinx). The comparative study of the egg-white proteins by Sibley and Ahlquist (1973) indicated that the Hoatzin was most closely allied to the Guirine cuckoos (Crotophagidae), but immunological data (Brush 1979) suggest a closer relationship with the Galliformes and it is retained here in a sub-order of its own. No systematic clues are given by the bird's parasites: the feather lice of the Hoatzin are allied to those of the Green Ibis *Mesembrinibis cayennensis*, found in the same habitat.

A curious anatomical feature is the wing structure of the chick; it recalls that of *Archaeopteryx* and led to the idea that the Hoatzin itself was an archaic relict. The first and second digits carry large claws, moveable by special muscles. These aid it to grasp branches like a climbing reptile, a technique that *Archaeopteryx* may well have used. Correspondingly, the development of the flight feathers is retarded, contrary to what happens in gallinaceous birds generally. As the young grow, they lose their wing-claws and the ability to swim and dive, but continue to use the spread wings to help them awkwardly about the branches, often breaking their primaries in the process.

Another very peculiar morphological character is the digestive tract. While in other vegetarian birds the food is broken up in the gizzard, the crop of the Hoatzin performs this function; it is of unusual size and consists of a number of separate sections which squeeze out and break up the food. To do this, the crop has thick muscular walls and a horny internal layer, whereas the true gizzard is much reduced. The size and weight of the full crop makes the Hoatzin top-heavy and when crouching on branches it keeps its balance by leaning on its sternum, which is covered by a specially-developed callosity. The pectoral girdle is totally transformed by the size of the crop. When the bird jumps from branch to branch, it maintains its equilibrium by spreading its wings and flapping its tail. The feet do not provide a sufficient grip on the branches, unlike the curassows' which can cling firmly even on thin branches.

Hoatzins have a musky odour varying in intensity with the individual and the season (hence the name 'stinking bird'). There is a widespread notion that the flesh also has this smell, which has caused the natives to leave the birds alone, except to use them as bait for fishing. Sometimes they are used for medicinal purposes. The eggs are always much in demand and Hoatzins are rapidly diminishing near human settlements.

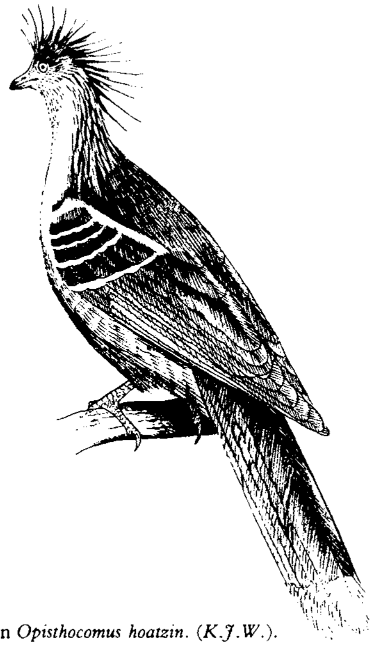
Habitat and food. The Hoatzin occurs from Guyana and Brazil to Ecuador and Bolivia, in permanently flooded forests along the overgrown shores of the Amazon, the Orinoco and rivers of the Guyanas; it can only exist where certain marshy plants are available as food; these include the great *Montrichardia* (Araceae) and the arboreal White Mangrove *Avicennia*. The birds feed on the tough, caustic leaves, flowers and fruit of these plants. Occasionally they take small animals, including fish and crabs, which they catch in the mud or shallow water under hanging vegetation. While so occupied they sometimes fall into the water, or even jump into it when shallow.

Behaviour. Hoatzins are sedentary; they consort in pairs but live in flocks of 10–20 (numbers up to 30 or more were formerly recorded). They are most active in the morning and evening and on moonlit nights. They like to climb to the tops of low trees along the shore, whence they look about them and fly clumsily across small bays and creeks, frequently gliding. During the hottest part of the day they rest hidden in the shadow of the dense woodland.

The Hoatzin has a very conspicuous display: it raises its enormous wings vertically, showing a big black area against a whitish background and contrasting sharply with the deep reddish colour of the rest of the wing and the flanks. It is a kind of 'eye effect', although the area is not round but square.

Voice. Their loud, hoarse cries and hissing sounds make their presence known from afar. The name 'Hoatzin' is said to be Indian and onomatopoeic, based on some of their cries. When calling, the birds usually spread wings and tail.

Breeding. Hoatzins breed more or less throughout the year in colonies and make their nests on branches 2–6 m above the water. The nest is flat, of dry twigs, loosely entwined. There are 2–4 eggs, relatively small, yellowish with pink spots; their shape varies considerably; the average size is 46 × 33 mm. The young hatch after about 4 weeks and have two successive down plumages. Although they stay in the nest for some weeks, they soon become adventurous and start making excursions, using their wings as hands. As, at that time, they also have a good grip with feet and bill, like parrots, they are able to clamber about without mishap. This method of locomotion is an excellent adaptation to the mangrove jungles. When danger threatens, the chicks let themselves fall into the water, where they dive and swim off, using both wings and feet. Afterwards they climb out again and continue their way through the branches.



Hoatzin *Opisthocomus hoatzin*. (*K.J.W.*).

The parents feed the young from the crop, the chick putting its head well into the widely gaping bill of the adult. As at times there are more than two mature birds visiting a nest and females exceed males in collections, some authors have suspected polygamy. H.S.

Beebe, W. 1909. A contribution to the ecology of the adult Hoatzin. Zoologica (N.Y.) 1: 45–66.

Brush, A.H. 1979. Comparison of egg-white proteins: effect of electrophoretic conditions. Biochem. Syst. and Ecology 7: 155–165.

Parker, W.K. 1891. On the morphology of a reptilian bird, *Opisthocomus cristatus*. Trans. Zool. Soc. 13 II.

Sibley, C.G. & Ahlquist, J.E. 1973. The relationships of the Hoatzin. Auk 90: 1–13.

Stegmann, B.C. 1978. Relationships of the Superorders Alectoromorphae and Charadriomorphae: a comparative study of the avian hand. Publ. Nuttall Ornith. Club 17: 1–119.

HOBBY: substantive name of certain small *Falco* spp.; used without qualification, in Britain, for *F. subbuteo* (see FALCON).

HOLARCTIC REGION: the Palearctic and Nearctic Regions combined—see DISTRIBUTION, GEOGRAPHICAL; NEARCTIC REGION; PALEARCTIC REGION.

HOLDING: using the feet to grasp food or other objects (except perches—see PERCHING). Most birds do not use the feet in this way, 'manual' functions devolving entirely on the bill (see BILL). Some birds indeed have feet obviously incapable of a prehensile function, e.g. when adapted to running or swimming (see LEG). Among the exceptions, parrots are specially notable, often using a foot very much as a hand when feeding. Birds-of-prey and owls make much use of the feet in seizing, killing, holding, and dismembering their food. To some extent this is true also of some of the 'minor raptors', such as figure prominently in the list of families given below. Tits *Parus* spp. not only hold food with the foot but can learn to pull up a hanging string with food at the end of it, the pulling being done with the bill but the successive lengths being secured on the perch with the feet. Further examples of use of the feet for holding food and so on are to be found among the toucans, nuthatches, shrikes, pepper-shrikes, shrike-vireos, drongos, wattle-birds, bell-magpies, and crows; this list is not necessarily exhaustive—the Purple Gallinule *Porphyrio porphyrio* (in Africa) is, rather unexpectedly, described as holding food up to its bill while it bites pieces off. In at least some of these cases the held object may be carried in flight (see CARRYING).

HOLORHINAL: see NARIS.

HOLOTHECAL: see BOOTED; LEG.

HOLOTYPE: see TYPE SPECIMEN.

HOMALOGONATAE: birds with an ambiens muscle (Garrod)—see MUSCULATURE.

HOME RANGE: the area occupied by an individual, a pair or a group of birds. When the area is defended, it is referred to as a TERRITORY.

HOMING PIGEON: a domestic pigeon *Columba livia* var. used for 'homing', either as a carrier of messages or in the sport of pigeon racing. Pigeons have been used to convey messages since the days of the ancient Egyptians, and were much used by the Greeks and in the Roman Empire and generally throughout the Middle East. Regular pigeon-posts were established and military operations were supported. The most famous siege use of pigeons was in Paris in 1870–1871, when 150,000 official and a million private messages (microphotographed) were passed. With the advent of telegraphy and wireless the civilian use of pigeon-post disappeared, but in both World Wars much use was made of them. In the 1939–45 war some 200,000 birds were supplied by private breeders to the British Services and 50,000 were reared by the US Army; nearly 17,000 were parachuted to the Resistance in German-occupied Europe and 2,000 returned safely. Many airmen owed their lives to the SOS messages carried by pigeons released when aircraft crash-landed at sea.

To fit pigeons for close support of modern warfare, birds were trained to home to mobile lofts, moved a short distance each day; only moderate success was obtained with intense training, and the birds were particularly likely to go astray if they were required to cross old flight lines, as in a retreat. Attempts were also made to establish a two-way message service by feeding the birds in one place and giving them grit, water, and roosts in another; this was useful only over short distances. Drastic selection provided pigeons that would fly short distances at night, up to 25 km. All these specialized techniques of training laid heavy emphasis on the birds being given an intimate knowledge of the country in which they were to fly. Pigeons sent long distances and returning to an established base were trained by a series of releases, at increasing distances, in the direction from which they would eventually have to return.

Directional training of that kind is also the basis of pigeon racing. This is an important sport and there are perhaps 100,000 pigeon fanciers in Britain alone, with something like 2 million pigeons in their lofts. The sport developed with the advent of the railways, which provided swift transport to distant release points. The first pigeon race over 150 km was held in 1818 in Belgium, and similar races had been established in England by 1875. Such distances are nowadays considered suitable for young birds of the year; yearlings will fly races of 480 km, and older birds up to 800 km. Because of heavier losses at sea-crossings the longer races, 1,000–1,300 km from the Faeroe Islands in the north and from San Sebastian (Spain) in the south, are seldom flown. In continental North America races of 1,600 km are often flown, although no birds return in one day. Only a small fraction, perhaps 1 in 20, of pigeons come through all the initial stages and return from the long-distance races.

Elaborate precautions are taken to ensure correct timing and to eliminate fraud. Before release a temporary rubber leg-band with a code number is put on each bird by officials. On its return the owner removes the band and drops it into a sealed time-check clock which marks the hour and minute of arrival. The distance from the release point to the home loft is measured to the nearest yard on a great circle, and the speed of the bird expressed in yards per minute. In good conditions homing speeds of 1,200 y.p.m. are common, while with tail winds they may be in excess of 2,000 y.p.m. Birds may, apparently, fly for up to 16 hours a day. Competition is within clubs and within area federations; prize money is relatively modest but is increased by systems of 'pooling' for the big national races. Birds that have been successful in such races are much in demand as breeders and can command extremely high prices. Much attention is paid to pedigrees, but there is general agreement that the only real test of an individual is its performance in races. Various fads about body shape and colour come and go; there is a school of thought that stresses 'eye-sign', the configuration of the ciliary muscle of the pupil, and in view of the overriding importance of the eye it is not impossible that there may be something in this idea. There are also numerous techniques that are supposed to increase the speed of homing, but little agreement as to whether, for instance, cocks or hens home faster or whether they should preferably be incubating eggs or feeding young. The 'widowhood' system seeks to send cocks off to a race in a frenzy of sexual passion.

Although pigeon races are essentially one-directional, the direction selected being that which gives the longest runs to the home area, it is well known that good homers can return, although not so swiftly or certainly, from other than the training direction. This indication of a more advanced form of navigational ability has been seized upon in testing theories of bird navigation (see NAVIGATION). The pigeon is certainly a bird readily amenable to experimental treatment, but a great deal of confusion has resulted from the use of birds of inferior stock. There is a wide range of individual variation in homing ability.

Other species have been used for message carrying. The Romans used swallows (Hirundinidae) to convey the winning colours of chariot-races, but these were wild birds caught at their nests on the day required. Pacific islanders, however, have tamed frigatebirds *Fregata* sp. and use them for inter-island communication.

In a different category were the 'shore-sighting' birds carried by ships of olden times. The technique was known in countries as far apart as Scandinavia and Ceylon. Ravens *Corvus corax* were particularly favoured and were released when land should be near; if the bird made off, it not only confirmed the presence of land but indicated its direction.

G.V.T.M.

Levi, W.M. 1951. The Pigeons. Columbia, S.C.

HOMOIOTHERMAL: 'warm-blooded', as contrasted with 'poikilothermal' or 'cold-blooded'; other spellings and alternative terminations are sometimes used (see ENERGETICS; HEAT REGULATION).

HOMOLOGUE: a structure basically equivalent to another (but possibly adapted in a different way)—compare ANALOGUE.

HOMOLOGY: a fundamental concept in comparative evolutionary studies, whether of morphological or behavioural features. Bock (1969) gives the following definition: 'Homologous features (or conditions of features) in two or more organisms are those that can be traced back phylogenetically to the same feature (or condition) in the immediate common ancestor of these organisms'. 'Analogy' is often taken as the opposite term but, as this term is used in a variety of other senses, Bock advocates the term 'non-homology' where attributes in two or more organisms cannot be traced phylogenetically to the same attribute in their immediate common ancestor. Discrimination of homologous features becomes a problem in morphologically uniform groups such as many bird taxa, and Bock has proposed the term 'pseudohomology' for some of the closely similar features or conditions that may arise independently in two or more members of such groups. P.J.K.B.

Bock, W.J. 1963. Evolution and phylogeny in morphologically uniform groups. Amer. Natur. 97: 265–285.

Bock, W.J. 1969. The concept of homology. Ann. N.Y. Acad. Sci. 167: 71–73.

Bock, W.J. 1974. The avian skeletomuscular system. *In* Farner, D.S. & King, J.R. (eds.). Avian Biology, vol. IV. New York.

HOMONYM: see NOMENCLATURE.

HOMOZYGOUS: see GENETICS.

HONEY-BUZZARD: name of *Pernis apivorus* and allies (see HAWK).

HONEYCREEPER: substantive name of some species of Thraupinae (see TANAGER), which were formerly combined with the BANANAQUIT, ORANGEQUIT, CONEBILLS and FLOWER-PIERCERS in the family Coerebidae (Passeriformes, suborder Oscines). In this older classification, 'honeycreepers' was the general term for the family. This term is inappropriate for the family Coerebidae as here recognized, since none of the 3 genera now included, *Coereba* (Bananaquit) and *Conirostrum* and *Oreomanes* (conebills), are generally known as honeycreepers. In what follows, the term 'honeycreeper' is restricted to the thraupine genera *Cyanerpes*, *Chlorophanes*, *Dacnis* and *Xenodacnis*, the last a little known genus represented by one species in the Andes and perhaps not closely related to the others. The 4 genera comprise 15 species, all confined to the American tropics.

The honeycreepers represent a line of specialization within the large assemblage of tanagers leading, from the typical tanagers' diet of insects and fruit, to nectar-eating. In *Dacnis* the bill is sharp, slightly decurved, and quite short, and thus not very different from that of some typical tanagers. *Chlorophanes* has a longer, more curved bill, and the extreme is reached in the Purple Honeycreeper *Cyanerpes caeruleus*, in which the bill is very long and curved and nectar and fruit juices are important elements in the diet. Together with the bill, the tongue is progressively modified into a tubular structure adapted for sucking. Even the most specialized honeycreepers, however, feed also on insects and small whole fruits, the long bill enabling them to probe for insects and to extract the arillate seeds from the splitting capsules of such plants as *Clusia*.

Male honeycreepers are brilliantly coloured, with unrivalled shades of deep blue, turquoise-blue and blue-green; the females are much duller, predominantly greenish. The male Blue (or Red-legged) Honeycreeper *Cyanerpes cyaneus* is peculiar in moulting, at least in parts of its range, into a female-type plumage during the non-breeding season. Honeycreepers are typically birds of forest and forest-edge, doing most of their foraging in the forest canopy; but cultivation with trees forms a suitable habitat for several species. In general behaviour they are typical TANAGERS; they live in pairs, have poorly developed, unmusical vocalizations, and build cup-shaped nests in trees and shrubs. D.W.S. (1)

Skutch, A.F. 1962. Life histories of honeycreepers. Condor 64: 92–116.

HONEYCREEPER, HAWAIIAN: see HAWAIIAN HONEYCREEPER.

HONEYEATER: substantive name of many species of Meliphagidae (Passeriformes, suborder Oscines); in the plural, general term for the family. This is a group of mainly arboreal, nectar-, insect- and fruit-eating birds of Australasian distribution.

Characteristics. The most striking family character is the brush-tongue, an adaptation to nectar feeding, but in its structure notably different from that of other major nectar-feeding groups of birds.

The tongue is prolonged and protrusible. The basal part is curled up on each side, forming two long grooves. The distal part is deeply cleft into 4 parts, which on their edges are delicately frayed and together form the 'brush' which licks up the nectar. The tongue is extended into nectar, or other liquids, about 10 times per second and liquid is taken up by capillary action. The tongue is then withdrawn into the beak which is closed, and projections on the roof of the beak appear to compress liquid from the brush along the groove to the throat. In spite of much variation and secondary changes, the basic characters of the tongue are present in all members of the family. A more rudimentary brush-tongue is found in other birds which feed on nectar less frequently e.g. silvereyes *Zosterops*, wood-swallows (Artamidae) and Australian chats (Ephthianuridae).

Other characters widespread in the family are the pervious nostrils, and the tendency to absence of feathers from parts of the face, on which develop bare spaces, or even lobes, wattles, or other appendages. The plumage is in most species rather dull, greenish, greyish brown, or streaked; the sexes being similar. The most notable exception to this is in several species of *Myzomela*, which possess contrasting patches of sanguineous red in the plumage and display a pronounced sexual dimorphism. In many honeyeaters there is a conspicuous yellow, golden or white patch on the posterior part of the ear region; this character is particularly well developed in the members of the large genus *Meliphaga*.

The honeyeaters display extraordinary variation in structure (lengths 9.5–32 cm), bill form, body proportions, and even mode of life. They include birds resembling goldcrests *Regulus* spp., other warblers (Sylviinae), and thrushes (Turdinae); species that could be mistaken for sunbirds (Nectariniidae) or hummingbirds (Trochilidae); species with falcate bills like Hawaiian honeycreepers (Drepanididae) or bee-eaters (Meropidae); larger species approaching the appearance of orioles (Oriolidae), jays and magpies (Corvidae); and even birds looking very similar to tits (Paridae), nuthatches (Sittidae), babblers (Timaliidae) and flycatchers (Muscicapinae). This extreme variation has been compared with that of the marsupials among mammals; and, although this may be exaggerated, there is obviously a striking parallelism in history and evolution in these two groups.

Habitat. In such a large and diversified group as the honeyeaters, ecology and behaviour are of course extremely varied. Common to almost all honeyeaters is their arboreal habit. Only a few descend to the ground for feeding e.g. *Manorina* and the Tawny-crowned Honeyeater *Phylidonyris melanops* and not a single species places its nest on the ground, although the latter species makes use of high grassy tussocks as nesting sites. Honeyeaters are mainly birds of forests and heathlands, where they frequent tree-tops and flowering trees and shrubs. Several species, most of them inhabiting the continent of Australia, have become adapted to the more open and arid woodlands. No species can exist in completely treeless country, however, but a single species, the Singing Honeyeater *Meliphaga virescens*, ranges right to the coastal sand-dunes and also inhabits the small islands off the barren south and west coasts of Australia. Many species are attached to the mangrove swamps, savannas, heathland and mallee, a few even to the mulga scrub, while in the desert-like spinifex country in the interior of Australia only one species, the Pied Honeyeater *Certhionyx variegatus*, is occasionally encountered. There is a tendency for different species in some genera, *Meliphaga, Melithreptus, Manorina*, to occur in separate, though often neighbouring habitats. Several species are restricted to the high mountains of New Guinea (*Melipotes, Melidectes* and others), while some, most of them belonging to the genera *Myzomela* and *Lichmera*, are inhabitants of small oceanic islands.

Tui *Prosthemadera novaeseelandiae*. (C.E.T.K.).

Distribution. Honeyeaters belong to the Australasian region, where they are widely distributed and form one of the most characteristic bird groups. Only one species, the Brown Honeyeater *Lichmera indistincta*, has crossed Wallace's Line and settled in Bali; another species, *Apalopteron familiaris*, inhabits the Bonin Islands, which are regarded as belonging to the Palearctic Region. To the east the range of the honeyeaters includes the greater part of Micronesia, Melanesia, Polynesia (east to Samoa and Tonga), the Hawaiian Islands, and the New Zealand islands.

The 167 species of honeyeaters (including a total of about 450 sub-species) are divided among 38 genera, of which 14 are monotypic. The largest genera are *Meliphaga* (36 species), *Myzomela* (24 species), and *Philemon* (16 species). New Guinea and the Australian mainland form the centres of distribution and are inhabited by an almost equal number of species—New Guinea (with satellite islands) by 63 species, Australia (with Tasmania) by 68 species. The New Guinea honeyeaters are generally more primitive and unspecialized, while the Australian (and New Zealand) forms include a great number of specialized and derivative types.

Food. Nectar and insects form the major part of the diet of most honeyeaters. In addition, many of the larger honeyeaters feed also on fruits and berries and may do some damage in Australian orchards. The tropical rainforest species are predominantly frugivorous. Pollen is consumed but probably not digested. Honeydew from scale insects, manna (sugary granules from damaged eucalypt leaves) and lerp (coats of sap-sucking insects) also form an important part of the diet of some species.

Behaviour and movements. Honeyeaters are more or less gregarious; no species is solitary. They tend to move around in small parties, especially outside the breeding season, and under certain conditions large swarms concentrate around flowering trees. Some open-country species are markedly nomadic; a few subtropical-temperate species make regular seasonal movements, whereas in many other species the movements are more complex and appear less regular. The flight may be swift in smaller species, and more clumsy and undulating in the larger species, almost like that of the Magpie *Pica pica*.

Voice. The vocal utterances differ widely. Many of the smaller species are excellent songsters, while the larger ones are not so musical and utter various harsh and noisy babbling sounds, usually characteristic of the genus. The Bell Miner *Manorina melanophrys* has a peculiar song, resembling the tinkling of a silver bell; the song of the New Zealand Bellbird *Anthornis melanura*, a distant ally, is somewhat similar. The strange Tui *Prosthemadura novaeseelandiae*, also of New Zealand, a glossy bluish-green bird like a Starling *Sturnus* sp. with 2 tufts of white curled feathers on the lower throat, is known to be an excellent mimic of other birds' songs. A few species frequenting open country have song-flights. Some of the species inhabiting dense rainforests are silent.

Breeding. The nest is a cup-shaped, sometimes pendulous, structure, varying considerably in composition and situation. It is placed in trees or bushes, often high up. In several species the nests are placed on branches overhanging water, along rivers or lake borders. Group nesting, in colonies up to 20 or more, is a rather frequent phenomenon, at least in Australian species. Many species of *Meliphaga* and probably all species of *Melithreptus* and *Manorina* are co-operative breeders with several adults, probably chiefly males, feeding the nestlings and fledglings from each nest. The Noisy Miner *Manorina melanocephala* has a particularly complex breeding system. The breeding season of honeyeaters in southern Australia is extended and late winter is the peak for the more nectarivorous species and spring for the more insectivorous ones. Breeding in autumn is quite frequent. A peculiar habit is developed in some species of *Melithreptus* and *Meliphaga*: to obtain nest material they habitually pull hairs off cows, larger marsupials (possums), and even man. The species of *Ramsayornis* are unique among honeyeaters in building closed nests, dome-shaped with a side entrance. The Blue-faced Honeyeater *Entomyzon cyanotis* of Australia differs from all other honeyeaters in using deserted nests of babblers (Timaliinae), preferably those of *Pomatostomus temporalis*, and it is known sometimes to oust the legitimate owners by force.

The eggs are spotted, most often with reddish brown. The clutch consists, in the tropical species, of 1 or 2 eggs, in the subtropical of 2, occasionally 3 eggs, in the larger species often of 4 eggs; and in the temperate species (in New Zealand) also usually of 4 eggs. The participation of the male in nest building and incubation differs widely, and in many species the female alone performs these duties. On the other hand, both sexes share in feeding the young. Incubation periods are from 12–16 days; and fledging periods 10–16 days.

Ecological relations. Many species of honeyeaters (e.g. *Phylidonyris, Acanthorhynchus* and *Anthochaera*) are dependent on the nectar of blossoms of trees and shrubs for a large part of the year. Insects are taken primarily as a source of protein. Others (e.g. *Meliphaga* and *Melithreptus*) feed more on insects, though they readily take nectar, especially in winter in southern Australia, and alternative sources of sugar (honeydew etc.). The species belonging to the Australian genus *Conopophila* have mostly given up nectar feeding and are mainly insectivorous, capturing their prey in the air like flycatchers (Muscicapinae). One species, the Painted Honeyeater *C. picta*, has specialized on mistletoe berries, apart from insects. The members of the New Guinean genus *Melipotes* have also become fruit-eaters; their tongue structure has been secondarily simplified. The 6 species of *Melithreptus* are tit-like, active birds, of which the Strong-billed Honeyeater *M. validirostris* of Tasmania has developed food habits and even a bill-form almost like that of a nuthatch *Sitta* sp. It runs up trunks, taking insects from under the bark, which it pulls off with its powerful bill. The O-o-aa *Moho braccatus* of Hawaii is predominantly insectivorous and searches for food by climbing the boles of trees like a woodpecker (Picidae), aided by its stiff tail-feathers. The spine-bills *Acanthorhynchus* spp. of Australia have long and extremely thin decurved bills, and during nectar feeding are able to hover in front of the blossoms like hummingbirds. The 4 miners *Manorina* spp. are jay-like, noisy, and inquisitive birds. The friar-birds or leatherheads *Philemon* spp. generally resemble jays or jackdaws (Corvidae) but have parts of the head naked and inky black, and many species have a horny protuberance on the bill. They are strange in appearance and utter loud and querulous chatterings. The wattle-birds *Anthochaera* have a pendent wattle on each side of the head, longest and most conspicuous in the Yellow Wattle-bird *A. paradoxa* of Tasmania; they utter peculiar guttural notes, resembling coughing or barking.

All 3 New Zealand honeyeaters feed on nectar, insects and fruit. The large Tui takes much nectar, often defending flowers from the 2 smaller species. The rare Stitchbird *Notiomystis cincta*, now only found on Little Barrier Island, visits the flowers of shrubs, while the Bellbird is more insectivorous.

Blossoms of trees and shrubs constitute the main feeding place of most honeyeaters. Owing to this fact they are very efficient pollinators; in fact they form, together with certain parrots, the most important agents in the fertilization of the greater part of the indigenous Australian tree and shrub flora, such as members of the Myrtaceae, Proteaceae, Epacridaceae, Loranthaceae, Rutaceae, Myoporaceae and Haemodoraceae (see POLLINATORS). An intimate connection exists between the plants and the honeyeaters, and the ornithophilous flowers have developed a number of adaptations to bird visits, just as the honeyeaters in their anatomy demonstrate striking adaptations to nectar feeding; this is true of the tongue, as mentioned above, and also of the alimentary tract. The intestinal canal is rather short and wide, the opening of the oesophagus into the stomach and that of the intestinal canal (pylorus) are placed very closely together, in a little chamber partly separated from the stomach proper. This structure permits nectar and other easily digestible matter to pass directly from the oesophagus to the intestines, while insect food can be retained in the stomach for the necessary period of digestion there.

The structure of the flowers visited by honeyeaters varies from simple and cup-shaped in *Eucalyptus* to long and gullet-shaped as in *Eremophila* and *Anigozanthos*. Pollen is chiefly deposited on the forehead and throat, but also on the crown and even the back, and the pollen of the Epacrids sticks to the beak and nostrils. Areas where nectar is abundant frequently attract large numbers of individuals and species of honeyeaters. Competition for nectar is often severe. Under these conditions larger species may defend territories around rich nectar sources, forcing smaller species into less rich areas.

Sugarbirds. The 2 sugarbirds *Promerops* spp. of South Africa, which are characterized by a long, curved bill and a prolonged, drooping tail, agree with the honeyeaters in most structural characters as well as in life-habits (nest, eggs, feeding). They have, therefore, been incorporated in the Meliphagidae until recently, but must for other reasons (for instance, electrophoresis) be regarded as a special family, not least on account of their remote breeding range (see SUGARBIRD (1)).

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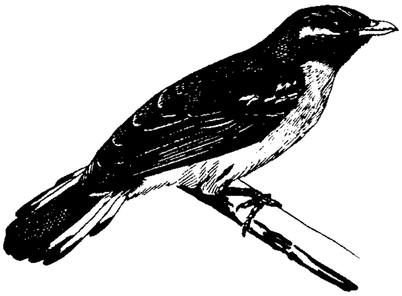
HONEYGUIDE: substantive name of the species of Indicatoridae (Piciformes, suborder Galbulae); in the plural, general term for the family. The family contains 16–19 species, depending on controversial taxonomic decisions exacerbated by inadequate knowledge of the biology of most forms; one (*Melignomon eisentrauti*) discovered as recently as 1965.

Characteristics. All honeyguides are small, 10–20 cm long and weighing 10–55 g. Plumage is dull and inconspicuous, generally olive, grey or brownish above, sometimes obscurely streaked, and lighter below, with dark or dull-coloured bill, legs and feet; *Indicator xanthonotus* has the forehead and rump orange. Most species have pale sides to the tail, often with a pale rump patch, and 2 species have yellow patches on the wing-coverts. Some species have a white spot on the lores and a black malar streak. Sexual dimorphism is usually slight, except in *I. indicator*



Greater Honeyguide *Indicator indicator*. (*C.E.T.K.*).

where the female is typically dull-coloured but the breeding male has the head boldly marked with white cheeks and black throat, and has yellow shoulder patches and a pink bill. The bill is typically stout and blunt, with raised edges around the nostrils except in the 3 small flycatcher-like *Prodotiscus* species which have a fine pointed bill. The legs are short, toes zygodactyl, with strong hooked claws. The wings are pointed, the flight rapid and often weakly undulating. The tail is graduated in most species; in *Melichneutes* it is lyre-shaped. The skin of some species is notably thick, possibly as a defence against insect stings.

Habitat and distribution. All 4 genera (*Indicator, Prodotiscus, Melignomon* and *Melichneutes*) inhabit evergreen forest or forest edge, the first 2 also occurring in more open woodland. All but 2 of the species are confined to Africa south of the Sahara; the 2 exceptions (both *Indicator*) are Oriental, one occurring in south-east Asia, the other in the Himalayas. Most of the African species form closely related groups whose members are so similar that taxonomic treatment remains controversial, especially as the groups themselves are very similar to each other. Within each group, there is a trend towards darker-plumaged species inhabiting evergreen forest and paler species occupying more open woodland. Three or more sibling species may be sympatric, and it is not known how they remain segregated.

Populations and movements. No information for any species.

Food. All the species whose food is known eat insects, but a characteristic peculiarity of the family is that they also eat wax, usually as bee comb but also, in *Prodotiscus* spp., as waxy scale-insects. Some species have been seen eating comb at bees' nests but in others 'cerophagy' (eating wax) is inferred from the presence of wax in the digestive system of collected specimens. Two species (*I. indicator* and *I. minor*) have been shown experimentally to digest wax and to survive for around 4 weeks on wax alone; *I. indicator* can also survive without wax for several months. It is not yet entirely clear whether the wax is digested by symbiotic bacteria, as one experiment suggests, or by an enzyme unique to honeyguides. The parts of the honeycomb most commonly eaten by *I. indicator* in captivity are the larvae and the wax; the honey that contributes to the family name, the pupae and adult bees are taken rarely or not at all. Bees' nests may be detected at least partly by scent since honeyguides can be attracted by the smoke from burning wax.

The habit of feeding on bee comb is associated in the 2 largest species, *I. indicator* and *I. variegatus*, with that of guiding man and other mammals to bees' nests. This behaviour is best known in *I. indicator*; the bird, usually alone, draws attention to itself by a distinctive chattering call, and then flies a short distance towards a bees' nest. This behaviour is repeated until the nest is reached, when the bird sits quietly nearby, coming down to feed at any comb that may be left after the follower has opened the nest. The usual follower apart from man is the Ratel or Honey-Badger *Mellivora capensis*, but baboons *Papio* and even mongooses (Herpestinae) may also respond. Tribesmen in many parts of Africa use honeyguides to lead them to bees' nests, but the habit seems to be declining as alternative sources of sugar become more available. The evolution and development of this complex symbiotic behaviour, especially surprising in a nest parasite, remain obscure.

Behaviour. So far as is known all honeyguides are solitary, individuals aggregating chiefly for mating or at localized food sources.

Voice. Poorly known; in several species the male song is a simple monotonous one repeated from an elevated song post. The guiding chatter of *I. indicator* is distinctive, and a variety of generally rather simple calls, often nasal or squeaky, is recorded from several species. Some species show vigorous vocal interactions with potential hosts even when hosts are not breeding.

Breeding. Of the 7 species whose breeding habits are known, 6 are certainly parasitic but *I. xanthonotus* of the Himalayas apparently is not; it may be significant that this species lacks the white outer tail feathers typical of honeyguides, supporting the possibility that these may be used in luring hosts away from their nest. An observation of an adult *Prodotiscus insignis* feeding a recently-fledged juvenile raises the intriguing possibility that parasitism may not always be complete even in habitually parasitic species (Brosset 1981). Most species parasitize hole-nesting birds, especially barbets, woodpeckers, hoopoes and wood-hoopoes, kingfishers, rollers, bee-eaters and starlings; but the small flycatcher-like *Prodotiscus* species (*P. insignis, P. zambesiae*) parasitize open-nesters such as white-eyes, and *P. regulus* parasitizes hosts with closed nests such as swallows, swifts and some *Cisticola* warblers.

The mating system is known only in *I. xanthonotus.* Males defend territories centred around bees' nests, to which they allow access only to females with which they have mated and their attendant young; this mating system has been described as 'resource-based non-harem polygyny'. Other species have been assumed to be promiscuous, but males of several species have been observed accompanying females attempting to enter host nests, a behaviour unlikely in a promiscuous species. No other honeyguide is known to defend either food sources or mating sites. In *I. indicator* and probably other species, males sing from a conspicuous 'stud post' where females come for mating, which is preceded by rudimentary courtship behaviour and may be followed in *I. indicator* by the male executing a dramatic circling flight in which a loud rattling noise is made by the wing feathers. In *Melichneutes* the lyre-shaped tail apparently also makes a distinctive sound. This may also be connected with courtship behaviour, which includes a display flight above the forest canopy.

Honeyguide eggs are normally thick-shelled and white, except in *P. zambesiae* where they are sometimes blue like those of the *Zosterops* host. Usually only one egg is laid in each nest but there are a few records of 2 honeyguides being reared in one nest. The incubation period is known only for *P. zambesiae* (less than 13 days) and *I. minor* (12 days). The fledging period is about 38 days for *I. minor*, 40 days for *I. indicator*. The chicks of several species bear on each mandible a hook, which is used to destroy host eggs or chicks. The chick is fed exclusively by the hosts at least until fledging; the begging call of nestling *I. indicator* resembles the combined calls of several chicks. A.W.D.

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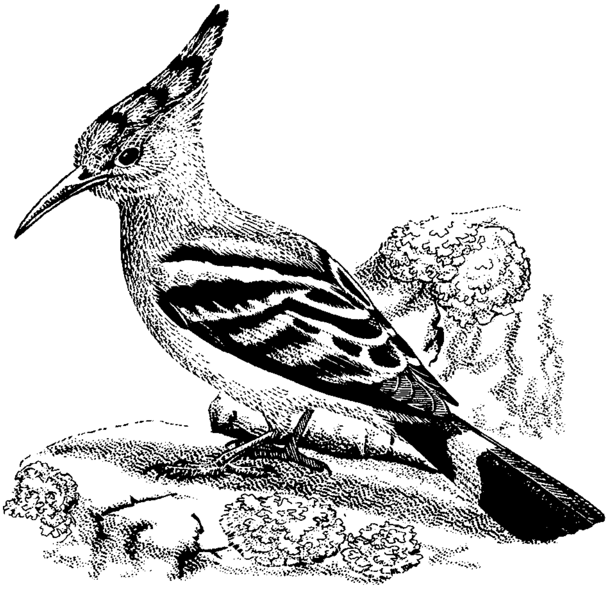
HONKER: name applied in North America to the Canada Goose *Branta canadensis* (see under DUCK).

HOOD: an area of distinctive colour, in some plumage patterns, covering a large part of the head (see TOPOGRAPHY).

HOOKBILL: *Ancistrops strigilatus* (see OVENBIRD (1)).

HOOPOE: *Upupa epops*, sole species of the family Upupidae (Coraciiformes, suborder Coracii), found in some 9 subspecies throughout most of the Palearctic, Afrotropical and Oriental Regions. The Hoopoe is such a striking and unmistakable bird that it has a long pedigree in human culture: it was used as a hieroglyphic in ancient Egypt, figured prominently in Aristophanes' *The Birds*, features widely in folklore, and has long been celebrated in literature. Both of the scientific names, and the vernacular names in several languages including English, are onomatopoeic.



Hoopoe *Upupa epops africana*. (*N.A.*).

Characteristics. Hoopoes are hole-nesting, ground-foraging, insectivorous birds with a long thin decurved beak, short legs and rather weak feet, and plumage of predominant hue varying geographically from pinkish through cinnamon to chestnut. The sexes, and the fledgling, look much alike. There is a long, black-tipped crest which is usually flat, but is opened into a conspicuous fan when the bird alights or is excited. The rump is white and the tail broad and black, with an inverted white chevron across it. The wings are rounded, black, with 1–4 broad bands of white across the secondaries and greater coverts and in some races a further white band crossing both primaries and secondaries subperipherally. Flight is distinctive, with erratic, butterfly-like flapping, the wings closed at each beat; it appears weak and indecisive, but Hoopoes are in fact strong fliers. They are about 31 cm long and weigh 50–60 g (range 40–70 g).

The mutual affinities of coraciiform and piciform families remain controversial (Sibley and Ahlquist 1972). But there is wide agreement that the Hoopoe's closest relatives are the Phoeniculidae (WOOD-HOOPOE), with which it agrees in feather structure (except the absence of an aftershaft), pterylosis, tongue, anatomy, egg-white proteins, visceral and skeletal characters; and there is good evidence also for allying these 2 families closely with the Bucerotidae (HORNBILL). However, *Upupa* differs from all other coraciiform birds in the absence of the expansor secondarium muscle, and in some characters it converges with passerine birds.

Hoopoes being migratory, at certain seasons and places 2 or more subspecies occur together. Where they are distinguishable in the field, it has led to them being treated as specifically distinct (e.g. *U. senegalensis*, *U. africana* and *U. epops* in Africa); but in the absence of breeding sympatry it accords better with current systematic practice to treat Hoopoes as a single polytypic species.

Distribution, habitat and movements. Hoopoes occur in open country in virtually the whole of Africa and Madagascar, and the Oriental and Palearctic Regions north to the Gulf of Finland, the Sakmara River, the southern shores of Lake Baikal, the middle Amur and Khungari Rivers. They breed in the Canaries and most Mediterranean islands, but only exceptionally in Britain and Scandinavia. In south-east Asia they breed throughout Sri Lanka, Indochina and Taiwan but rarely further south in the Malayan peninsula than Pattani. Borneo has only one record, probably a migrant; but a few may nest in northern Sumatra. They do not occur in Korea or Japan. Throughout their breeding range, they prefer open land with scattered trees and some short grass sward or bare soil: pastures, parkland, orchards, steppe, dry and wooded savannas, and broken ground with scattered shrubs to an altitude of 2,500 m. In Africa, drier regions are favoured and lush evergreen woods and forests are shunned. West Palearctic Hoopoes winter in sub-Saharan Africa south to 10°S, and central and east Palearctic populations winter in south Asia from Mesopotamia to southern India and south China. African races are migratory within the tropics. The bird is a diurnal migrant, and over the Mediterranean commonly falls prey to falcons.

Food. Mainly small insects, particularly soft larvae; cockchafers and smaller beetles (larvae and imagines), grasshopper nymphs, caterpillars, ants, flies, termites, earwigs, ant-lions. Also spiders, occasionally earthworms and woodlice, and rarely larger items like centipedes, which have to be broken up before being eaten. Evidently Hoopoes do not regurgitate pellets, but void arthropod sclerites with the faeces. They feed mainly on the ground, walking over turf, dusty or moist soil, pecking and probing assiduously, and may insert the beak full-length into soft soil and dig small holes with the beak to extract prey. Sometimes Hoopoes hawk flying insects, and search the ground beneath flicked-over refuse and dry cow-pats.

Behaviour and voice. Hoopoes are monogamous, and territorial when breeding. No winter territories appear to be held. They occur in pairs or solitarily, but immigrants to breeding grounds form parties up to 9 before reproductive behaviour commences. The young do not feed themselves at all for 6 days after fledging, and thereafter remain in loose family parties with their parents for some weeks. Sexual behaviour is heralded by males beginning to call even when still in prebreeding flocks—a far-carrying, dove-like *hoo hoo* (2–4 notes) given inside or on top of a tree. As territories are established, favoured song-posts are adopted and rival males advertise from 300 m or more apart. 'Swizzle' and 'rattle' calls are given during male–male and male–female chases, and these and other calls during courtship feeding and nest-hole-demonstration by the male to the female (Hirschfeld and Hirschfeld 1973; Skead 1950). There is no additional courtship display; and copulation takes place on the ground.

Nestlings defend themselves by: hissing; rapid upward poking of the head with beak-clapping; a single rapid wing-strike; a stinking secretion of the preen gland (Löhrl 1977); and by the aimed spraying of excreta. Adults have a striking defence posture with the wings and tail widespread on the ground, the head thrown back and the beak upward.

Breeding. Hoopoes nest in holes in trees and walls, or crevices in boulders and old buildings; sometimes in nest-boxes. Nest holes are found and cleared by the male. Sometimes no nest material is used (although droppings accumulate) but at others a distinct bed of grass-bents is made. The whitish eggs are laid daily, clutch sizes being 4–7 in the tropics and 5–8, exceptionally 12, in Europe. The female incubates and is fed by the male, occasionally emerging to feed herself too. She remains in the nest for about a week after the last egg hatches, then both parents provide food. The incubation period is 17 days and the nestling period 26–32 days (South Africa). Nest sanitation is primitive. The species is double, possibly treble, brooded. C.H.F.

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HOOTING: term applied, where appropriate, to the calling of certain birds, especially owls (Strigiformes).

HOPPING: see LEG; LOCOMOTION, TERRESTRIAL.

HORIZONTAL AND VERTICAL CLASSIFICATION: a horizontal system of CLASSIFICATION is one that includes only birds existing at the same level of geological time. A system thoroughly phylogenetic in its scope must, however, take into account also those fossil forms that produce a vertical arrangement in which, so to speak, time is a dimension. Such an arrangement can be depicted as a branching tree.

HORMONES: internal secretions having specific physiological actions (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

HORNBILL: substantive name of all members of Bucerotidae (Coraciiformes, suborder Bucerotes). A discrete and distinctive family, most closely allied to the hoopoes (Phoeniculidae, Upupidae), but not related to the toucans (Ramphastidae) of the New World, although they may be their ecological counterpart.

Characteristics. Hornbills have fused axis and atlas vertebrae, and are noted for their long, heavy bills, each with a casque on top. In some species the bill has ridges or notches on its sides. The casque is light and hollow, supported internally by thin bony struts, and may be elaborately shaped and as large as the bill. Hornbills have long eyelashes, short legs with syndactylous toes and broad soles, broad, rather short wings, and long tails which are graduated in some species. The flight is direct and consists of bouts of flapping and gliding, and is often noisy as air rushes through the bases of the flight feathers not covered by stiff coverts. Most species hop on the ground, but a few terrestrial ones walk. The plumage is white, black or brown, sometimes with a metallic sheen. Bare areas of skin on the face and throat, the eyes, and the bill and casque are often brightly coloured, the colours changing with age. Differences in these colours also occur between the sexes which are dimorphic, to a greater or lesser extent, through size (males being slightly larger than females), through differences in plumage, and through the shape and size of the casque. All hornbills (apart from 2 ground hornbills in *Bucorvus*) seal the entrance of their nesthole.

These characteristics have made hornbills mystical birds. Some African tribes place *Bucorvus* heads on their own heads as camouflage when hunting game, and many taboos exist about who may eat hornbills, when and for what reasons. Asian and Polynesian tribes use tail feathers of the large hornbills for head-dress and cloak ornamentation. In Borneo the Rhinoceros Hornbill *Buceros rhinoceros* is revered, the recurved casque being symbolized as spirals on large carved effigies, and it forms the centre-piece of the coat-of-arms of Sarawak. Ivory from the casque of the Helmeted Hornbill *Rhinoplax vigil* is intricately carved as earrings, belt buckles and other trinkets, and has been a highly valued export from the region to China since at least the 12th century. As a result hornbills are being protected, legally or by taboo, in many areas. (See also ORNAMENTATION, BIRDS IN HUMAN.)

Systematic characteristics. The 45 species of hornbills are usually placed in 14 genera; *Tockus* (14), *Rhyticeros* (7), *Bycanistes* (5), *Anthracoceros* (4), *Buceros* (3), *Penelopides* (2), *Bucorvus* (2), *Ceratogymna* (2), and the monotypic genera *Aceros, Anorrhinus, Berenicornis, Ptilolaemus, Rhinoplax* and *Tropicranus*. As far as is known all nestlings of *Tockus, Anthracoceros, Penelopides, Anorrhinus, Berenicornis, Ptilolaemus* and *Tropicranus* have pink skin on hatching and this remains pink, whereas in the remaining genera the pink coloration changes to a deep purple–black within a few days of hatching.

Hornbills vary in size from the relatively small *Tockus* species (*c.* 38–46 cm), through the medium-sized species in *Anorrhinus, Anthracoceros, Berenicornis, Ptilolaemus* and *Tropicranus* (range *c.* 68–92 cm), to the very large species in *Aceros, Buceros, Bucorvus* and *Rhinoplax* (*c.* 116–126 cm).

The African *Tockus* species and the closely related Long-crested Hornbill *Tropicranus albicristatus*, with its white crest and long graduated tail, are the only hornbills that bring single items of food to the nest. The others, apart from the ground hornbills, regurgitate food at the nest, item by item, from the gullet. The Asian species of *Tockus* may deserve their own genus for they differ from the African species in having young with yellow bills, as do other Asian genera, and when calling do not display, whereas the African species are very vocal and do display. They appear to be linked to the poorly defined *Anthracoceros* genus, most of which have very large casques in both sexes, but differ among themselves in calls, behaviour and breeding biology.

Although the Bushy-crested Hornbill *Anorrhinus galeritus* and the Brown-backed Hornbill *Ptilolaemus tickelli* have similar calls and share their own genus of louse, they are kept in monotypic genera as their colour and breeding biology are different.

Sexual dimorphism is pronounced in the White-crested Hornbill *Berenicornis comatus, Penelopides* spp., the Rufous-necked Hornbill *Aceros nipalensis* and in *Rhyticeros* spp. In the last 2 genera the head and neck are brown and white in males and black in females, and the immatures are like adult males. In most species their tails are short and white. Each species of *Rhyticeros* has a distinctive casque shape, variously wreathed and wrinkled, and the bare areas on the face are often extensive and colourful. The White-crested Hornbill has a long crest and a long graduated tail. Little is known about it, and it may be related to *Anorrhinus* and *Ptilolaemus*. The *Penelopides* species, one highly polymorphic, have similar calls and tail patterns to *Anorrhinus* and both may be closely linked.

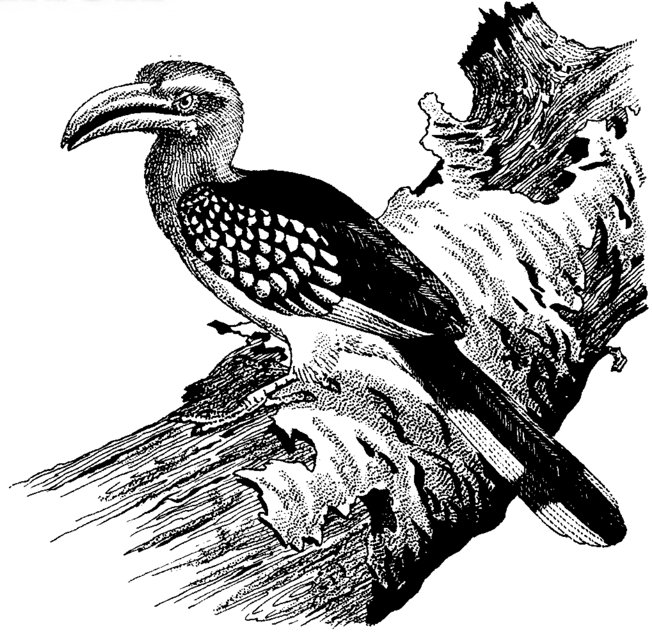
Several species of hornbills, the Helmeted Hornbill *Rhinoplax vigil, Buceros*, and *Bucorvus*, have oil glands which provide cosmetic coloration for bills, casques and white areas of plumage. In *Buceros* the yellow and orange coloration is applied using a special tuft of feathers that surrounds the gland. All *Buceros* species and the Helmeted Hornbill have brightly coloured feet, greenish-yellow in *Buceros*, reddish-brown in *Rhinoplax* and usually dark slate grey in other genera, white tails with a black band, and elaborate and large casques. The Helmeted Hornbill differs in having extensive bare skin on the head and neck, greatly elongated tail feathers, and the front of the casque composed of solid 'ivory' so that its skull is 10% of the body mass. These 3 genera also share a unique genus of louse, although *Buceros* and the Helmeted Hornbill are arboreal while *Bucorvus* species are terrestrial. The ground hornbills are aberrant: in addition to the differences already mentioned, they have an extra cervical vertebra (15 instead of 14), long tarsi and a short tail, and extensive and inflatable facial skin areas. They walk on the tips of their toes, and scrape and dig the ground with their bills in search of food. They are the only hornbills that excavate their own nest hole if required, and show no nest sanitation. They also deliver the food to the nest as a collection of items in the bill.

Seven species in the genera *Bycanistes* and *Ceratogymna* are closely allied. Immatures resemble adult females in having brown on the head and neck, and males have greatly enlarged casques. *Bycanistes* species are distinguishable by their white rumps, and *Ceratogymna* species by the throat wattles of loose skin.

Habitat. All but 11 of the 45 species occupy forest of one type or other, although some of these (in *Tockus, Bycanistes* and *Anthracoceros*) show wide habitat tolerance and may be found along forest edge and in riparian woodland extending into savanna areas. The savanna species (9 *Tockus*, 2 *Bucorvus*) are found in habitat ranging from woodland to arid grassland and even semi desert in south-west Africa where Monteiro's Hornbill *Tockus monteiri* occurs. All are confined to Africa except the Indian Grey Hornbill *Tockus birostris*.

Distribution. There are 22 hornbills in the Afrotropical region, 19 in the Oriental region and 4 species in the Australasian region. The genera *Tropicranus, Bycanistes, Ceratogymna*, and *Bucorvus* are African. The majority of *Tockus* species are African but 2, not considered closely related, are Oriental. The remaining genera are Oriental, with representative species in *Rhyticeros* (3) and *Penelopides* (1) extending into the Australasian region. Two species of *Rhyticeros* (the Narcondam Hornbill *R. narcondami* and Sumba Hornbill *R. everetti*) have a very restricted range, each confined to a South East Asian island. A fossil hornbill is known from Germany.

Movements. Most species seem to be sedentary and territorial throughout the year. Some savanna *Tockus* species form into flocks in the non-breeding season, moving locally in search of food, and these movements may entail regular local or altitudinal migrations in some areas. In Nigeria, the resident population of the Grey Hornbill *Tockus nasutus* in the Sudan zone (11°–13°N) is joined by immigrants from the



Yellow-billed Hornbill *Tockus flavirostris*. (*N.A.*).

Guinea zone (8°–11°N) after breeding there. Frugivorous species in forest, such as *Bycanistes*, *Ceratogymna* and *Rhyticeros*, may never hold territories, ranging randomly over a wide area in search of fruiting trees.

Food. Most species are omnivorous, eating fruit as well as small animals. *Tockus* and *Tropicranus* species are largely insectivorous, some of them following army ants or troops of monkeys for the insects they disturb. The ground hornbills appear to be entirely carnivorous, catching reptiles, including large and venomous snakes, birds, squirrels, rodents and animals the size of hares. Tortoises are dug out of their shells as well as fossorial toads and beetles from the ground. Their main diet, however, is insects, especially grasshoppers and beetles. Most of the forest species rely on fruit as their main diet but supplement it with any small animal disturbed in the foliage. Many are known to increase the amount of animal prey during the breeding season but this is minimal for *Bycanistes* and *Ceratogymna* species. During the nesting period of the Silvery-cheeked Hornbill *Bycanistes brevis*, it has been estimated that the male makes 1,600 deliveries of food with average loads of 15 fruits.

Food is simply picked up or plucked where found, the long bill being an effective pair of forceps to handle sticky or dangerous items. Some species dig out their food, and the more aerial species hawk or capture food while in flight. Limited observations suggest that *Rhinoplax* may use its bill in the manner of a giant woodpecker.

Only *Ceratogymna* species have been recorded drinking water and then only twice, once in natural habitat and the other in a zoo.

Behaviour. Most species are sedentary and live as pairs within their territory, which ranges from 10 ha in small *Tockus* species to 10,000 ha in *Bucorvus*. Some species form flocks during the non-breeding season but these break up into pairs at the beginning of the breeding season. In a few species there are social groups which defend a common territory and breed co-operatively, a breeding pair being assisted throughout the year by other members in defence of the territory and in bringing food to the nest. This is known to occur in *Anorrhinus* and *Bucorvus* species and probably in some *Berenicornis*, *Buceros* and *Tockus* species. Hornbills display threat by raising the bill and exposing the throat, which is often coloured distinctively, at other times by beating on a log, and occasionally by bill-grappling and fighting. Submission is shown by bowing the head, and often leads on to ALLOPREENING between pairs or group members. Dominance within a group may be mediated by gestures either of food acceptance or its refusal. Several species have special warming postures. Bathing in standing water is unknown, but several species bathe in wet foliage or in rain and so become soaked. The majority of species sunbathe regularly with outstretched wings.

Voice. Hornbills are very vocal and have a variety of calls. Most of the smaller species, which are probably the most primitive, utter a series of clucks with the head bowed. They also use high pitched cries and whistles while raising their heads and pointing their bills vertically upwards. These vocal displays are often accompanied either by wing-flapping or flicking movements of the tail or head, or by fanning the tail over the back as found in Hemprich's Hornbill *Tockus hemprichii* and *Aceros*, 2 unrelated birds. The larger species utter soft hoots (*Berenicornis*), short barks (*Rhyticeros* and *Aceros*), a variety of whistles, wails, clicks and brays (*Bycanistes* and *Ceratogymna*), and deep booming noises, usually before dawn, which may be heard at 5 km distance (*Bucorvus*). Calls of *Buceros* species and *Rhinoplax vigil* are given often as duets. The latter has a most striking call, an accelerating series of hoots, breaking into maniacal laughter, which makes it one of the never-to-be-forgotten noises of the Asian forests.

Breeding. Apart from the ground hornbills, it is usual for a pair of hornbills to select a natural hole in a tree, sometimes in a rock face, as a nest site. The entrance is sealed to form a vertical slit. In most species this is the task of the female, although males in some species may assist, and in *Bycanistes* and *Ceratogymna* they supply the female with specially prepared sealing material. The sealing proceeds in stages, often initially with mud from the outside, until the female is just able to enter the nest hole. The timing of the final entrance of the female, before she seals herself in, is probably determined to some extent by the amount of food she receives from the male during courtship. The male may now pass lining, such as leaves and bark, through the slit to the female and mollusc shells that may be important as a source of calcium for egg production. The sealed nest protects the female and chicks from predators, but, in addition to this, most nests have a long funk-hole above them into which the female and chick can crawl out of reach. Ventilation in the nest is maintained by convection.

Egg-laying may be delayed for several days after the female has sealed herself in, but once started occurs at intervals of a day in *Tockus* species but at longer intervals in the larger species. Females of *Bycanistes*, *Ceratogymna* and *Bucorvus* species do not moult while breeding but have a normal successive replacement of feathers as do males and non-breeding females. They are, therefore, able to fly at all times and this may be a result of an unpredictable food supply or predation risk, both making flight necessary at times. Although not thoroughly studied, many breeding females of other genera, possibly all, are flightless within a few days of laying because of a rapid moult of rectrices followed by the remiges. A staggered moult of the body feathers also begins. By the time the females leave the nest, their flight feathers are renewed.

The breeding of many species is little known and only a few species have been studied thoroughly. Incubation of the white eggs, which are oval and rather pitted, begins with the first egg, and the incubation period ranges from 25 days (*Tockus*) to 40 days (*Bucorvus*). Some species lay 1 or 2 eggs, usually 2, but others may lay more (*Anthracoceros* 3–4, *Aceros* 3, *Penelopides* 4, Asian *Tockus* species 4, and *Ptilolaemus* 5) and African *Tockus* species may lay up to 7. The nestling periods range from 45 days (*Tockus*) to 86 days (*Bucorvus*). The long breeding periods exclude second broods except in some forest species, which have no fixed breeding season and show co-operative breeding behaviour. Females of *Bycanistes* remain in the nest with the young and they all emerge together after a period of 4 months or more. In *Tockus*, *Tropicranus*, some *Anthracoceros* and *Buceros* species the females emerge before the chicks are full grown. In *Bucorvus* the female, when incubating or brooding, is brought food by the male or group members and only leaves the nest 3 or 4 times a day, mainly to defaecate.

The chicks hatch at intervals, are naked and blind at hatching, and their upper mandibles are markedly shorter than the lower. Their legs develop rapidly and this enables them to sit and beg for food from the male, rather than from the female inside, and lift their anus, as does the female, to the entrance in order to squirt out their droppings. The nest is kept clean of food remains and debris by throwing these out through the slit; any left is eaten by insects. The feathers on the chicks remain for some time in quill, giving a porcupine-like appearance but, when they burst out, the feathers develop rapidly. In species where the female emerges before the chicks, the nestlings re-seal the entrance themselves (without help from the parents) using their own droppings. The chicks fly as soon as they leave the nest and do not return there. Food is brought to the nest entirely by the male except in those species where the female emerges from the nest before the chick. In *Bucorvus* members of the group bring food to the nest in addition to the male. Smaller chicks often die of starvation and this seems to be obligatory in *Bucorvus* and may be so in the other species (*Bycanistes*, *Ceratogymna*, *Buceros* and *Rhyticeros*) which lay 2 eggs but rear only 1 chick. A.C.K. and L.G.G.

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HORNERO: South American substantive name of the true ovenbirds *Furnarius* spp., especially *F. leucopus*, now used also as English substantive name (see OVENBIRD (1)).

HOST: see BROOD-PARASITISM; ECTOPARASITE; ENDOPARASITE.

HOT SEARCHING: term used to describe finding nests by working vegetation so as to flush the sitting bird; sometimes after watching it back to the nest area; contrasted with 'cold searching', when the nest is found by close examination of likely habitat.

HOUBARA: sometimes used alone as the name of the Houbara Bustard *Chlamydotis undulata* (see BUSTARD).

HOVERING: see FLIGHT.

HUET-HUET: *Pteroptochos tarnii* (see TAPACULO).

HUIA: *Heteralocha acutirostris* (see WATTLEBIRD (2); EXTINCT BIRDS).

HUMAN IMITATION OF BIRD SOUNDS: for a number of reasons and by a variety of means. Perhaps the commonest form is onomatopoeia, when we speak bird names that are intended to sound like the sounds of the birds, e.g. Cuckoo *Cuculus canorus*, Chiffchaff *Phylloscopus collybita*, Killdeer *Charadrius vociferus* and Bobwhite *Colinus virginianus*. The human vocal cords can be employed to copy, for example, the song of the male Cuckoo. Imitation may be otherwise effected by whistling through the lips, 'spishing' through the teeth or 'squeaking' by sucking in air between lips held against the back of the hand. By cupping the hands together and blowing between thumbs held parallel and against the lips, calls such as those of the Tawny Owl *Strix aluco* and the Cuckoo can be reproduced.

Among the various 'bird-calls', the commonest is the whistle or pipe. The simplest design is a tube with a mouth aperture and a single outlet hole. Some whistles may have a 'pea' inside or may incorporate a reed. The pipe known as the 'Nightingale' (and used in the music of Scarlatti and Haydn) involves blowing through a container partly filled with water. The small thin circular instruments used, for example, to copy the distinctive *wheooo*! of the drake Wigeon *Anas penelope* are sucked rather than blown. Diaphragm callers (e.g. for Wild Turkeys *Meleagris gallopavo*) are held inside the mouth against the palate. A few whistles have bellows (e.g. the French Quail *Coturnix coturnix* pipe); or a compressible bulb (the British Quail pipe) both of which are operated with the hands. In the case of a large bellows (as in the American 'Scotch' make of Mallard *Anas platyrhynchos* call) a foot may be used (thus leaving two hands free for a gun?).

Quite different instruments are those that rely on friction for the creation of sound. An Irish Corncrake *Crex crex* caller comprises two mammalian rib bones; one has saw-teeth, across which the other bone is rhythmically drawn to reproduce the rasping 'song'. The 'Audubon' bird call consists of a small cylindrical piece of birch wood into which is inserted (and then turned) a resined small pewter plug; its high-pitched squeaks are reputed to attract song birds. A common design of Wild Turkey call involves scraping a piece of wood across a slate. Box calls are operated by hand; one side of the box is pivoted at one end and elongated at the other to form a handle and its flat side is drawn across an upright edge, the box acting as a resonator. These are used mainly for Wild Turkeys and wild geese. One French company sells 25 different bird-calls, a Brazilian one, 40. Although 'electronic callers' are not strictly relevant they do represent the reproduction of bird sounds by human agency and they have come to replace earlier manual callers. These consist of recordings of real birds reproduced from a disc or tape on a portable battery-operated gramophone or player. The use of this method for hunting is now illegal in the USA and Britain.

Siffleurs use a siffler—'a song whistle' with a moveable 'plunger'—to give generalized impressions of bird song accompanying music. The copying of birds in human music is done with conventional instruments, or (recently) with synthesizers for radiophonic music. One recent and highly original example of human imitation of bird voice combines the simplest with the most sophisticated technique: human vocal mimicry recorded on tape and then electronically enhanced to increase its verisimilitude before being published on disc and cassette as an identification aid for birdwatchers (Ward *et al* 1980).

Primitive peoples imitate birds, either in their ceremonies, or to locate or decoy them. For example, the American Indians of the north-west Pacific coast have a dance in which they imitate the voice and the actions of the Raven *Corvus corax*. The Cree Indians use callers to decoy Canada Geese *Branta canadensis*. The Esquimo of the Canadian Belcher Islands attract them vocally. There is a published recording of the Kayabi tribe of the Paranatinga River in the Matto Grosso of Brazil mimicking 4 species of bird. Tribespeople in Laos use a bird-call fashioned from bamboo to attract the Bamboo Partridge *Bambusicola fytchii* within range of a weapon. Whistles made from bone and found in a few prehistoric sites in Europe, and more commonly across North America, may well have been used for the purpose of attracting birds. Indeed, whistles similar to those found by archaeologists in New Mexico were still used by the Pueblos to lure Wild Turkeys in the early 20th century.

Present day hunters use a variety of means to decoy their quarry, but nowhere more elaborately than in North America, where the sales of duck and goose calls and, most of all, of Wild Turkey calls must be considerable. Schorger (1966) gives a detailed account of turkey calling from prehistoric times to the present day. Not only are the food species decoyed, so too are so-called 'vermin'. Hunters may copy the species they are pursuing or they may attract them by mimicking a predator that the birds assemble to mob. Thus plumage hunters in Trinidad used to call up hummingbirds by mimicking the call of a local owl. Human imitations are usually intended to attract the birds but, in the case of dove calling, they merely cause the bird to answer from its perch and thus give away its location to the hunter. Bird-trappers on the south-west coast of France, and no doubt elsewhere, lure birds to the catching areas of their clap nets with a decoy whistle.

For bird-watchers to call up owls for a better view is comparatively simple, and in North America 'spishing' and 'squeaking' are commonly employed, usually to put wild birds on view for the purpose of identification, and occasionally to census (Smith 1975, Tucker 1978). The reproduction in the field of tape recordings is widely used, e.g. for censusing and ringing. For example, Swallows *Hirundo rustica* approaching a roost location before sunset can be very effectively drawn in the direction of the ringer and his mist net by playing the 'Swallow roost twitter' recording. Even more remarkable is the success achieved by reproducing from coastal headlands at night the purring call of the Storm Petrel *Hydrobates pelagicus*. Although well away from nesting colonies, 3 workers in 6 years mist-netted 16,000 birds (Fowler *et al* 1982). The use of tape PLAYBACK in the breeding season, particularly with rare species, needs scientific investigation to determine how easily, if at all, harm may be done.

Bird impressionists—notably in mid 20th century Britain, Percy Edwards—provided entertainment on stage, radio and television. Gramophone records of avian imitators have been issued surprisingly often since the earliest one in 1891 (Copeland and Boswall 1983). Mechanical birds that sang from little French enamel boxes appeared in the late 18th century in France, and 'automaton' mechanical caged birds were no doubt a familiar sight in Victorian drawing-rooms. Two of the jewelled eggs of Imperial Russia were designed by Fabergé to feature birds (a Nightingale *Luscinia megarhynchos* and a cockerel) that appeared by clockwork to offer the world mechanical utterances.

The direct imitation by human composers dates from the 13th century and is dealt with in detail under MUSIC, BIRDS IN. See also SCARING and VOCALIZATION.

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HUMERUS: a bone of the fore-limb (see SKELETON, POST-CRANIAL; WING). The flight feathers ('tertials') borne on this part of the limb are sometimes called 'humerals'.

HUMIDITY: see WEATHER AND BIRDS.

HUMMINGBIRD: substantive name of many species of Trochilidae (Apodiformes); in the plural general term for the family. The name derives from the noise made by the wings when hovering.

Characteristics. All hummingbirds feed by extracting nectar from flowers with their specialized tongues and usually elongated bills and nearly all hover while doing so. This feeding method accounts for the most striking characteristics of the family. These are: wings adapted for hovering both forwards and backwards, long bills, and very small legs and feet. In addition most hummingbirds have brilliant glittering or iridescent plumage. Hummingbirds are mostly small (6–13 cm long) and range in weight between 2 and 9 g. Two genera with specialized bills, *Ensifera* and *Eutoxeres*, are larger (12–13 g), and the substantially larger Giant Hummingbird *Patagona gigas* weighs 20 g.

The wing structure of hummingbirds differs from other birds, except swifts, by a great reduction in length of the humerus, radius and ulna and an elongation of the hand bones to which the flight feathers are attached. This modified wing moves freely in all directions at the shoulder attachment so that a rotary movement is possible. The wing-beat rates of hummingbirds vary between 22 and 78 per second (Greenewalt 1962); and they have a forward speed in level flight of about 45 km/h. The high wing-beat rate, small size and high temperature (39–42°C) means that hummingbirds have a high rate of metabolism, requiring the frequent intake of energy-rich food. In order to conserve energy, hummingbirds are capable of becoming torpid at night when their temperature falls close to that of the surrounding air.

Most hummingbirds show striking sexual dimorphism, the females having a relatively plain, and the males a more brilliant, plumage, with glittering patches particularly on the throat and crown. In some species males have other special adornments, such as elongated and brilliant tail feathers and crests. In most of the hermit hummingbirds, sometimes placed in a separate subfamily Phaethorninae, the sexes are the same or only slightly different in plumage; this is also true of the violet-ears *Colibri* and many emeralds *Amazilia*.

The 320 species of hummingbird have been placed in 112 genera, 63 of which are represented by only a single species. Eighty-eight genera occur in South America and 24 additional genera occur to the north, mostly in middle America but also the Caribbean islands and North America.

Habitat. Hummingbirds occupy a wide range of habitats from the open paramos of the Andes, over 4,000 m, to the tropical forests of Amazonia, arid scrublands and coastal mangrove swamps. Most species are resident, but a few migrate to breed in such diverse habitats as the deserts of Arizona and the coniferous forests of Canada and Alaska. The essential ingredient of all these habitats is a sufficient abundance of nectar-secreting flowers to supply the energy which the birds need. Although a large and variable proportion of insect food is taken by hummingbirds, most habitats are soon deserted when flowers become scarce.

While most hummingbird nests are small simple cups which may be sited in almost any vegetation and even on overhead electric wires, a few species have more exact nest-site requirements. Thus the hillstars *Oreotrochilus* of the high Andes require a cave roof or a rocky overhang on which to affix their pendent nests. The long-billed hermit hummingbirds of the forests (Phaethorninae) attach their pendent nests to the underside of large tapering leaves such as palms or the wild banana *Heliconia* spp. While this type of leaf is abundant in unaltered forest habitat, it may be absent from areas highly modified by man so that they become largely unsuitable for the Phaethorninae.

Distribution. Hummingbirds occur only in the New World, where they range from Alaska and Labrador in the north to Tierra del Fuego in the south, and from Barbados in the east to the Juan Fernandes group of islands 650 km from the western seaboard of Chile. Very few species, however, occur at high latitudes, the Green-backed Firecrown *Sephanoides sephanoides* in the south (to *c.* 54°S) and the Rufous Hummingbird *Selasphorus rufus* (*c.* 60°N) and the Rubythroat *Archilochus colubris* (*c.* 54°N) in the north. The great majority of species inhabit the latitudes between 10°N and 25°S, with the greatest diversity in Colombia and Ecuador.

Of the 88 South American genera, 5 genera with 8 species occur in the arid coastal zones of the western and northern seaboards, 41 genera with 119 species occur mainly at tropical levels (sea level to 1,525 m), 15 genera with 26 species occur mainly at subtropical levels (1,525–2,580 m, also including 4 genera inhabiting subtropical habitats due to latitude), and 19 genera with 62 species occur mainly at temperate levels (2,580–3,500 m) with the monotypic *Sephanoides* occupying a temperate habitat due to latitude. The number of species decreases sharply in the paramo and puna zones (from the tree line up to the snow line); here 3 genera, *Oreotrochilus*, *Oxypogon* and *Chalcostigma*, show special adaptations to high altitudes (Carpenter 1976) but some temperate-zone species make seasonal visits. This breakdown of species by habitat shows the importance of the Andean mountain range for hummingbird speciation; no other bird family is represented by so many species at temperate levels in the Andes as are the Trochilidae.

Within the Trochilidae there is great variation in the geographical range of different species. The Brown Violetear *Colibri delphinae*, for example, is nowhere abundant but ranges from Guatemala to Bolivia at subtropical and tropical levels. Others have extremely restricted ranges, such as the Spatule-tail *Loddigesia mirabilis* which is known only from the temperate zone of one valley in Peru. Further species with restricted ranges may yet be discovered. As recently as the 1970s, a new species of sunangel, *Heliangelus regalis*, was discovered at subtropical levels in one locality in N. Peru and a metaltail, *Metallura odomae*, at temperate levels in one range in N. Peru.

Movements. The few hummingbird species that breed at high latitudes undertake long migrations. The Rubythroat of eastern N. America migrates for the winter to middle America, reaching as far as Panama. For some populations this journey includes a 1,000 km crossing of the Gulf of Mexico. The Rufous Hummingbird, which breeds as far north as Alaska, winters in southern Mexico 3,500 km away. The Green-backed Firecrown, which breeds as far south as the Straits of Magellan, moves north in the southern winter, some birds at least as far as 23°S.

Besides long-distance movements, many species of hummingbird make more local movements in response to the flowering season of nectar-rich flowers. This has been well documented for the Anna Hummingbird *Calypte anna* in the Santa Monica mountains of California, with its winter breeding season in the chaparral linked to the flowering of a species of *Ribes*, followed by a movement in mid-summer to the high mountain meadows. In the highlands of Costa Rica (2,950–3,200 m) 4 species of hummingbird breed, but only one, *Panterpe insignis*, is present in large numbers throughout the year; the other 3 species make seasonal movements related to flower abundance (Wolf *et al* 1976). At much higher altitudes around 4,000 m on the altiplano of Peru the Sparkling Violetear *Colibri coruscans* is present only in the summer and migrates to lower altitudes in the winter (Carpenter 1976).

In rain forest at tropical levels most hummingbird species appear to be sedentary. This has been proved by marking individuals of the Hairy Hermit *Glaucis hirsuta* and Guy's Hermit *Phaethornis guy* in Trinidad, and the Long-tailed Hermit *P. superciliosus* in Costa Rica.

Food. The diet of hummingbirds consists of nectar supplemented with insects and sometimes spiders. This is true of all species that have been studied in any detail but the proportion of insect to nectar food, the method of capturing insects, the flowers from which nectar is extracted and the behavioural factors which secure this nectar supply, are extremely varied. This variation allows a very large range of feeding niches, which must be the major factor accounting for the large number of hummingbird species.

The structure of hummingbird flowers, especially the length and shape of the corolla tube, is in many cases adapted to permit exploitation by particular kinds of hummingbirds, which pollinate the flowers while feeding at them. A large number of plant genera in the Americas have flowers adapted for pollination by hummingbirds, among the most important being *Heliconia*, *Passiflora* and many genera in the families Bromeliaceae and Gesneriaceae. In several plant genera there is a clear distinction between insect-pollinated species (presumed to be the primitive condition) and species with longer, usually red, corolla tubes adapted for pollination by hummingbirds. (See also POLLINATORS.)

One of the major divisions in feeding methods is between territorial and trap-line feeding. For territorial behaviour to develop, a flower species must provide sufficient nectar to fulfil the energy needs of an individual hummingbird in an area small enough to defend from other nectar feeders. Medium-sized hummingbirds with medium-length bills, such as the emeralds *Amazilia* at tropical levels and the sunangels *Heliangelus* and pufflegs *Eriocnemis* at subtropical and temperate levels, are typical territorial feeders. Trap-line feeders do not defend a nectar resource but travel round visiting scattered flowers rich in nectar. Typically they are hummingbirds with long bills which may be curved, and most show a high degree of co-evolutionary development with the flowers they visit, which have correspondingly long or curved corolla tubes. The hermit hummingbirds are typical trap-line feeders. An advanced degree of co-evolutionary development is shown between 2 hummingbird genera with the most extreme bills, the Swordbill *Ensifera* with a bill length which may exceed 100 mm and the sicklebills *Eutoxeres* with extremely curved bills, and the flowers they visit, which have respectively extremely long and extremely curved corollas. The nectar in such flowers is not available to other hummingbirds if they use the legitimate corolla aperture, but a few genera, e.g. *Heliothryx*, have evolved short and exceptionally sharp bills and habitually pierce long or curved corolla tubes to gain access to the nectar.

In addition to the relatively large, long-billed trap-line feeders, many small hummingbirds, with relatively small unspecialized bills, trap-line feed at insect-pollinated flowers or the less specialized hummingbird flowers which are too scattered to be defended by territorial hummingbirds.

In North America 4 species of hummingbird are known to take sap from trees where it is made available by sap-sucking woodpeckers (Picidae); and hummingbirds have also been recorded taking juice from ripe fruit.

Hummingbirds employ 2 methods of capturing insects: hawking insects in flight, and gleaning resting insects and spiders from the vegetation and from spider's webs. The hermit hummingbirds, nearly all of which have curved bills, employ the gleaning method almost entirely, hovering to search the undersides, edges and tips of leaves low down in the forest or in the middle canopy. A specialized form of insect gleaning while clambering over the ground is employed by 3 species of hummingbirds inhabiting the high Andes, where the bare hillsides are suitable for such methods and the energetic cost of hovering in the thin cool air is particularly heavy. Hawking for airborne insects has been observed in many straight-billed species, some of which also glean for resting insects in the same way as hermit hummingbirds. Hawking is especially prevalent among species with relatively long wings and short bills such as the Green-tailed Trainbearer *Lesbia nuna* and the Buff-tailed Coronet *Boissonneaua flavescens*. Methods and vantage points for hawking vary between species, some species using high exposed perches above the canopy, and others lower perches near or within vegetation or in the open. Some species catch a single flying insect at a sally, others make a number of captures per sally or attempt to do so.

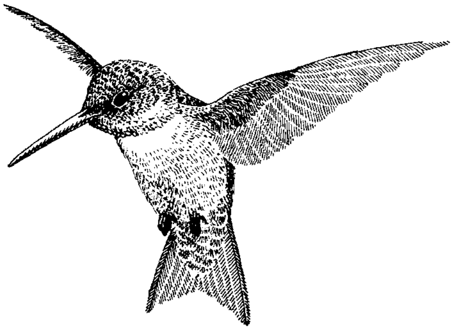
Behaviour. Hummingbirds are polygamous, the males advertising themselves by song and display either at traditional leks (singing assemblies) or at more scattered song posts or at their feeding territories. Spectacular aerial diving displays are characteristic of species that inhabit open country, as in North America. The female's visits to advertising males culminate in copulation. In all except one of the species that have been studied, the female builds, incubates the eggs and rears the young unaided by the male. The exception is the Sparkling Violetear. Males of this species are reported to guard the nest, and one took over incubation when the female was shot at the nest (Moore 1947). At another nest 2 adults shared incubation; one of them the observer believed to be the male (Schäfer 1954).

A LEK mating system is usual among species, such as many of the hermits, that feed by trap-lining. The size of leks varies greatly; T.A.W. Davis noted assemblies of 100 or more Long-tailed Hermits in Guyana, while a lek of the same species in Costa Rica censused for 5 years varied between 14 and 23 males (Stiles and Wolf 1979). Leks of the Reddish Hermit *Phaethornis ruber* may consist of only 5 males, and the Barbthroat *Threnetes ruckeri* may sing at solitary perches or within sound of 1 or 2 conspecifics. Within a hermit hummingbird's lek, each male defends several song perches, which are slender horizontal twigs in the undergrowth. Song, display, territorial encounters with other males and copulation take place on or near these perches. During courtship and other encounters, the plain-coloured hermits nearly all display their brightly coloured gapes. The many species with brilliant plumage and iridescent patches display these, usually when airborne.

In the Purple-throated Carib *Eulampis jugularis* mating takes place within the male's feeding territory where the female is permitted to feed prior to copulation (Wolf 1975). The male Hairy Hermit forms loose pair-bonds with one or two females that nest along a section of stream side which he defends from other hermits (Snow and Snow 1973). Prior to mating, the female Andean Hillstar *Oreotrochilus estella* feeds the male in her territory. In this species only females hold territories in the breeding season.

Voice. Both male and female hummingbirds call in flight. Flight calls are usually monosyllabic, lasting about half a second; they are uttered by a bird flying alone and not near leks or assemblies. It is characteristic of hummingbirds which defend floral feeding territories to utter a brief monosyllabic note between feeding probes. Many species utter a chase call, a chattering series of rapid notes uttered when attacking and chasing intruders at their feeding territories or at lek territories. There are strong aggressive elements in these two calls, which may be employed by either sex, are particular to a species and appear to be innate.

Most hummingbird advertising song is short and simple, lasting from a fraction of a second to 1½ s. These short songs are frequently repeated, the brief monosyllabic ones typically up to 70 times a minute and the longer 1–1½ s phrases some 30 times a minute. The songs are often of high frequency and sound squeaky and thin to human ears. Some species sing longer more musical songs with longer intervals between them: the Barbthroat has a warbling song lasting 4–5 s and the Wine-throated Hummingbird *Atthis ellioti* has a song of nearly a minute's duration.



Rubythroat *Archilochus colubris*. (*N.A.*).

Many species, particularly the Phaethorninae, are extremely persistent singers, and sing throughout much of the day and throughout the often long breeding season. An extremely low-volume continuous warbling sub-song has been heard from many species; recently fledged birds and adults of both sexes may sing this sub-song. Some displays are accompanied by vocalizations not heard at other times. Duet singing, with first the male then the female uttering a phrase, occurs in the Hairy Hermit.

All evidence indicates that the advertising song of males is not innate but learnt, becoming fixed in young males probably in their first year. Abnormal songs may apparently be developed by individuals that learn from the wrong species. Skutch (1974) reported a striking example, of a male *Amazilia amabilis* which for 7 years sang the song of *Amazilia tzacatl* but at the tempo usual to his own species. In the lek-forming hermit hummingbirds, young males learn the song form of their closest neighbours. Even when the song is a monosyllabic note lasting less than a quarter of a second, as in the Long-tailed Hermit, many audibly distinct forms are sung. One lek of 20 males had 4 distinct song forms, adjacent males all singing alike.

Breeding. The unaided female builds the nest, incubates the eggs and rears the young. Throughout the Trochilidae the clutch consists of 2 eggs which are always white and of an elongated shape; there is normally a 48-hour interval before the second egg is laid. In two hermit hummingbird genera *Glaucis* and *Threnetes*, nests with 3 or 4 eggs are not uncommon; these are apparently attributable to more than one female.

There are 2 basic nest-types. The commoner, built by all species except the Phaethorninae and some cave-nesting species, is a small compact open cup placed astride a stem or twig. The nest is composed of vegetable down and sometimes moss and is bound together and to its support with cobweb.

The Phaethorninae build pendent nests which are fastened by cobweb to the underside of a blade-shaped leaf or strip of leaf, so that the leaf forms the inner wall. The nest tapers to a tail, to which twigs and debris are attached to act as a balancing weight. Species that nest in caves and buildings, such as the hillstars, have thick-walled pendent nests attached to the rock by a glue. The only known nest of the Blue-fronted Lancebill *Doryfera johannae* was also pendent and attached by cobweb to a rocky overhang near the bottom of a 75 m shaft. Normally hummingbirds nest solitarily except those that need specialized nest-sites such as caves.

Incubation begins when the second egg is laid and ranges from 14–19 days. The altricial young are sparsely covered with down at hatching, and are brooded frequently, but by 8–12 days brooding ceases even at night. Small nestlings defaecate in the nest and the female removes the droppings, older nestlings defaecate over the rim of the nest. The female regurgitates food to the young, inserting her bill into their throats. Fledging periods vary between 18 and 28 days. H.O. Wagner, studying the Green Violetear *Colibri thalassinus* in Mexico, found the fledging period varied from season to season with different weather conditions. The female continues to feed the young after they have fledged, the longest recorded period being 41 days (Skutch 1974).

Hummingbird breeding seasons are linked with the flowering seasons of their main sources of nectar. In the far north and south of their range the main flowering seasons have a simple relationship with day length and temperature, corresponding to the northern and southern summers. At 34°N in California, 2 migratory species have a typical northern breeding season starting March/April with a peak in May, while the non-migratory Anna Hummingbird has a peak of breeding from January to March coinciding with the peak of precipitation in this dry region and the peak flowering season of 2 species of *Ribes* (Stiles 1973).

In the humid tropics and subtropics the hummingbirds which build open cup nests liable to saturation do not nest at the peak of the rainy seasons when day-long rain may occur. This group of hummingbirds breeds mainly in the dry season, but not towards the end of a long or severe one when flowers become scarce. The beginning and end of rainy seasons, when both sun and rain are usually intermittent, are important breeding periods as hummingbirds are well able to protect the nest and its contents for limited periods of rain.

The nests of hermit hummingbirds are protected from rain by the living leaf to which they are attached, so excessive rain is not a limiting factor of the breeding season. Thus at 600–900 m in Costa Rica the Hairy Hermit and the Barbthroat nest almost entirely in the rainy season (Skutch). In the lowlands of Costa Rica the Long-tailed Hermit breeds from January to August, well into the wet season. In Trinidad the Hairy Hermit also breeds from January to August, which spans the main dry season, but with a peak of laying in the first 2 months of the wet season. Nests of Guy's Hermit in the same locality were found in all months except August to October. All these hermit breeding seasons show correlations with the flowering of the mainly herbaceous plants on which these species feed.

Individual female Hairy Hermits and Guy's Hermits in Trinidad may make 3 nesting attempts in a season, as deduced from the reuse of repaired nests. A female Anna Hummingbird in California successfully raised 2 broods in a season, as did a Black-throated Mango *Anthracothorax nigricollis* in Trinidad.

See photo FEEDING HABITS. B.K.S.

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HUNGER TRACE: see PLUMAGE, ABNORMAL.

HUNTING: see FEEDING HABITS.

HWAMEI: *Garrulax canorus* (see BABBLER).

HYBRID: term used to denote the product of a cross between individuals of unlike genetic constitution, usually distinct morphologically. It is often restricted to a cross between individuals of different species, but this begs the question of the taxonomic status of the forms before one can designate the products of their crossing. Genetically the term denotes a first generation product but in practice it is impossible under field conditions to distinguish such F^1 hybrids from second generation hybrids (resulting from a cross between hybrids) and from backcross products, i.e. individuals resulting from crossing hybrids with individuals of the parental forms (see GENETICS).

Interspecific and intraspecific hybrids are generally uncommon but may involve some 10% of the world's bird species. Interspecific hybrids between distantly related species that occur sympatrically are rare, but are usually easily distinguishable, and readily come to the attention of ornithologists. More common are hybrids between closely related species, either in zones of parapatry (where their ranges meet) or in zones of overlap and hybridization between geographically replacing allospecies that together form a superspecies (see HYBRIDIZATION, ZONE OF SECONDARY; INTROGRESSION; SPECIATION). Intraspecific hybridization results in zones of secondary contact between morphologically and genetically distinct subspecies; the hybrids are variable, occurring in a hybrid zone that both genetically connects and geographically separates the parental SUBSPECIES.

Generally, the more distantly related 2 species are, the more dissimilar they are genetically and hence the less likely they are to hybridize. Under captive conditions, and in the wild at borders of the ranges of species where choice of mates may be restricted, barriers to interbreeding can break down, resulting occasionally in hybridization. Another factor that promotes hybridization is mating systems in which pair formation occurs rapidly and males take no part in the nesting effort, as in many ducks, birds-of-paradise and hummingbirds (see also PAIR FORMATION).

Hybrids between species that manage to interbreed, despite behavioural or other factors tending to reduce mixed pairing, may be eliminated at various stages of development, from the period of fertilization onward. There is usually reduced fertility of the eggs of hybridizing individuals, and hybrid embryos often fail to develop to hatching. Anomalies often occur in hybrids that do hatch, reducing their chances of survival and breeding. Those hybrids that survive vary greatly in their degree of viability. They may be intermediate in their morphological, behavioural and other characteristics between those of their parents, but often show a variable array of traits, some like one or other parent, some intermediate, and others occasionally unlike either parent. Hybrids that do survive may exhibit 'hybrid vigour', being larger, or stronger, or faster growing, or more aggressive than either parental species, but as they usually have reduced viability, this prevents or limits introgression (passage of genes from the gene pool of one species into that of another). Fertile interspecific hybrids seem more frequent in some orders of birds than in others, and certain large genera such as *Anas*, that contain a number of relatively closely related species, show numerous natural hybrids as well as hybrids produced under captive conditions.

Although hybrids are of behavioural, physiological and genetic interest they are of little significance in terms of evolution unless they exhibit some degree of fertility and backcrossing occurs. Frequent hybridization with backcrossing is significant in an evolutionary sense to the degree that the interbreeding allows gene flow, giving the gene pool of each parental species some access to favourable genes and gene combinations of the other species.

There is no more recent list of bird hybrids than that of A.P. Gray (1958), although reports treating various aspects and occurrences of hybrids and hybridization are frequent in ornithological literature. Mayr and Short (1970) analyzed the North American avifauna of 516 breeding non-marine birds and found 24 cases of interspecific hybridization and 30 instances of intraspecific hybridization involving a total of 73 species, roughly 10% of all North American species. L.L.S.

Gray, A.P. 1958. Bird Hybrids: a Check-list with Bibliography. Farnham Royal.
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HYBRIDIZATION, ZONE OF SECONDARY: an area in which 2 or more closely related forms contact and interbreed with backcrossing, having earlier differentiated under conditions of geographical isolation (see SPECIATION). It is not clear that the isolation need be complete, as strong selection could counter gene flow if the contact between the differentiating forms is restricted. Such zones are characterized by great individual variability.

Short (1969) classed these zones into 2 types: a zone of overlap and hybridization, and a hybrid zone. The zone of overlap and hybridization involves forms that hybridize to a greater or lesser degree, but the hybridization is incomplete, both parental forms occurring along with the hybrids. In this case the 2 forms remain sympatric and the continued occurrence and in some instances the preponderance of parental-type individuals indicate the presence of some barrier to interbreeding, or hybrid breakdown—the forms are considered to represent hybridizing species, designated allospecies, and together these allospecies form a superspecies (Amadon 1966). The hybrid zone is an area of greater or lesser extent populated entirely by hybrids between well-differentiated but freely interbreeding forms. This type of zone both genetically connects and geographically separates the parental forms, which are conspecific. The conspecific hybridizing forms often are so distinct that they have been considered full species at one time or another, and Amadon and Short (1976) have designated such differentiates as 'mega-subspecies'.

Examples of zones of overlap and hybridization are rather numerous and include those involving the Rose-breasted Grosbeak *Pheucticus ludovicianus* and Black-headed Grosbeak *P. melanocephalus*, and the Mallard *Anas platyrhynchos* and the American Black Duck *A. rubripes* in North America, and the Azure Tit *Parus cyanus* and Blue Tit *P. caeruleus* in Europe. Hybrid zones occur between the megasubspecies *cafer* and *auratus* of the North American Northern Flicker *Colaptes auratus*, and between the megasubspecies *cornix* and *corone* of the Carrion/Hooded Crow *Corvus corone*, of Eurasia. The extent of these zones depends upon a variety of factors, not the least of which is the availability of characters used in defining the zone. When characters are few, as in the case of the crows, the zone defined by the one or two characters may be narrow. The use of other, especially biochemical characters may show that the zones actually are broader than they appear, as has been found in lizards and other animals. Topographical and ecological factors may severely limit the possibility of contact and thus affect the size of the zone. There are several cases of range expansion that increase the area of a zone of overlap and hybridization, in the course of which hybridization is prevalent mainly at the edge of the range of the expanding species, followed by lessened interbreeding in the area of overlap, as in *Parus caeruleus-cyanus*, and in the European Syrian Woodpecker *Dendrocopos* (*Picoides*) *syriacus*, and Great Spotted Woodpecker *D. major*. Another peculiar situation is that of a range extension with very frequent hybridization accompanying it, followed by replacement of one species by the other, the example here being that of the Blue-winged Warbler *Vermivora pinus*, hybridizing with and largely or entirely replacing the Golden-winged Warbler *V. chrysoptera* in eastern North America (see also RANGE CHANGES).

A few situations are so complex as to defy any attempt to categorize them. The Rufous-sided Towhee *Pipilo erythrophthalmus*, and Collared Towhee *P. ocai*, are 2 strikingly differently plumaged finches, the former occupying much of North America and the latter inhabiting highlands of Mexico. In Mexico there is generally an ecological and altitudinal separation of the 2 forms, but they meet in many places with varying outcomes. In a few small areas they occur together, overlapping in range without interbreeding. In many areas they hybridize apparently freely, forming hybrid zones. Some entirely hybrid populations are geographically isolated, forming 'hybrid swarms' totally out of genetic contact with their parental forms. Certain of the hybrid swarm populations show by their distribution and gradation of their average characters the effects of a hybrid zone, but with geographical gaps among the isolated populations. The diverse situations probably reflect differences in the time of occurrence of the contacts relative to the development of reproductive isolating mechanisms, although some may have occurred as the result of a local breakdown in reproductive isolation.

The Crimson Rosella *Platycercus elegans* of wet eastern and south-eastern Australian woodlands and the Yellow Rosella *P. flaveolus* of the interior Murray River system meet and sporadically hybridize west and north of Australia's Great Dividing Range. The range involved is massively modified by man's activities, but at least one tenuous hybrid zone exists between them along the Murrumbidgee River. In South Australia's Adelaide Hills and the Flinders Range occurs a variable population that clearly represents a huge hybrid swarm; often treated as a species, the 'Adelaide' Rosella *P. adelaidae*, this population interbreeds freely but narrowly with the Yellow Rosella, destruction of habitat limiting the contact possibilities near the lower Murray River. There is no extant contact between the 'Adelaide' Rosella and the Crimson Rosella but 'Adelaide' Rosellas grade from yellowish in the north to red in the south, tending strongly toward *P. elegans*. This situation has been regarded by some as a 'ring' in which the extremes (*flaveolus* and *elegans*) are connected by an intermediate population but do not interbreed at the ends of their ranges (in the east). Actually the 'ring' is broken in the lack of contact of '*adelaidae*' with *elegans*, and *elegans* and *flaveolus* do hybridize in eastern Australia, so they appear to represent well-differentiated megasubspecies.

A true ring of races appears to exist between the Herring Gull *Larus argentatus* and the Lesser Black-backed Gull *L. fuscus*. These are sympatric in parts of northern Europe, and usually do not interbreed. However, from eastern Europe across Siberia to North America occur connecting, interbreeding populations, and thus the northern European situation would seem to represent the non-interbreeding ends of a chain of genetically connected populations. All of the connections have not been thoroughly studied and the complexity of this problem is enhanced by the propensity of the Herring Gull to interbreed with the Glaucous-winged Gull *L. glaucescens* in western North America, with the Glaucous Gull *L. hyperboreus* in Iceland, and with the Slaty-backed Gull *L. schistisagus* in eastern Siberia.

The matter of hybridization is of great interest and is directly involved in the matter of defining species (see SPECIATION). Many of the situations are highly dynamic and subject to modification through man's effects on habitats. Mayr and Short (1970) note that many hybridizing species of temperate regions seem biologically very successful, even in the face of man's activities. L.L.S.

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HYDROBATIDAE: see under PROCELLARIIFORMES; PETREL.

HYLIA: substantive name of *Hylia prasina*, an African warbler-like bird of uncertain affinities.

HYOID: see MUSCULATURE; SKELETON, POST-CRANIAL; TONGUE.

HYPAXIAL: see MUSCULATURE.

HYPHENS: as regards their use in vernacular or scientific names of birds, see NAME, ENGLISH; NOMENCLATURE.

HYPOCOLIINAE: see BOMBYCILLIDAE; and below.

HYPOCOLIUS: generic name used as common name of *Hypocolius ampelinus*, sole member of subfamily Hypocoliinae of the Bombycillidae (Passeriformes, suborder Oscines); an aberrant species placed near the waxwings (see under BOMBYCILLIDAE). Its home is south-western Asia, whence irregular migrations take place to north-western India and perhaps casually to north-eastern Africa.

Characteristics. The plumage is pale grey, tinged blue on the back and buff on the forehead and underparts. A black band extends from the bill through the lores and round the back of the neck, where it can be erected into a small crest. The primaries are black, tipped white; the tail is grey, tipped black. Females lack the black on face and neck. Juveniles are buffy-brown without black markings, except for the tips of the rectrices; the tips of the remiges are marked buff as well as white.

The Hypocolius is about 23 cm in length with a long tail and short, broad, slightly hooked bill; the feet and legs are short and strong. The wings are relatively short and rounded; the tenth primary is relatively

Hypocolius *Hypocolius ampelinus*. (*C.E.T.K.*).

longer than in the waxwings. The flight is strong, swift and direct, not undulating, but the birds are sluggish, shy and sociable except in the breeding season. Fruits and berries are staple foods, although insects are also taken.

Voice. Vocalizations include mewing calls, associated with pair formation, and a continuous loud *kirrrkirrrkirrr*, uttered by pairs during courtship flights over the nesting territory.

Breeding. Nests have been found in the Tigris–Euphrates valley of Iraq and in south-western Arabia. Large and loosely built of twigs, they are lined with soft vegetable matter and sometimes hair, like those of waxwings; they are usually well hidden among the leaves of palm trees, but sometimes in other bushy trees. The 4–5 eggs are laid in mid-June and the parents are prone to desert if disturbed. The eggs are very pale slaty grey, with darker blotches and spots at the larger end; occasionally these form a ring or cover the whole egg. (J.C.G. Jr). D.W.S. (1)

Bunni, M.K. & Siman, H.Y. 1979. Pair formation and courtship activities in Grey Hypocolius, *Hypocolius ampelinus* Bonaparte. Bull. Nat. Hist. Res. Centre, Univ. Baghdad 7(3): 73–82.

Delacour, J. & Amadon, D. 1949. The relationships of *Hypocolius*. Ibis 91: 427–429.

Meinertzhagen, R. 1954. Birds of Arabia. Edinburgh.

HYPOPHYSIS: the pituitary gland (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

HYPORACHIS: see AFTERSHAFT.

HYPOSITTIDAE: a monotypic family separated by some authors, but of doubtful affinities and now provisionally merged with the Vangidae (for family see VANGA).

HYPOTHALAMUS: part of the forebrain (see NERVOUS SYSTEM).

I

IBIDORHYNCHIDAE: see CHARADRIIFORMES; IBISBILL.

IBIS: substantive name for most of the approximately 23 species and 16 genera in the subfamily Threskiornithinae of the family Threskiornithidae (Ciconiiformes, suborder Ciconiae).

Characteristics. Ibises are medium-sized water or terrestrial birds, about 50 to 100 cm in total length, including medium to long legs, long necks, and long, decurved bills. All species have heads that are partially or wholly bare, and some species are crested or have other modified feathers. The wings are relatively long and broad, and the tail is short. The flight is strong and rapid with neck extended. Among the more gregarious species, flocks often fly in long lines or V's with all birds flapping or gliding in unison. Sexes are similar except that the males of some species are slightly larger than the females. Immature birds are often darker than adults, and may be more extensively feathered on the head.

Systematic characteristics and distribution. Ibises are widespread in the warmer parts of the world, with 9 genera restricted to the Old World, 6 to the New World, and one that is cosmopolitan.

In the Old World, the genus *Threskiornis* contains 4 species, the Sacred Ibis *T. aethiopicus* occurring primarily in Africa south of the Sahara, the Straw-necked Ibis *T. spinicollis* of Australia, the Australian White Ibis *T. molucca* found between Indonesia and Australia, and the similar Oriental White Ibis *T. melanocephalus* in southern Asia. The species of *Threskiornis* are primarily black and white in colour, with entirely bare heads and upper necks.

Also in Asia is the Black (or White-shouldered) Ibis *Pseudibis papillosa* of India, south-eastern Asia and southern China, the Giant Ibis *Thaumatibis gigantea* of Indo-China, and the Crested Ibis *Nipponia nippon* of Japan, China, and Korea. The Black and Giant Ibises are dark species, the former having a patch of red papillae on the bare skin of the crown, and the latter characterized by its large size and barred nape and hind neck. The Crested Ibis is white, with the anterior half of the head bare red skin, and a crest of elongate white feathers at the nape.

In addition to the Sacred Ibis, 7 other species occur entirely or in large part within Africa. The endangered Waldrapp *Geronticus eremita* survives as a breeding bird of Morocco and Turkey, while the Bald Ibis *G. calvus* is restricted to mountains of South Africa. Both are large, dark ibises with strong metallic sheens to their plumage, red bills and entirely bare heads and upper necks. Three crested species are the Olive (or Green) Ibis *Lompribis olivacea*, the Spotted-breasted Ibis *L. rara* and the Crested Wood Ibis *Lophotibis cristata*, endemic to Malagasy. The Hadada *Hagedashia hagedash*, widespread in Africa south of the Sahara, is a broad-winged, all dark bird, and the Wattled Ibis *Bostrychia carunculata* in the Afrotropical Region, also a dark species, has a wattle hanging from the throat.

In the New World are 2 species of *Eudocimus*, the American White Ibis *E. albus*, a mostly white species with bare red face, which occurs between the south-eastern United States and northern South America, and the Scarlet Ibis *E. ruber* with a brilliant red plumage, found along the north-eastern coast of South America and in Trinidad. Immatures of both species are dark brown above.

Six species belonging to monotypic genera are essentially South American. The Plumbeous Ibis *Harpiprion caerulescens*, occurring in the southern continent east of the Andes, is a slaty grey bird with a bushy crest, while the Buff-necked Ibis *Theristicus caudatus*, found throughout tropical South America, is a grey and white species with buffy head and neck and large white wing patches. Four mostly blackish species are the Green Ibis *Mesembrinibis cayennensis* and the Bare-faced Ibis *Phimosus infuscatus*, both ranging throughout most of tropical South America, the Sharp-tailed Ibis *Cercibis oxycerca*, occurring from eastern Colombia to northern Brazil, and the Puna Ibis *Plegadis ridgwayi*, a high altitude species of the central and southern Andes. All 4 have feathered heads with varying amounts of bare skin on the face or chin, which is red on the Sharp-tailed and Bare-faced and dark in the other two.

The one cosmopolitan species is the Glossy Ibis *Plegadis falcinellus*, occurring in warmer regions of Eurasia, Africa, Australia and the New World, although the population that breeds from South America to the western United States is separated by some taxonomists as *P. chihi*, the White-faced Ibis. The Glossy Ibis is a dark, chestnut-coloured bird, glossy green on the wings, and with the head mostly feathered.

Habitat. Most ibises feed in a broad range of shallow, wetland habitats, primarily freshwater or estuarine, including swamps, marshes, rain-flooded agricultural lands, rice fields and river and lake edges. Exceptions include the 2 *Geronticus* species, the Buff-necked Ibis and the Black Ibis, which feed in dry pastures, savannas or other open, upland habitats. Most ibises place their nests in patches of low woody or herbaceous vegetation in either permanently or seasonally flooded sites, although *Geronticus* nests on ledges of cliffs or in piles of boulders, and the Crested Ibis and Black Ibis nest in large trees near water.

Population. Although several species of ibis are known to have experienced slow and persistent declines in numbers and some loss of range, in part due to habitat loss, shooting and pesticide problems, most species remain fairly common in large portions of their ranges. Two species, however, have become seriously threatened with extinction. The last 5 remaining Crested Ibis in Japan were live-trapped in 1981 in an attempt to increase numbers through a captive breeding programme; the species has become extremely rare in other parts of its range. Waldrapps had disappeared from their central European range by the 17th century, and declined in north Africa and the Near East until less than 300 nesting pairs remained by the late 1970s. On the other hand, the Glossy Ibis in North America has experienced a tenfold increase in numbers and has greatly extended its breeding range along the Atlantic Coast since the 1940s.

Movements. In more tropical regions, ibises are generally non-migratory. Instead, they may be resident or perform somewhat irregular movements apparently regulated by the influence which rainfall patterns and water levels have upon food resources and nesting sites. Ibises that nest in temperate regions, including populations of Glossy Ibis, American White Ibis and Crested Ibis, are migratory, and move into warmer regions during winter. Post-breeding dispersals, including northward movements in some North Temperate populations, are also characteristic of ibises, especially among younger age-classes.

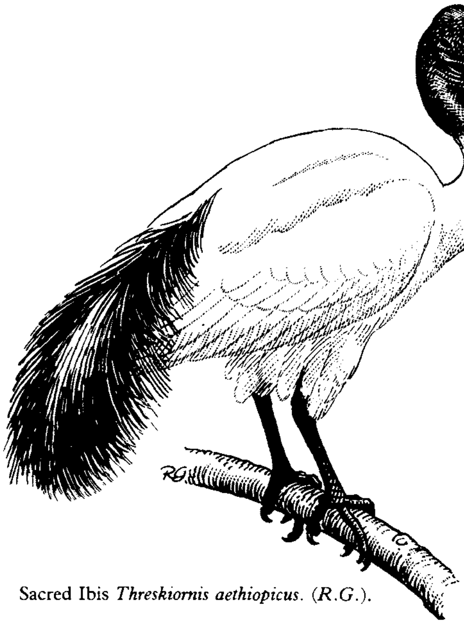
Food. In aquatic habitats, ibises feed primarily on crustaceans, molluscs, aquatic insects, and insect larvae, small fish and frogs. Prey taken at upland sites includes numerous grasshoppers, locusts, beetles, ants and other insects, spiders, molluscs, reptiles, and occasionally carrion, bird and reptile eggs or small rodents. Most food is captured by probing the long bill along the bottom in shallow flooded areas or in terrestrial sites. Feeding sites may be some distance from nesting or roosting locations, entailing flights of 10–25 km each way.

Voice. Ibises utter a variety of harsh, guttural or grunting calls, usually when in flight or during social interactions in colonies. Most species are otherwise quiet, although an exception is the Hadada, which is extremely loud and vociferous.

Behaviour. Ibises tend to be highly gregarious, although the degree of social behaviour varies between species. Roosting and feeding occur in small to large flocks, although some tropical species such as the Sharp-tailed and Green Ibis in South America and Black Ibis in India are usually seen as pairs or in small groups of less than 10 birds.

Breeding. Most species nest in colonies, either single-species or mixed with other species of long-legged water birds. Nesting colonies vary considerably in size, depending upon local habitat conditions and the species of ibis, with colonies of a few nests to several hundred the most common. The extremes are represented by the Crested Ibis which once nested as single pairs in the eastern USSR, to the American White Ibis which forms colonies containing tens of thousands of pairs covering many hectares of swampland forest. In the few species whose breeding behaviour has been studied, pair bonds are monogamous and of seasonal duration. Pairing occurs at the nesting site, and may include a display with head and neck stretched low and forward by one or both adults, and intertwining of the head and neck by the pair. During incubation, nest exchanges may include mutual billing and allopreening. Pairs defend immediate nest sites only. Both sexes participate in incubation and care of the young.

Nesting occurs on an annual cycle in temperate zones, but on less



Sacred Ibis *Threskiornis aethiopicus*. (*R.G.*).

well-defined cycles in tropical regions where local water conditions may greatly influence its timing. Pairs generally are single-brooded during each breeding cycle. Clutch size generally ranges from 2–5 eggs, incubation starting with the first egg in the Glossy Ibis and Waldrapp, and with the last egg laid by the American White Ibis and Sacred Ibis. Incubation lasts from 21–29 days. Nestlings are nidicolous and semi-altricial, and are fed by regurgitation either directly between adult and nestling or into the nest bottom. Nestlings are brooded for the first 5–7 days after hatching, begin to move away from the nest by 14–21 days, but will return to it to be fed, and are capable of full flight between 30 and 50 days of age. Nesting success in individual colonies ranges from complete failure when rapid deterioration of feeding conditions occurs, to as high as 80% of nests producing 1 or more young in years of good feeding conditions. Young ibises of most species apparently reach maturity by at least 3 years of age. J.C.O.

Carrick, R. 1959. The food and feeding habits of the Straw-necked Ibis *Threskiornis spinicollis* (Jameson) and the White Ibis *T. molucca* (Cuvier), in Australia. CSIRO Wildl. Res. 4: 69–92.

Dement'ev, G.P. & Gladkov, N.A. 1951. Birds of the Soviet Union. Vol. 2. Israel Prog. for Scientific Translations, Jerusalem, 1968.

Kushlan, J.A. 1977. Populations energetics of the American White Ibis. Auk 94: 114–122.

Palmer, R.S. (ed.) 1962. Handbook of North American Birds. Vol. 1. New Haven.

IBISBILL: *Ibidorhyncha struthersii*, sole member of the family Ibidorhynchidae (Charadriiformes, suborder Charadrii). Formerly grouped with avocets and stilts in the Recurvirostridae, this aberrant wader of the high plateaux of central Asia, from Turkestan to Kashmir and northern Burma, is rather over 17 cm in length, greyish brown above, bluish grey to white below, with a black face and broad black gorget. The decurved bill, 7–8 cm long, is bright red, the legs are blood red, the eyes dark red.

Small parties of birds remain by the slower-flowing reaches of mountain streams all the year, but a few descend into the foothills in winter. They feed, both on the banks and by wading deep into the water or swimming, on a variety of invertebrate animals. In the light elegant flight the neck is stretched out and white patches show on the wings, and a repeated whistling call is uttered.

The Ibisbill breeds from the end of March to early June according to the season. A shallow scrape is made among stones and shingle and the clutch of 4 eggs, brown-spotted on a grey ground, is incubated by both parents for an as yet unknown period. H.B.

Grzimek, B. 1972. Grzimek's Animal Life Encyclopaedia: Birds II, vol. 8. New York.

Étchécopar, R.D. & Hüe, F. 1978. Les Oiseaux de Chine. Non-passereaux. Tahiti.

IBIS, WOOD-: see STORK; WOOD-IBIS.

ICE-BIRD: sailors' name for some prions *Pachyptila* spp. (see PETREL). Note, however, that the German name 'Eisvogel' applies to the Kingfisher *Alcedo atthis*.

ICHTHYORNITHIFORMES: order erected to include such fossil forms as *Ichthyornis* and *Apatornis* (see FOSSIL BIRDS).

ICTERIDAE: a family of the Passeriformes, suborder Oscines; ORIOLE (2).

IIWI: *Vestiaria coccinea* (see HAWAIIAN HONEYCREEPER).

ILEUM: the posterior part of the small intestine (see ALIMENTARY SYSTEM).

ILIUM: a paired bone of the pelvic girdle, partly fused with the other elements (see SKELETON, POST-CRANIAL).

ILLADOPSIS: substantive name of African BABBLERS of the genus *Trichastoma*, in West Africa known as Adalats.

ILLUSTRATION, BIRD: the pictorial representation of birds. Birds were among the first subjects to be drawn by Neolithic man on the walls of his cave. It is thought that these pictures of birds and other animals may have had some mystical significance, being sympathetic or restitutive magic, shamanism, totemism or a representation of the duality of male and female. It is even possible that they may have been just home decoration or Art for its own sake.

Representations of birds were found in several ancient cultures, but most notable must be those from Ancient Egypt. These usually depicted recognizable species. On the fresco of the tomb of Ne-Few-Maat at Medum are very life-like illustrations of Bean Goose *Anser fabalis*, Red-breasted Goose *A. ruficollis* and White-fronted Goose *A. albifrons*. Each bird has a specific JIZZ, suggesting that the artist, working at least as long ago as 3,000 BC, was familiar with his subjects.

It was not until the Middle Ages that the first didactic bird illustrations appeared in medieval bestiaries. The monastic manuscripts also contained accurate representations of species that are recognizable today. There are excellent marginal decorations of birds in *De Arte Venandi cum Avibus* (*c.* 1248) by the German Emperor Frederick II (see also FALCONRY). Probably the best representations of this period are to be found in the Sherborne Missal (*c.* 1400). Of the 170 decorations, two-thirds are identifiable and cover 40 species.

The invention of printing brought bird illustrations to a wider readership. Notable among the earliest printed books to contain bird pictures were *Das Buch der Natur* (Augsburg, 1475) and *De Proprietatibus Rerum* of Bartholomaeus Anglicus, printed in England by Wynkyn de Worde (*c.* 1495). A third significant book at this period was *Hortus Sanitatis*, printed by Jacob Meydenbach at Mainz in 1491, which contained 103 figures of birds.

The first book that can be described as an 'ornithological treatise' was by Pierre Belon of Le Mans, whose *Histoire de la Nature des Oyseaux* was published in Paris in 1555. The 160 woodcut illustrations were described by the author as 'simple portraits of birds, the nature of which no one else has illustrated before'. More accurate and sophisticated woodcuts by the Strasbourg artist Lukas Schan are to be found in Conrad Gesner's *Historia Animalium* (Zurich, 1565), the third volume of which was devoted to birds. Gesner, in describing Schan as equally skilled in painting and in fowling, summed up the essential truth that the best bird illustrators know as much about birds as they do about painting and drawing.

It was not until 1676 that the first illustrated text book of birds appeared in England, when Willughby and Ray's *Ornithologiae Libri Tres*, was published. It was significant because in it the authors attempted a scientific classification of birds. The illustrations were not of a very high quality, but they were attempts at clear representations of birds.

Engraving on metal, which had begun to supersede wood towards the end of the 16th century enabled the artist to achieve finer detail. This development coincided with the great 17th and 18th century voyages of discovery, which gave rise to books with magnificent, hand-coloured plates. Excellent examples of these are Mark Catesby's *Natural History of Carolina* (2 volumes, London 1731–43) and Eleazer Albin's *Natural History of Birds* (1738).

In France the work of Buffon had provoked enormous interest with the publication of the collection of plates of animals drawn and engraved under Buffon's supervision by F.N. Martinet. Work began in 1765 and by 1783 1,000 plates had been published, 973 of which contained figures of birds. This comprehensive ornithological iconography is usually referred to as *Les Planches Enluminées, Executées par Daubenton le Jeune* or *Buffon's Planches Enluminées*. This was the period of the *de luxe* monograph in France. Works of great beauty, such as *Oiseaux Dorés* (Paris 1800–2) by J.D. Audebert, F. Levaillant's *Histoire Naturelle des Perroquets* (1801–5) with figures by J. Barraband, and A.G. Desmarest's *Histoire Naturelle de Tangaras* (1805–7) with plates by Barraband's pupil, Pauline de Courcelles, made the Empire the golden age of ornithological illustration in France.

The foremost bird illustrator at this time was Thomas Bewick, who by 1800 was developing wood engraving. By cutting into the end grain he obtained from the wood the delicacy of shadowing that only intaglio copperplates had achieved before. He also attempted by means of detailed backgrounds to indicate the bird's habitat. Bewick was a major influence on both wildlife illustration and the art of engraving.

The first and, arguably, the finest of the great colour-illustrated books of the 19th century was *The Birds of America*, a four-volume elephant folio illustrated with 435 aquatint engravings. This book was the work of John James Audubon, who as well as being the greatest 19th century bird illustrator must also have been the most romantic. He was born in Haiti, son of a Creole woman and a French sea captain who later made a considerable fortune as a merchant. Educated in France, he went to live in the United States at the age of 18 and it was only after various business ventures had failed that he thought of publishing a book. Unable to interest American publishers, he sought subscribers in Europe and *The Birds of America* was published in London. The carefully composed plates often contain several birds and are full of action, showing that as well as being a very skilled artist, Audubon was a skilful observer of bird behaviour.

The invention of lithography brought a means of reproducing tone successfully and one of the pioneers of the process was Edward Lear, whose illustrations of the *Family Psittacidae* (1830–32) contains 42 large lithographic plates 'drawn from life and on stone'. These plates were beautifully and laboriously coloured by hand.

Lear was one of a stable of artists used by John Gould to prepare plates for his books. Gould's first book *A Century of Birds from the Himalaya Mountains* was published in 1832 and when he died in 1881 he had published more than 40 illustrated books. Although he prepared preliminary sketches and completed some very fine finished drawings, most of the illustrations were the work of his wife Elizabeth, Edward Lear, Joseph Wolf, William Hart, H.C. Richter and, latterly, J.G. Keulemans and Joseph Smit.

The portraits of birds in the school of Gould showed an adult or, especially in the case of sexually dimorphic species, two adults in the foreground with a scene suggesting the habitat or an interesting aspect of the species's habits. This formula for composition became accepted and was used by many artists for many years after Gould's death.

The paintings for exhibition or commission by Joseph Wolf and others were on an heroic scale, the fashionable obsession with the macabre and with the Scottish Highlands producing many dramatic paintings of Golden Eagles *Aquila chrysaetos* feeding on dead Red Deer *Cervus elaphus* or harrying Ptarmigan *Lagopus mutus*.

The invention of chromolithography meant that colour illustrations could be produced in greater quantities than before. One of the earlier bird books to take advantage of this development was Lord Lilford's *Coloured Figures of Birds of the British Islands* (1891–98). The chromolithographs were made from drawings by Keulemans and Archibald Thorburn with a small number by G.E. Lodge and W. Foster. These illustrations must have been seen by hundreds of thousands of birdwatchers, because they subsequently appeared in all 3 volumes of T.A. Coward's *The Birds of the British Isles and Their Eggs*, which was almost continuously in print for 40 years from 1920 and *The Observer's Book of Birds*, published in 1937. Thorburn in his own *British Birds*, published in 4 volumes in 1915–16, produced plates in which several species could be compared. On one plate there might be up to 11 species seen in appropriate habitat.

With his illustrations for the first two volumes of E.D. Cumming's *The Bodley Head Natural History* (1913) J.A. Shepherd suggested that it might be possible to identify birds from illustrations that show them as living and moving animals. No one else has tried to do this as an aid to identification, but Shepherd's work has influenced some of today's leading British illustrators, particularly John Busby.

Generally, North American bird artists of the early part of this century were more adventurous in approach than the Europeans. Louis Agassiz Fuertes, for example, showed great understanding of light and shade and his gallery paintings were the equal of any European contemporary, with the possible exception of Bruno Liljefors.

Fuertes was then, and still is, a major influence on American bird art and his death at the age of 53 in 1927 was a tragedy. At this time other leading North American bird artists included Lynne Bogue Hunt, Bruce Horsfall, Francis Lee Jaques and two Canadians, Allan Brooks and Frank Hennessy. All were among the exhibitors at the Cooper Ornithological Club's 1926 Annual Meeting in Los Angeles. Among the newcomers was an eighteen-year-old who was to revolutionize birdwatching with his system of illustrating for identification. His name was Roger Tory Peterson.

Peterson in *A Field Guide to the Birds* set a pattern which was to be followed for 40 years at least. In this revolutionary book he showed birds in profile with an arrow indicating diagnostic characters. Peterson, with Guy Mountfort and P.A.D. Hollom, did the same for European birds in *A Field Guide to the Birds of Britain and Europe*, published by Collins in 1954. These field guides have set a format for books on birds of various parts of the world as well as for those about other classes of animals.

Although there have been imitators of Peterson, none has been able to better his technique. Two artists, however, have developed further dimensions to illustration for identification by recognizing that not all birds present their watchers with a perfect profile. They are Peter Hayman, whose illustrations for *The Birdlife of Britain* (Mitchell Beazley, 1976) and *What's That Bird?* (RSPB, 1979) show birds in a variety of postures and Lars Jonsson, a Swedish artist, whose *Fåglar i Naturen* series of identification guides, first published in Sweden from 1977 to 1980, effectively capture the jizz of birds.

As well as book illustrations, Thorburn produced paintings for exhibitions. These often portrayed gamebirds and birds of prey, for it was sportsmen rather than ornithologists who made up the greatest market for bird paintings at the beginning of the century. These pictures showing birds in landscapes were much less dramatic (and, despite his reputation, less accurate) than the oil paintings of his Swedish contemporary, Bruno Liljefors, whose knowledge of birds and other animals and creative ability must make him one of the greatest of all wildlife painters. Other excellent bird painters, who both illustrated books and painted pictures for the private collector at this period, included Winifred Austen, G.E. Lodge, Allen W. Seaby and Frank Southgate.

Thorburn died in 1935, Liljefors 2 years later, by which time the paintings of Peter Scott had become popular, both as illustrations to his books and also reproduced as prints. This work as an artist, together with his conservation activities, helped to create a fertile ground in which the post-war interest in birds could grow. Among other books published in the 1930s were R.B. Talbot Kelly's *The Way of Birds* (1937) and Mary Priestley's *A Book of Birds* (1937) with illustrations by C.F. Tunnicliffe, who later wrote and illustrated several significant books of his own, notably *Shorelands Summer Diary* (1957). R.B. Talbot Kelly's distillation of birds to a few lines and flat colours and Eric Ennion's outstanding ability to catch the movement of birds and commit it to paper have influenced several of today's leading wildlife artists.

C.F. Tunnicliffe had first come to notice as an etcher of country subjects and then as a wood engraver, illustrating the nature books of Henry Williamson. Another expert wood-engraver still working is the Swiss, Robert Hainard, all of whose prints, often in several colours, are based on events that he has seen.

Print-making is not popular among bird illustrators today, but Robert Gillmor has made strong lino-cut prints and Robert Greenhalf uses birds in landscapes as subjects for his etchings.

While European bird art has become freer, in North America there seems to be a vogue for minutely accurate, often rather romanticized portrayals of birds. There is certainly work of a high ornithological standard from Roger Tory Peterson, George Miksch Sutton, Don Eckelberrry, Guy Coheleach and Al Gilbert, and Canada has produced two first-class bird artists in Robert Bateman and J. Fenwick Lansdowne. Australasia has produced several artists in the realistic genre; perhaps the most notable are Peter Trusler, William Cooper and Raymond Harris Ching, a New Zealander whose skilful drawing shows to great advantage when he tackles subjects with which he is familiar.

The contribution of bird illustrators to the creation of an interest in birds and their conservation has always been considerable, but in the last 50 years this contribution has been particularly impressive. The wide popularity of the work of Peter Scott and Roger Tory Peterson, the illustrations of Don Eckelberry, the vast commercial output of C.F. Tunnicliffe, the paintings and prints by Keith Shackleton and the book illustrations, calendars and cards by Robert Gillmor have all been notable.

Never has the demand for bird illustrations been so great nor have there been so many illustrators. However, not all the published bird illustrations are as accurate as they might be. The wonderfully detailed studies by David Reid Henry have yet to be matched by any living wildlife artist. While the growth of nature photography has encouraged some artists to adopt a more abstract approach, photographs have had the unfortunate effect of providing a source for other artists to copy. Sadly, some also use as models mounted specimens which they faithfully reproduce with all their unpreened feathers, shrunken soft parts and sometimes unrealistic poses. However, thanks to the Society of Wildlife Artists, whose inaugural exhibition was held in 1964, standards are improving. The SWLA and in the USA the Society of Animal Artists mount annual ornithological exhibitions and, with conservation societies holding exhibitions and a growing number of privately run galleries, there is plenty of opportunity for bird watchers to acquire original work. With an increasing number of bird books being published and the decorative opportunities presented by the use of birds on gifts and cards there has never been such wide scope for bird artists to have their work used. N.H.

Anker, J. 1938. Bird Books and Bird Art. Copenhagen.
Jackson, C.E. 1975. Bird Illustrators. London.
Jackson, C.E. 1978. Wood Engravings. London.
Kelly, R.B. Talbot. 1955. Birdlife and the Painter. London.
Harris, H. 1926. Examples of recent American bird art. Condor, 28: 191–206.
Niall, I. 1980. Portrait of a Country Artist. London.
Norelli, Martina R. 1975. American Wildlife Painting. New York.
Yapp, B. 1981. Birds in Medieval Manuscripts. London.

IMAGE-FIGHTING: term used to describe attacks by a bird against its reflection in a window, mirror or other reflecting surface, e.g. the hub-cap of a motor-car. The attacks may be brief and not repeated or become an obsession, persisting over months, and are usually but by no means always made by male birds, presumably against a territorial 'rival'. Attacks by a number of passeriform species, notably crows *Corvus* and wagtails *Motacilla*, are on record; also by game-birds such as the Capercaillie *Tetrao urogallus*. So far the phenomenon has not attracted more than anecdotal attention.

IMITATION: see under COMFORT BEHAVIOUR; FACILITATION, SOCIAL; FOOD SELECTION; HUMAN IMITATION OF BIRD SOUNDS; LEARNING; MIMICRY, VOCAL.

IMMATURITY: see under YOUNG BIRD.

IMMIGRATION: migration into an area (see MIGRATION; and IRRUPTION).

IMPENNES: a superorder recognized by some authorities (see under CLASS; PENGUIN).

IMPERVIOUS: as applied to nostrils, see NARIS.

IMPING: a technique in FALCONRY for mending broken feathers, also useful for rehabilitating flight-impaired birds. There are 3 main methods. (1) The broken feather's calamus is severed at the widest, most distal, hollow part; a whole moulted feather is cut at the same point, and a shaped wooded plug glued into the vane of each to join them. (2) The broken feather's calamus is cut as in (1) and the 'new' feather's calamus is not cut but trimmed to fit inside the original calamus, retained by glue and a thread tie. This method has been used to attach small transmitters (see RADIO-TRACKING AND BIOTELEMETRY). (3) The rachis is severed proximal to the break, a moulted feather cut to match, and a needle, pointed at each end, inserted with glue to make the join. Severely bent but unbroken feathers can be similarly mended by pushing the needle into the distal rachis at the bend, and ventrally slitting the proximal rachis to insert the needle lengthways.

IMPRINTING: a special case of exploratory or latent learning that has particular relevance for the student of ornithology (see also LEARNING). Like latent learning and insight learning, it is characterized by the absence of any reward in the usual sense of something which satisfies one of the primary physiological needs of the animal. The name 'imprinting' ('Prägung' in German) was originally given to a type of learning characteristic of the development of the following response of the young of nidifugous birds such as geese and ducks and rails. Heinroth, in 1910, found that young geese reared from the egg in isolation reacted to their human keepers, or to the first relatively large moving objects that they saw, by following them as they would their parents. In extreme cases it seems that this need happen perhaps for only a few minutes for the young bird to come to accept a human being as its proper associate and to retain for the rest of its life a tendency to regard human beings as fellow-members of its species. Thus a bird, as a result of this first experience, may when it becomes mature—months or years later—be found to be irreversibly fixated sexually to human beings; and Lorenz (1935) assumed from his work on geese that this was characteristic of imprinting. Subsequent investigation seems to show that such fixations based solely on the experience of the first few hours or days of life are extremely rare. Although many examples have been reported, it is evident that in almost all cases there has been a long subsequent history of rearing and attending by human keepers, so that there has been continual opportunity for the bird to learn to respond to human beings as a result of other types of LEARNING. The important point emerges, however, that when the young bird first follows the parent or substitute parent the attachment is not to an individual (although this will usually come later as a result of conditioning) but to the 'species' in a very general manner. Thus, we can sum up the characteristics of the process of imprinting, in the sense originally proposed by Lorenz, as:

(1) A learning process confined to a very definite and brief period of the individual life.

(2) One that, once accomplished, is often very stable and perhaps in some rare cases irreversible.

(3) A process that is often completed long before the various specific reactions to which the imprinted pattern will ultimately become linked are established.

(4) Learning that is generalized in the sense of leading to an ability to respond to the broad characteristics of the species.

On the whole, subsequent research has tended to emphasize the importance of conclusion (1) and to suggest that (2) and (3) apply only in exceptional cases. Recent developments concerning conclusion (4) will be discussed later.

As regards the first point, it has been shown that the critical age for imprinting Mallard *Anas platyrhynchos* ducklings, by the process of following, is between 13 and 16 hours; and that if the first experience is delayed beyond the latter age then the percentage of ducklings that can be imprinted falls rapidly to zero (Figure). It is known, however, that by holding the birds in complete isolation, or by giving doses of drugs such as meprobamate that reduce metabolism and act as muscle relaxants, the critical age for imprinting can be extended (E.H. Hess). Similar evidence for the existence of a critical period early in life has been found in chicks and goslings, as well as in the young of Tufted Duck *Aythya fuligula*, Moorhen *Gallinula chloropus*, Coot *Fulica atra*, and others.

The importance of internal processes of maturation in determining the start of the sensitive period is indicated by the observation that the start is more closely related to developmental age (time since conception) than to time since hatching.

A wide variety of stimuli will elicit a following response in ducklings and domestic chicks, ranging from a slowly walking person to a flashing light. The optimal stimulus in terms of colour and size varies from species to species, and the efficacy of a particular stimulus is influenced by the rearing environment. P.P.G. Bateson, for example, found that exposure of chicks to a colour pattern in their home pens subsequently facilitated imprinting to that pattern.

As the young bird becomes attached to one stimulus, a tendency to avoid other stimuli develops. In part, the onset of avoidance of new stimuli is a consequence of the imprinting process itself: when one object becomes familiar, others, by definition are unfamiliar and avoided. Thus the sensitive period is to some extent self-terminating and by depriving young birds the chance to become imprinted (e.g. by rearing them in diffuse light) the sensitive period can be extended. However it cannot be extended indefinitely, so it seems likely that the endogenous maturation

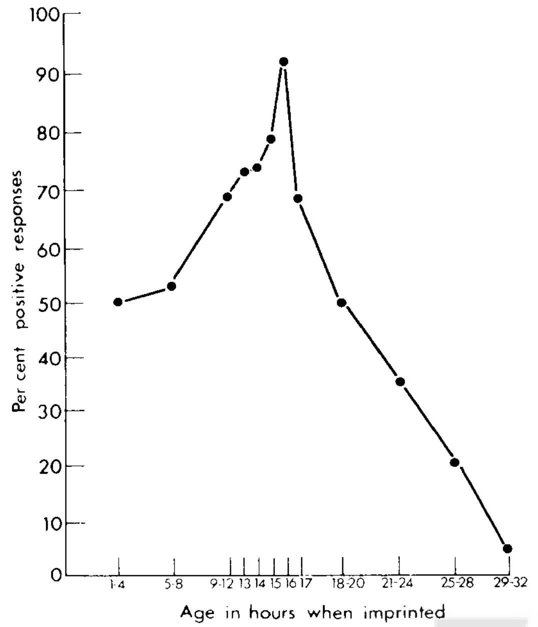


Fig. 1. Critical age for imprinting in Mallards *Anas platyrhynchos* expressed as a percentage of positive responses. (Redrawn from Hess 1957).

of 'fear' also plays a role in terminating it.

More detailed investigations of the stimuli eliciting the following response have shown that in fact the most effective stimulus for an imprinted chick is one that is very slightly different from the original imprinting stimulus; for example a chick imprinted on a yellow flashing light, and then offered the choice between approaching yellow or orange lights, prefers the orange. Thus there is a trade-off between familiarity and novelty and slight novelty provides the optimal stimulus.

Imprinting is not restricted to visual stimuli. In the cavity-nesting Wood Duck *Aix sponsa* exposure to sound signals can lead to a subsequent preference for that sound; further, this imprinted response to sound is not altered or reinforced by visual stimuli. This fits well with the natural life of the Wood Duck, since the first response of the young ducklings inside the dark nest cavity to their mother must be based on auditory rather than visual stimuli.

Sexual imprinting. For Lorenz, one of the key characteristics of imprinting was that later sexual preference could be determined by a rather brief exposure in early life. Subsequent work has shown that sexual imprinting does occur, but that it requires longer exposure to the imprinting stimulus than does so-called filial imprinting of the young bird on its parent. Once established, however, imprinted sexual preference can be very strong. In one experiment Zebra and Bengalese Finches (*Poephila guttata* and *Lonchura striata*) were cross-fostered and then maintained with their own species for a number of years. Even though the cross-fostered birds bred with their own species, when eventually given a choice between their own and their foster species, they strongly preferred to court the latter. Sexual imprinting, does, however, seem to be biassed towards the animal's own species. When the two finch species referred to above are raised by a mixed pair, they always imprint on their own species.

The sexual imprintability of the two sexes may differ in some cases. F. Schütz, for example, reported that in sexually dimorphic duck species only the males show sexual imprinting as a result of cross-fostering, while in the monomorphic Chilean Teal *Anas flavirostris* both sexes imprint.

The biological significance of imprinting. Why should the chancy business of learning be used instead of a fixed genetic instruction to determine filial and sexual preference? One proposal for filial imprinting is that the young bird sees its parent from so many different angles and distances that it would be hard to programme a genetic instruction for recognizing the parent under all conceivable circumstances: learning is more flexible. A second idea refers primarily to sexual imprinting. Recent work with Japanese Quail *Coturnix coturnix japonica* has shown that sexual imprinting is not, after all, simply a matter of learning supra-individual, species-specific chararacters. P. P. G. Bateson has shown that Quail prefer to mate with partners that differ slightly in plumage pattern from those with which they have been reared. This preference for slight novelty may prevent inbreeding, while ensuring that a mate of the correct species is chosen. The flexibility of learning may be better suited to cope with this compromise than a genetically fixed rule.

Other kinds of imprinting. Although most of the research on imprinting has been concerned with filial and sexual imprinting, analogous forms of learning (latent learning in a sensitive period) are known to influence other kinds of behaviour, for example, food preferences and habitat selection.

The concept of a sensitive period also emerges from studies of song development in birds (see VOCALIZATION): young Chaffinches *Fringilla coelebs* are capable of learning songs during their first year of life, but not subsequently. In this case the termination of the sensitive period seems to be under the hormonal control—gonadectomized Chaffinches have a greatly extended learning period. W.H.T. and J.R.K.

Bateson, P.P.G. 1979. How do sensitive periods arise and what are they for? Anim. Behav. 27: 470–486.

Chalmers, N. 1983. The development of social relationships. *In* Halliday, T.R. & Slater, P.J.B. (eds). Animal Behaviour, vol. 3. Genes, development and learning. Pp. 114–148. Oxford.

Heinroth, O. 1910. Beiträge zur Biologie, namentlich Ethologie und Physiologie der Anatiden. Verh. V. Internat. Orn. Kongr., Berlin 1910: 589–702.

Lorenz, K. 1935. Der Kumpan in der Umwelt des Vogels. J. Orn. 83: 137–214; 289–413.

INCA: substantive name of some *Coeligena* spp. (for family see HUMMINGBIRD).

INCA-FINCH: substantive name of Andean finches of the genus *Incaspiza* (for family see BUNTING).

INCA-TERN: see TERN.

INCERTAE SEDIS: term used in taxonomy to mean 'of uncertain taxonomic position'.

INCUBATION: the process whereby the heat necessary for embryonic development is applied to an egg after it has been laid. Such heat is usually derived from the body of one or both of the parent birds although species in several groups use foster parents (see BROOD-PARASITISM). The Megapodiidae utilize natural sources of heat such as solar radiation, volcanoes or the heat of fermentation of decaying organic matter (see MEGAPODE).

In the majority of birds heat transfer is effected by the close application to the eggs of the incubation or brood patch. Some birds have a single patch that covers all the eggs whilst others have a discrete patch for each egg. Generally this area on the ventral surface of the bird becomes denuded of feathers, and becomes oedematous and highly vascular through the action of steroid hormones in conjunction with prolactin (for reviews see Lofts and Murton 1973, Drent 1975). The release of these hormones appears to be related to the onset of breeding behaviour, e.g. the manipulation of nest material and stimulation by the mate during courtship. In some species, e.g. pigeons and doves (Columbidae), the incubation patch is an area naturally devoid of feathers and is bare the year round whilst in waterfowl there are no true incubation patches but the feathers in an area on the ventral surface are often plucked out by the parent. There are numerous observations on the way the incubation patch is brought into the right relationship with the eggs. The 'resettling' movements performed when a bird sits on the eggs include ruffling or lowering of the abdominal feathers to expose the patch and a waggling or quivering action as or after the bird lowers itself to adjust the tightness of sit. Some birds lack incubation patches (e.g. pelicans *Pelecanus* spp.) and in the Sulidae (gannets and boobies) the cradling of the egg in the webs of the feet has led to the suggestion that these birds incubate with their feet. The ventral body surface, although lacking an incubation patch, probably contributes to the warming of the egg for, as Drent points out, blood flow through the feet is usually highly variable since the legs and feet are used as heat dissipators for thermoregulation (see HEAT REGULATION).

Kendeigh (1952) surveyed a large body of data collected from all groups on such points as the division of labour between the parents and the patterns of attentiveness and inattentiveness i.e. intervals spent on and off the nest. Almost all the possible arrangements are exemplified from equal sharing of incubation between the sexes (most birds) to either

Magellanic Plover *Pluvianellus socialis* incubating. (*Photo: J.R. Jehl Jr.*).

Double-banded Courser *Cursorius africanus* incubating. (*Photo: G.L. Maclean*).

female (e.g. Galliformes, Strigiformes) or male (e.g. phalaropes, Tinamiformes) taking sole charge. Incubating males generally develop incubation patches (e.g. phalaropes and passerines—Skutch 1957) although several exceptions are listed by Lofts and Murton and by Drent. There are numerous examples of adaptive specialization, for instance, species in which only one member of a pair incubates are in many cases sexually dimorphic; the incubating bird is coloured cryptically and its mate conspicuously.

In bisexual incubation the eggs are generally attended at all times by one or the other parent except, for example, when the weather is mild. In single sex intermittent incubation the time is divided between attending the eggs and inattentive periods usually spent foraging; the nests of these species are usually of complex structure providing good heat retention during the inattentive periods.

Periods spent sitting on the eggs vary enormously between species (Lack 1968), from less than one hour in many passerines e.g. European Robin *Erithacus rubecula*, to a few hours in most seabirds which feed inshore, e.g. gulls and terns, between 2 and 12 days in offshore feeding seabirds, e.g. shearwaters, storm-petrels (Procellariidae), spells of 2½ to 3 weeks in the albatrosses *Diomedea nigripes* and *D. immutabilis* and the 64 days of the male Emperor Penguin *Aptenodytes forsteri*. Incubating birds do not adjust their heat production to regulate egg temperatures, but instead adjust the amount of time they spend in contact with the eggs. Consequently adjustments in the time (number and/or duration of sitting spells) spent attending the eggs are related to the ambient air temperature, degree of nest insulation, and the time required for foraging (White and Kinney 1974). The time spent off the nest foraging is reduced in some cases by the non-incubating member feeding its sitting mate.

When the parent leaves the nest to forage, the eggs lose heat at a rate dependent on their size, arrangement in the nest, degree of nest insulation, ambient temperature, and possibly egg colour. Resistance of the embryo to chilling has been demonstrated clearly in the Procellariiformes and seems to be a feature of bird embryos in general. In the latter half of incubation, when embryonic metabolism is increasing, the heat so produced, whilst not able to maintain the egg temperature, may at least slow its rate of decrease when the parent leaves the nest. Drent points out that in the energy budget for incubation not only is the rate of cooling of the eggs important, but the time required to reheat the eggs when the parent returns may also influence the pattern of foraging.

In birds with open nests on the ground the eggs may be exposed to the danger of overheating due to solar radiation when the parents leave the nest. Many of these species, however, have cryptic egg coloration as a protection against predators, and the pigments responsible for the markings tend to reflect the potentially harmful near-infrared rays and thus minimize solar heating. The bright blue eggs of some tree-nesting species also show high reflectance in the near-infrared. In some instances the ambient/egg temperature may be so high that cooling of the eggs by shading, wetting of the abdominal feathers (see BELLY-SOAKING) or through the brood-patch, with or without accompanying panting or gular flutter, may be necessary. Such species tend additionally to locate their nests to take advantage of prevailing shade and cooling winds and to orient their sitting posture to minimize insulation and maximize cooling by breezes.

The definitive incubation temperature (generally between 34 and 39°C depending on the species) is achieved only after a warm-up period, the length of which may be related to the tightness of sit and the time required for the incubation patch to become fully functional. Maintaining an adequate incubation temperature is, however, only one ingredient in the recipe for successful incubation, for it is clear from a consideration of the artificial incubation of eggs that other criteria must be satisfied through the behaviour of the incubating bird, the particular nest environment or adaptation of the egg. Thus, most eggs irrespective of size lose about 15% of their fresh weight during incubation (due to the loss of water from the contents across the porous shell) which suggests either a regulation of the nest humidity or an adaptation of shell porosity to the humidity conditions characteristic of the species. Control of water loss from the egg may be obligatory if the water content of the hatchling is to be similar to that of the fresh egg and successful hatching maximal. Thus, for example, the eggs of coots *Fulica*, divers (Gaviidae) and grebes have a shell of high porosity as an adaptation to the humidity pertaining in the nest. Species nesting at altitude have a reduced eggshell porosity compared to their sea-level counterparts to compensate for the changes that would result in embryonic respiratory gas exchange and water loss from the egg as a consequence of the lower barometric pressure (for these and other examples see Rahn and Paganelli 1981).

Nest ventilation (achieved presumably during the frequent rising and shuffling by the incubating parent) is important to maintain an optimum gaseous environment and egg turning, 'poking' or 'shifting' behaviour is important for a number of reasons. For example, it helps counteract the temperature gradients which occur in the nest and during early incubation it prevents premature adhesions between the extra-embryonic membranes and the shell membranes. These may result in distortions in subsequent development, with the embryo perhaps dying during incubation or finding itself in a position from which it is unable to escape when hatching. During the latter part of incubation the egg develops an asymmetrical distribution of weight so that in spite of egg-turning by the parent the egg probably resettles in a particular attitude. This may facilitate attainment of a correct pre-hatching position by the embryo (Drent; see HATCHING).

The incubation period is strictly defined as the time which, with regular uninterrupted incubation, elapses from the laying of the last egg in a clutch to the hatching of that egg. Accurate determination of the period of incubation demands marking of the eggs and vigilant observation and many documented periods have not been assessed according to the definition above. Incubation periods vary from 11 days in some of the smaller passerines (egg weight below 1 g) to about 80 days in the Royal

Water Rail *Rallus aquaticus* moving egg during incubation. (*Photo: K.J. Carlson*).

Albatross *Diomedea epomophora* (egg weight about 450 g). There exists a general relationship between egg weight and incubation period: each doubling of species egg weight increases incubation time by 16% on average. However, various factors have been suggested that modulate the relationship. Some of these are the egg temperature during incubation, stage of the development of the chick at hatching, relative risk of predation, type of nest, climate, season and food supply, with the result that there is a wide range of incubation period about any given egg weight. Nice (1954), reviewing these factors, concluded that the crucial one was the rate of development of the embryo. This rate of development is a product of natural selection and ultimate causes may be located in the bird's ecological relationships e.g. the availability of food and growth rate of the young. Thus Lack, commenting on the correlation between the fledging period and incubation period, suggested that the easiest or perhaps the only way to evolve a particular growth rate of the young was to alter the whole rate of development including that of the embryo in the egg (see DEVELOPMENT, EMBRYONIC; GROWTH).

See photos BELLY SOAKING; COLONIALITY; COLORATION, ADAPTIVE; ENERGETICS. S.G.T.

Drent, R.H. 1975. Incubation. *In* Farner, D.S. & King, J.R. (eds.). Avian Biology V. London.
Kendeigh, S.C. 1952. Parental care and its evolution in birds. Illinois Biol. Monog. 22(1–3): 1–356.
Lack, D. 1968. Ecological Adaptations for Breeding in Birds. London.
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Nice, M.M. 1954. Problems of incubation in North American birds. Condor 56: 173–197.
Rahn, H. & Paganelli, C.V. 1981. Gas Exchange in Avian Eggs. Buffalo.
Skutch, A.F. 1957. The incubation patterns of birds. Ibis 99: 69–93.
White, F.N. & Kinney, J.L. 1974. Avian incubation. Science 186: 107–115.

INCUBATOR BIRD: see MEGAPODE.

INDETERMINATE LAYER: species in which the number of eggs laid in a clutch can be altered by the addition or removal of eggs during laying (see LAYING).

INDEX: term sometimes applied to the second digit of the manus, but by a few authors to the first (see WING).

INDIAN REGION: alternative name for ORIENTAL REGION.

INDICATORIDAE: see PICIFORMES; HONEYGUIDE.

INDICATOR SPECIES: species whose ecological requirements are such that their presence more or less guarantees the existence of particular environmental conditions. It may then be easier to observe the presence or the absence of the indicator species than to measure the environmental conditions themselves.

INDIGENOUS: term applied to species, etc., meaning native to the area under reference.

INDIGO-BIRD: substantive name, alternatively 'indigo-finch' or 'combassou', used in East Africa for *Hypochera* spp. (for family see WHYDAH (1)).

INDIGO BUNTING: *Passerina cyanea* of North America (see CARDINAL GROSBEAK).

INDIRECT HEAD SCRATCHING: see COMFORT BEHAVIOUR.

INDIVIDUAL DISTANCE: the minimum distance at which an individual will tolerate the presence of another (usually, conspecific) individual. The term was introduced into ornithology by Conder (1949), who defined it widely so as to include the distance maintained between individuals in various other circumstances; but it is now most often applied to resting, or otherwise inactive, birds. Individual distance tends to be a specific characteristic; it is perhaps most obvious in gregarious birds roosting or perching together, for example on a telegraph line.

Conder, P.J. 1949. Individual distance. Ibis 91: 649–655.

INFECTION: see DISEASE.

INFESTATION: see ECTOPARASITE; ENDOPARASITE.

INFORMATION CENTRE: a phrase coined by P. Ward and A. Zahavi (following J. Fisher) to refer to the idea that birds nesting in colonies or gathering in communal roosts may learn from each other about the location of good feeding sites. The idea is that unsuccessful foragers could follow more successful individuals on their next trip. It has generated a considerable amount of data and theoretical controversy. Most of the evidence pertaining to the idea is inconclusive.

INFRA-ORDER: a systematic category between suborder and superfamily (if used) or family. The use of this category is not obligatory and the grouping of presumed families into a suborder in fact is rather subjective.

INFRA-SOUND: sounds of too low frequency to be detected by the human ear: below 20–30 Hz (waves per second). Recent experiments have shown that pigeons can detect sounds down to 0.05 Hz (1 wave in 20 s). If this proves to be common in birds, it may be related to the presence in their cochlea of a third otolith, the lagena, which has been lost in mammals. It has been suggested that natural infra-sound, which carries for very long distances, may give pigeons cues that help them in homing (see HOMING PIGEON; ULTRASOUND).

INGLUVIES: the crop (see ALIMENTARY SYSTEM).

INHAMBU: name used in Latin America for *Crypturellus* spp. (see TINAMOU).

INHERITANCE: see GENETICS.

INJURED BIRDS: see CARE OF SICK, INJURED AND ORPHANED BIRDS.

INJURY FEIGNING: see DISTRACTION BEHAVIOUR.

INNATE BEHAVIOUR: see BEHAVIOUR, HISTORY OF.

INNER TOE: see LEG.

INSECTICIDES: see TOXIC CHEMICALS.

INSECTIVOROUS: insect-eating; usually assumed to include other terrestrial arthropods.

INSESSORES: former ordinal name, applied to an assemblage of so-called 'perching birds' comprising the Passeriformes of today and various other groups.

INSHORE HABITAT: see under OCEANIC BIRDS.

INSIGHT: see LEARNING.

INSTINCT: an innate capacity for forms of behaviour that do not have to be learnt by the individual—a word falling into disuse as a scientific term because it represents an over-simplified concept and has acquired a variety of meanings.

INSTRUMENTAL SOUNDS: see MECHANICAL SOUNDS.

INTEGUMENTARY STRUCTURES: outgrowths from the skin (see SKIN). Of these the chief are feathers (see FEATHER; PLUMAGE), the rhamphotheca covering the bill, sometimes with horny excrescences or extensions such as casques and frontal shields (see BILL), the podothecae covering the feet (see LEG), and the oil gland (see OIL GLAND); these are dealt with elsewhere, as indicated. So also are the claws growing on the toes and sometimes on the digits of the manus, and the spurs that are present on the tarsus or on the carpal joint in some species (see LEG; WING). There remain to be considered various accessory structures found in certain species, especially about the head and neck; these are of several kinds. See photo BELLY-SOAKING.

Combs, Wattles, and Lappets. These are unfeathered flaps or appendages, usually of a fleshy texture and brightly coloured. Their function must lie in display and recognition; they often show sexual dimorphism; and their state may be subject to hormonal control. They are included in the general term 'caruncle'. A familiar example of a comb—an erect process situated longitudinally on the crown—is that of the domestic fowl, largest in the cock; the name derives from the serrated margin. Wattles are often pendulous from the angles of the mouth ('rictal lappets'), and there may be more than one on each side. Or they may be harder, more warty excrescences, variously situated—rictally, frontally, near the eye, or anywhere on the patches of bare skin found in some species, chiefly on the face and neck. Some of these, as with others adorning the bill, are moulted seasonally (see MOULT). Wattles are found in many species, particularly among the pheasants, turkeys, plovers, jacanas, cotingas, honeyeaters, starlings, and wattle-birds. The Turkey *Meleagris gallopavo* has a varied assortment, comprising a distensible frontal caruncle, tubercles on head and neck, and a throat wattle.

Pouches and Sacs. These are of different kinds. The gular pouches of pelicans and, less markedly, of cormorants play a part in the capture and swallowing of prey. Others are ornamental, such as the long red pouch depending from the almost naked neck of the Marabou *Leptoptilos crumeniferus*; or the inflatable sac, covered with bright red skin, on the front of the throat in male frigatebirds *Fregata* spp. Others again are concealed by feathers and are used in the production of booming calls, such as that uttered in spring by the male Prairie Chicken *Tympanuchus cupido* with the aid of two inflatable sacs on the sides of the neck.

INTELLIGENCE: a term without precise connotation for the study of bird behaviour, its place being taken by 'insight learning' (see LEARNING; also NERVOUS SYSTEM).

INTENTION MOVEMENTS: the incomplete initial phases of a behaviour pattern. For example when a bird is about to take off it crouches, withdraws its head and raises its tail, and then reverses these movements as it takes off. Such incomplete movements may be repeated several times as the bird prepares to take off, in particular if the bird is in a conflict about whether to fly or not. The primary interest of intention movements to students of bird behaviour is that they are thought to be the raw material from which some courtship and threat displays have evolved by RITUALIZATION.

INTERBREEDING: see GENETICS; HYBRID; HYBRIDIZATION, ZONE OF SECONDARY; ISOLATING MECHANISM; REPRODUCTIVE ISOLATION; SPECIATION.

INTERMEWED: term used in FALCONRY.

INTERNATIONAL CODE; INTERNATIONAL COMMISSION: see NOMENCLATURE.

INTERSPECIFIC: between two or more species.

INTESTINE: the posterior part of the gut or digestive tract, comprising the small intestine (duodenum and ileum) and the large intestine (rectum)—see ALIMENTARY SYSTEM.

INTRASPECIFIC: within a single species.

INTRODUCTION, ARTIFICIAL: see NATURALIZED BIRDS.

INTROGRESSION: gene flow between genetically divergent populations, often used technically for gene flow occurring only between species, but that usage begs the question of the exact taxonomic status of the two populations before one can employ the term, and such taxonomic determination is not always easy. In cases of avian hybridization in nature there is frequently little difference between introgression affecting species and that affecting subspecies, although theoretically greater introgession is to be expected between genetically more similar conspecific subspecies than between genetically more divergent species. One complication is that evaluation of hybridization and introgression is usually based upon a few morphological or other traits representing but a small fraction of genetic determinants which may be linked, and hence possibly biased (the fewer the characters studied the more difficult it is to appreciate actual gene flow). Other complications include intrinsic factors such as various reproductive isolating mechanisms, population structure, heterosis, selection for or against certain alien genes and gene combinations, and extrinsic factors such as topography or gene flow in one direction or another (see GENETICS; HYBRID; HYBRIDIZATION, ZONE OF SECONDARY).

Biochemical and other sophisticated techniques applied to cases involving hybridization usually disclose greater introgession than is superficially apparent from analysis of plumage and other morphological traits. Not only are different traits apt to show different degrees of introgression in a given case, but introgression may affect one population more than another. In the Northern Flicker *Colaptes auratus* of North America there is extensive hybridization between the eastern ('yellow-shafted') and western ('red-shafted') subspecies groups: traits such as shaft colour and colour of the facial moustache of males show extensive introgression into the eastern populations, whereas restriction of the nape patch shows little introgression beyond the hybrid zone. Also, the western populations show much more introgression than do the eastern populations. Other notable cases of introgression involve the Yellow-rumped Warbler *Dendroica coronata*, and the Blue-winged Warbler *Vermivora pinus* and Golden-winged Warbler *V. chrysoptera* in North America, the House Sparrow *Passer domesticus* and Spanish Sparrow *P. hispaniolensis* of Europe, and the Pale-headed Rosella *Platycercus adscitus* and Eastern Rosella *P. eximius* of Australia.

Introgression is suspected as a cause of observed variation when hybridization is known to occur between two populations, and the variation encountered shows gradients for traits within each population that involve characteristics of the other population and run toward the area of contact and hybridization between the two populations. Often the gradients in each population, with their gradual increase in characteristics of the other population toward the region of their interbreeding, run counter to all other patterns of clinal variation within each of them.

L.L.S.

INVASION: a term best reserved for an expansion of range into a new area; but sometimes used as synonymous with IRRUPTION.

IORA: substantive name of *Aegithina* spp. (see LEAFBIRD).

IRENIDAE: a family of the Passeriformes, suborder Oscines; LEAFBIRD.

IRIS: a thin, opaque annulus of tissue in front of the lens of the eye, which by its state of contraction determines the size of the aperture (pupil) in its centre (plural 'irides'; see VISION). As in reptiles, but in contrast to mammals, the musculature of the bird iris is striated.

IRIS COLORATION: often a noticeable character of the living bird at close range or of the newly dead specimen, but lost in the museum skin and not always accurately represented by the artificial eyes of mounted exhibits. The character may show SEXUAL DIMORPHISM, and changes with age and sometimes with season. Even more rapid colour changes are reported to occur in the eyes of some species, perhaps corresponding to different emotional states. Although eye colour sometimes matches the coloration of the head, possibly in order to camouflage the eye, brilliant lipochrome pigments in the irides of many birds often make the eye more conspicuous. The function of iris coloration is unclear; as in other vertebrates, the iris of birds is opaque, and its colour can apparently have no effect on vision. In different birds, eye colour may be used for sex or age recognition, in display behaviour, or simply as an integral part of the head plumage coloration.

The pigment of the iris epithelium in birds is brown, but there are nearly always stromal pigment cells (i.e. chromatophores in the stromal connective tissue of the iris) containing various amounts of melanin and/or coloured oils. The iris coloration is the result of both pigmentary factors and differential absorption or reflection by the different layers of the iris (see COLOUR); the red or reddish eyes observed in many species may be due (as in the Rock Dove *Columba livia*) more to richness of the superficial blood vessels than to pigmentation of the iris itself. On close examination, iris coloration may often be seen to be variegated and, interestingly, the iris of most birds has a black edge which may seem to make the pupil appear larger.

Among birds a brown iris coloration, resembling that found in mammals, is very common especially among song birds. In general, the irides of birds of prey are often yellow while many herons, parrots and pheasants have reddish eyes due to oil droplets of different refractions. Dark (brown or black) eyes are even reported to be especially common in birds that fly fast or feed on the wing (Worthy 1978). Despite these generalizations, however, a wide variety of colours occurs in many kinds of birds.

Some examples of birds showing various colours other than brown may be mentioned. Yellow irides are found, for instance, in most owls (Strigiformes), some 'waders' (Charadrii), some pigeons, and some herons, but also in many other groups. The Jackdaw *Corvus monedula* is a familiar example of a species in which the iris is almost white (pearl-grey in the adult). In adult Budgerigars *Melopsittacus undulatus* the iris is white peripherally, and chocolate-brown with white concentric lines in the pupillary part. In the Honey Buzzard *Pernis apivorus* a layer of guanine-containing cells in the yellow iris makes the latter appear brilliant white in reflected light.

An example of a bird in which the irides are green—a relatively infrequent colour—is the Cormorant *Phalacrocorax carbo*. Blue irides are found in, for example, the Oilbird *Steatornis caripensis*, the Blue-eyed Shag *Phalacrocorax atriceps*, the Ariel Toucan *Ramphastos vitellinus ariel*, and the Monkey-eating Eagle *Pithecophaga jefferyi*.

Many groups include red-eyed birds, e.g. rails, pigeons, grebes, herons, coucals (Centropinae), barbets, puffbirds, vireos, and mocking-thrushes; the White-winged Cough *Corcorax melanoramphos* (Grallinidae) has a bright red eye.

Sexual dimorphism in iris coloration is not infrequent. In Brewer's Blackbird *Euphagus cyanocephalus* (Icteridae), the iris is white in the male and dark in the female; whereas in two species of finfoots (Heliornithidae), it is dark brown in the male and bright yellow in the female. In the Wood Duck *Aix sponsa* the iris is orange-red in the male and dark brown in the female. A striking case is that of the Saddlebill *Ephippiorhynchus senegalensis* (Ciconiidae); the brown eye of the male tones with the dark plumage of the head, while the chrome yellow iris of the female is a conspicuous character.

Iris coloration often varies with age. The iris usually begins as blue, grey, grey-brown, brown or yellow, but in many species gradually changes after fledging to reddish-brown, brown, red, orange, yellow, white or green. These age-related changes in iris coloration in birds usually take place over a relatively short period. In the Gannet *Sula bassana*, for example, the iris is dark brown in the nestling, grey-blue in the juvenile, and nearly white—with a fine black outer ring—in the adult. In certain hawks, however, iris coloration may continue to change for several years. There may sometimes be seasonal change; for instance in the Rockhopper Penguin *Eudyptes crestatus* the colour of the iris, with that of the bill, varies from red to yellow with the seasons (see also HERON). As in fish, more rapid changes in iris coloration may sometimes accompany changes in emotional state. For example, the yellow irides of the Eagle Owl *Bubo bubo* are reported to turn red when the bird becomes agitated.

To be distinguished from iris coloration is the colour of the orbital ring of bare (sometimes hardened) skin around the eye in some species, e.g. among the cormorants, or in any circular pattern in the plumage in that position. The white-eyes (Zosteropidae) take their name from a white ring around the eye. J.T.E.

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Worthy, M. 1978. Eye color, size and quick-versus-deliberate behavior of birds. Percep. Motor Skills, 47: 60–62.

IRRUPTION: a form of MIGRATION in which the proportion of birds leaving the breeding range, and the distance travelled, varies greatly from year to year. Noted mainly in northern regions, irruptions occur in responses to annual, as well as to seasonal, fluctuations in food. Most migrations are regular, taking place at the same season each year, with individuals moving between fixed breeding and wintering areas. In irruptions, individuals may breed or winter in widely separated areas in different years. Regular migrations are associated with regular and predictable food supplies, whereas irruptions are associated with sporadic food supplies, which are much more plentiful in certain years than in others, or are plentiful in one region in one year and in a different region the next (Newton 1972). Strictly the term 'irruption' (or invasion) is applicable only to the region receiving the birds, whereas 'eruption' is often applied to the region losing them, but for general discussion it is convenient to use a single term.

Typically, irruptive species have diets based on one or two food types, which fluctuate from year to year. They include certain finches and other fruit-eating birds of boreal regions, certain raptors and owls that depend on cyclic prey, and a few steppe species, which occasionally experience extreme food shortages through drought (Table 1). All these species appear in strength in particular areas only in certain years.

Seed-eaters. The seed crops of trees vary enormously from year to year, and in some years fail completely. The cropping depends partly on the natural rhythm of the trees themselves, and partly on the weather. Most trees require more than one year to accumulate the reserves necessary to produce fruit, and crop at longer intervals towards the north, where the growing seasons are shorter. Spruce, for example, tends to crop well every 2–3 years in central Europe, every 3–4 years in southern Sweden, and less frequently further north. For a good crop, the weather must also be fine and warm in the preceding autumn when the fruit buds form, and again in the spring when the flowers set; otherwise the crop is delayed for another year. In any one area, most of the trees of a species fruit in phase with one another because they come under the same weather, and often those of a different species also crop in phase. The result is an enormous profusion of fruits in certain years, and practically none in others.

The trees in widely separated areas may be on different cropping regimes, partly because of regional variations in weather, so good crops in some areas may coincide with poor crops in others. Usually each productive area extends over thousands or millions of km^2, and is separated from the next by terrain which, in that year, is almost devoid of seeds. In some years, moreover, the productive patches are plentiful and widespread, and in others few and far between, so that the total production of seeds over a continent varies greatly from year to year.

The birds that depend on such seeds generally concentrate wherever their food is plentiful at the time. The majority of individuals migrate regularly in spring and autumn, but may breed and winter in different areas in successive years. Their local populations therefore fluctuate greatly from year to year in parallel with local seed crops. In winter quarters, too, populations range between total absence in years when appropriate tree seeds are lacking, to thousands of birds per km^2 in years when such seeds are plentiful. The bird species involved seem to move each autumn only until they find areas rich in food, then settle there. In consequence, the distance travelled by the bulk of the migrants varies from year to year, according to where the crops are good, and only when the migrants are exceptionally numerous, or their food is generally scarce, do they reach the furthest parts of their wintering range, as an irruption. Often several species irrupt in the same years, coinciding with the simultaneous failure of their respective food-plants (Bock and Lepthien 1976).

The food shortage which leads to a long and heavy migration is accentuated if the birds are especially numerous at the time. This situation is frequent, because good seed crops are usually followed by poor ones. The good crops in the first year lead to high survival among the birds over winter and to a large breeding population the next summer, and these same birds and their young then encounter the widespread poor crops in the next autumn, so have to move further than usual then. How far irruptive species move northward in spring also depends partly on how much food they meet on the way. The Mealy Redpoll *Carduelis f. flammea* provides the most striking example, for this subspecies curtails its usual migration by up to several hundred km to breed in southern Fennoscandia in years when the spruce crop there is good.

Compared with other migrants in autumn, irruptive finches tend to show more spread in their departure directions, and birds from a particular breeding area may spread over a large part of Europe on migration. Bullfinches *Pyrrhula pyrrhula* ringed in Fennoscandia have been recovered the following winter anywhere between south-west, through south, to east of their breeding place in the previous summer, and similar but less marked trends have been noted in other species. Individuals breeding or wintering in widely separated areas in different years have been confirmed by ringing. For example, one Siskin *Carduelis spinus* was found in successive breeding seasons at places 120 km apart, and 2 Mealy Redpolls were found at places 280 and 550 km apart. Wintering recoveries are even more striking, and Bramblings *Fringilla montifringilla* and Siskins have been caught in Belgium in one winter and as far east as Turkey and the Balkans in a later one. Another Siskin was ringed in Germany one February and recovered 2,200 km to the east in Russia the next, and a Bullfinch was recovered one winter in Russia 2,000 km to the west of where it had been ringed in the winter of the previous year. Three Mealy Redpolls are known to have wintered in different years at places 1,300, 1,500 and 1,800 km apart. Similarly, a Waxwing *Bombycilla garrulus* ringed in Poland one February was recovered in the next winter 4,500 km further east in Siberia, and a Cedar Waxwing *B. cedrorum* ringed in California in April was recovered in Alabama 3,000 km to the east two years later. Presumably all these birds had returned to the breeding range in the meantime, and took quite different directions in the two years.

The extent to which an irruptive finch will wander for food is well shown by the North American Evening Grosbeak *Hesperiphona vespertina*, which breeds in conifer forests and moves south or south-east in autumn. This species feeds mainly on large, hard tree-fruits, but also visits feeding trays for sunflower seeds, a habit which makes it easy to catch. Over 14 winters, 17,000 Grosbeaks were ringed at a site in Pennsylvania. Of these, only 48 were recovered at the same place in subsequent winters, yet 451 others were scattered among 17 American states and 4 Canadian provinces. Another 348 birds that had been ringed elsewhere were caught at this same locality, and these had come from 14 different states and 4 provinces. These recoveries show both how widely individual Grosbeaks range and how weak is their tendency to return to the same place in later years.

The wide wintering range, less rigid directional tendencies, and the poor homing shown by irruptive species are all ways of coping with a sporadic food supply. They contrast with the marked directional tendencies, narrow migration routes and strong homing shown by birds which feed on more predictable food supplies.

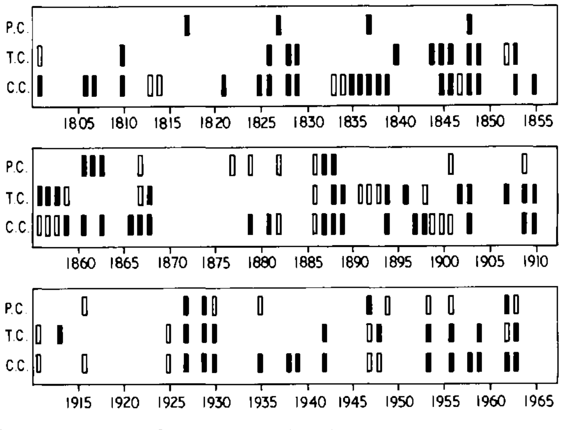

Fig. 1. The dates of crossbill invasions into south-west Europe. Filled blocks show large invasions, open blocks small ones. P.C., T.C. and C.C. refer to Parrot Crossbill *Loxia pytyopsittacus*, Two-barred Crossbill *L. leucoptera* and Common Crossbill *L. curvirostra*.

The most famous of the irruptive migrants are the crossbills, which feed almost entirely on conifer seeds, and leave the boreal region in large numbers only in exceptional years. Between 1800 and 1965, Common Crossbills *Loxia curvirostra* irrupted into south-west Europe at least 67 times; sometimes they came in successive years, and at other times at intervals up to 11 years (Newton 1972). Parrot *L. pytyopsittacus* and Two-barred Crossbills *L. leucoptera* often came in the same years as Common Crossbills, though less frequently. The ultimate cause (adaptive value) of mass emigration is presumably to avoid food shortage on the regular range, but while some authors have speculated that food shortage is the proximate factor releasing the flight (Svärdson 1957), others believe that over-population and crowding present the stimulus to leave (Lack 1954). The hypothesis that best fits the facts is that high numbers are necessary for eruptive migrations of crossbills, but the size of the food crop modifies this (Newton 1972). Once the population is high, emigration probably occurs in response to the first inadequate crop, and only an exceptionally good crop over a wide area will prevent the flight.

Once on the move, some birds reach the extreme south-west of Europe, some 4,000 km from their breeding range. Such mass movements by crossbills were formerly regarded as 'death-wanderings', because most birds failed to find areas of suitable food. However, ringing has now confirmed that some individuals return successfully to the boreal forests in a later year. Moreover, those emigrants which find areas with conifers often stay for a year or two and breed, if the cone crops permit.

In many irruptive species, the young predominate in invading flocks, and among the adults females outnumber males. This has given rise to the ideas (a) that irruptions follow good breeding seasons, (b) that the young emigrate in greater proportion than the adults, and (c) that more adult hens than cocks leave. In general, this is probably true, as in many regular migrants, but recent information on the composition of irruptive flocks is conflicting. While some certainly contain a high proportion of young, others do not, suggesting that not all movements follow good breeding. Some authors have suggested a cyclic rhythm to the irruptions of seed-eating species, but in most cases there is little evidence for this. This is in contrast to the owls and raptors discussed below.

Owls and raptors. Irruptive movements are known from those species which feed on cyclic prey, mass emigration occurring in the 'low' years, when prey are scarce (Newton 1979). Two main cycles are recognized: (a) an approximately 4-year cycle of small rodents on the northern tundras and temperate grasslands; and (b) an approximately 10-year cycle of Snowshoe Hares *Lepus americanus* in the boreal forests of North America. Some grouse-like birds are also involved, but whereas in some regions they follow the 4-year rodent cycle, with peaks in the same years, in others they follow the 10-year hare cycle. The populations of these various animals do not reach a peak simultaneously over their whole range, but the peak may be synchronized over tens or many thousands of km^2. Why such prey species fluctuate with fairly regular periodicity is uncertain, but there is no question that they cause mass movements by their avian predators. Among owls and raptors, the majority of individuals stay in the north of the wintering range in years when prey is plentiful there, and move further south in years when prey is scarce. As in the finches, the food shortage caused by a crash in the prey population is often accentuated because the predators themselves tend to be numerous at such times, as a result of good breeding and survival in the previous few years, when prey was abundant.

The main invasions by the Rough-legged Buzzard *Buteo lagopus* occur at about 4-year intervals, whereas those of the Goshawk *Accipter gentilis* in North America occur roughly every 10 years, corresponding with the 4-year and 10-year prey cycles respectively. Invasions may occur in only one autumn, or in two successive ones if prey remains sparse. Invasions by Rough-legged Buzzards often occur in the same years as those by Snowy Owls *Nyctea scandiaca* (both species eat rodents), while in parts of North America the invasions by Goshawks show a similar periodicity to those by Horned Owls *Bubo virginianus* (both eat hares and grouse). Since the lows in prey populations are not synchronized over the whole range, invasions by any one species tend to come in different years in different regions. Those by the Rough-legged Buzzard and Snowy Owl are also more marked in North America than in Europe, presumably because the birds are more numerous in North America, having a greater area of breeding habitat (tundra) on that continent.

Some Irregular Migrants of the Northern Hemisphere	*Preferred Food*	*Distribution*
SEED-EATERS		
Great Spotted Woodpecker *Dendrocopos major*	Spruce, Pine and other seeds	Palearctic
Waxwing *Bombycilla garrulus*	Berries, especially Rowan	Holarctic
Cedar Waxwing *B. cedrorum*	Berries	Nearctic
Pine Grosbeak *Pinicola enucleator*	Conifer seeds, berries	Holarctic
Fieldfare *Turdus pilaris*	Berries	Palearctic
Coal Tit *Parus ater*	Spruce seeds, insects	Palearctic
Black-capped and Boreal Chickadees *Parus atricapillus* and *P. hudsonicus littoralis*	Various seeds, insects	Nearctic
Nuthatch *Sitta europaea* (Siberian populations)	Spruce seeds	Siberia
Red-breasted Nuthatch *S. canadensis*	Pine, Spruce seeds	Nearctic
Brambling *Fringilla montifringilla*	Beech seeds	Palearctic
Siskin *Carduelis spinus*	Birch, Alder and Conifer seeds	Palearctic
Pine Siskin *Carduelis pinus*	Conifer, Birch and Alder seeds	Nearctic
Northern Bullfinch *Pyrrhula pyrrhula*	Various tree-seeds and berries	Palearctic
Evening Grosbeak *Hesperiphona vespertina*	Maple and other tree-seeds	Nearctic
Redpoll *Carduelis flammea*	Birch seeds	Holarctic
Arctic Redpoll *C. hornemanni*	Birch seeds	Holarctic
Purple Finch *Carpodacus purpureus*	Various tree-seeds	Nearctic
Crossbill *Loxia curvirostra*	Spruce and other Conifer seeds	Holarctic
Two-barred Crossbill *L. leucoptera*	Larch and other Conifer seeds	Holarctic
Parrot Crossbill *L. pytyopsittacus*	Pine seeds	Europe
Jay *Garrulus glandarius*	Oak fruits	Palearctic
Thick-billed Nutcracker *Nucifraga caryocatactes macrorhynchos*	Hazel fruits	Scandinavia
Thin-billed Nutcracker *N. c. caryocatactes*	Arolla Pine seeds	Siberia
Clark's Nutcracker *N. columbiana*	Whitebark Pine and other Conifer seeds	Nearctic
RAPTORS AND OTHER PREDATORS		
Goshawk *Accipiter gentilis*	Various Grouse and Hares	Palearctic
Rough-legged Buzzard *Buteo lagopus*	Lemmings, Voles	Holarctic
Snowy Owl *Nyctea scandiaca*	Lemmings, Voles	Holarctic
Horned Owl *Bubo virginianus*	Varying Hares	Nearctic
Short-eared Owl *Asio flammeus*	Voles	Holarctic
Great Grey (or Northern) Shrike *Lanius excubitor*	Voles	Holarctic
STEPPE BIRDS		
Pallas's Sandgrouse *Syrrhaptes paradoxus*	*Agriophyllum gobicum*	Central Asia
Rosy Pastor *Sturnus ('Pastor') roseus*	Locusts (in breeding season)	Turkestan

Many individual raptors must winter in widely separated areas in different years, as in the finches. On their breeding grounds, too, some rodent-eating species concentrate to breed wherever food is plentiful at the time, so that their local populations fluctuate greatly from year to year. This implies that at least some individuals breed (as well as winter) in widely separated areas in different years. So far, however, ringing recoveries of owls and raptors lend no support to this idea because they nearly all refer to birds handled only once as adults.

Steppe species. The Rosy Pastor *Sturnus roseus* is a regular migrant to India from the Asian steppes, but it is sporadic in its breeding, as thousands of birds may settle in a suitable locality, breed and then desert it again. It feeds its young on locusts, and its irruptions occur in spring and early summer, presumably on occasions when it returns on its normal spring migration to find a failure of the locust hatch. The movements of Pallas's Sandgrouse *Syrrhaptes paradoxus* are probably caused by prolonged drought. Major invasions of sandgrouse into western Europe occurred in 1863, 1872, 1876, 1888 and 1908, and there have been a few other occurrences. Breeding was recorded in Britain in 1888–89 following an irruption.

It seems probable that irregular migration is far more widespread than is generally supposed. There is every gradation between irruption and conventional migration, and even species which are normally fairly sedentary perform irruptive movements on occasion. Unexpected movements of this type have been noted, for example, among Blue Tits *Parus caeruleus* and Bearded Tits *Panurus biarmicus*. They tend to occur when the birds are especially numerous, or in obvious imbalance with their food-supply. I.N.

Bock, C.E. & Lepthien, L.W. 1976. Synchronous eruptions of boreal seed-eating birds. Am. Nat., 110: 559–71.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford.

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Svärdson, G. 1957. The 'invasion' type of bird migration. Br. Birds, 50: 314–43.

ISCHIUM: a paired bone of the pelvic girdle, partly fused with the other elements (see SKELETON, POST-CRANIAL).

ISLAND BIOGEOGRAPHY: see DISTRIBUTION, GEOGRAPHICAL.

ISOCHRONAL LINE: a line joining geographical localities at which the same event occurs simultaneously; applied, notably, to the mean date of arrival of a given migratory species (see MIGRATION).

ISOLATING MECHANISM: a difference between species, or populations of a species, that tends to prevent cross-mating and so to maintain reproductive isolation; such differences are often in factors concerned in recognition, i.e. in appearance (plumage) or behaviour (display, voice). An isolating mechanism is said to be 'specific' when it is adaptively built up between two populations that are genetically capable of interbreeding and of producing fertile hybrids; this can occur only when there is some contact between the two populations, with the production of hybrids that are at a selective disadvantage as compared with the parent stocks. Such specific isolating mechanisms often play an important part in speciation (see SPECIATION; also HYBRID; HYBRIDIZATION, ZONE OF SECONDARY; RECOGNITION; REPRODUCTIVE ISOLATION; VOCALIZATION).

ISOPHENE: a geographical line along which a character of a polytypic species has the same value; 'a line of equal phenotype'. Isophenes run roughly at right angles to the direction of a CLINE.

ISOTHERM: a line connecting points of equal air temperature (commonly in terms of the mean temperature for a stated day or month of the year)—see WEATHER AND BIRDS.

ITALICS: as regards their use in printing scientific names of birds (represented by single underlining in manuscript or typescript), see NOMENCLATURE.

ITINERANT BREEDING: a series of breeding attempts by the same individual in two or more different geographical areas during the course of the same annual reproductive period, and recurring year after year as a normal event in the annual cycle of the species. The seasonal movement between the successive breeding areas has been termed the 'breeding migration'.

Conclusive proof of itinerant breeding, e.g. from ringed individuals, is still lacking but circumstantial evidence points to its occurrence in several tropical and temperate species. The phenomenon was first recognized in the European Quail *Coturnix coturnix*, where females arriving in Italy in June and July, apparently to breed, often showed regressing incubation patches from a recent breeding attempt and were frequently accompanied by young no more than 2 months old. These young must have hatched from clutches begun in March but at so early a date breeding could have been possible only in North Africa. Reports of a general exodus of Quail from Tunisia in spring after breeding support this and birds ringed there in May and early June have been recovered in Italy and Albania 2–3 months later. It has been suggested that late clutches laid in Britain and northern Europe in August and September could result from an influx in midsummer of birds that have already bred around the Mediterranean.

Among tropical species the most suggestive evidence for itinerant breeding is for the Red-billed Quelea *Quelea quelea* of Africa. The different races of queleas perform migrations whose patterns are determined by the movements of rainfronts across the continent. The birds congregate during the dry season in certain areas where they subsist on the dry grass seed produced during the previous rains. When the next rains break, however, this abundance of dry seed suddenly germinates and is unavailable as food, forcing the birds to leave the area. Queleas are normally able to perform an 'early-rains migration' to areas over which the rainfront has already passed some two months previously and where the new grass has already set seed. The new seed and insects associated with the growing vegetation enable some birds to begin their first breeding attempt straight away, while others begin the slow return movement, the 'breeding migration'. This follows the course taken by the rainfront at the start of the wet season, in the wake of which is now developing a 'front' of seeding grasses. By remaining within this slowly shifting zone of seeding grass all birds soon reach breeding condition, halt the migration, and establish colonies. Feeding conditions suitable for rearing young do not last long, however, and despite an abbreviated breeding schedule of only 5 weeks, there is not time to rear 2 broods in the same place. The adults abandon the young at 3 weeks old with enough fat reserves to ensure their survival, and continue the 'breeding migration'. On catching up once more with the zone of seeding grasses it is thought that the adults can begin a second breeding attempt, perhaps some hundreds of km from the site of the first, and almost certainly with a different mate.

The evidence is circumstantial but compelling; many females begin developing the yolks of a second clutch while still feeding the first brood, yet do not breed again in the vicinity, and in those regions where colonies are likely to contain a majority of birds breeding for the second time on the 'breeding migration', most adults arrive in already very worn plumage, consistent with a previous breeding attempt. In West and southern Africa there is time in wet years for up to 3 broods to be raised in different places along a 'breeding migration' and in East Africa up to 5, though it is unknown if these maxima could often be achieved.

It is likely that itinerant breeding will be found amongst other birds living in seasonal environments which offer local opportunities for breeding for too limited a period for more than one brood to be reared. Such species may nevertheless be multibrooded if, by performing a 'breeding migration', they can utilize in turn adjacent regions that become suitable at different times during the annual reproductive period. Prerequisites for such a breeding strategy would be a short breeding schedule with early independence of the young. Species that require a long period of territorial establishment, or which undertake prolonged postfledging parental care, would not be expected to be itinerant breeders. P.J.J.

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Ward, P. 1971. The migration patterns of *Quelea quelea* in Africa. Ibis 113: 275–297.

J

JABIRU: *Jabiru mycteria* of South America; in the Old World the name is sometimes applied to the Saddlebill *Ephippiorhynchus senegalensis* or the Black-necked Stork *E. asiaticus*. For all these species of Ciconiidae see STORK.

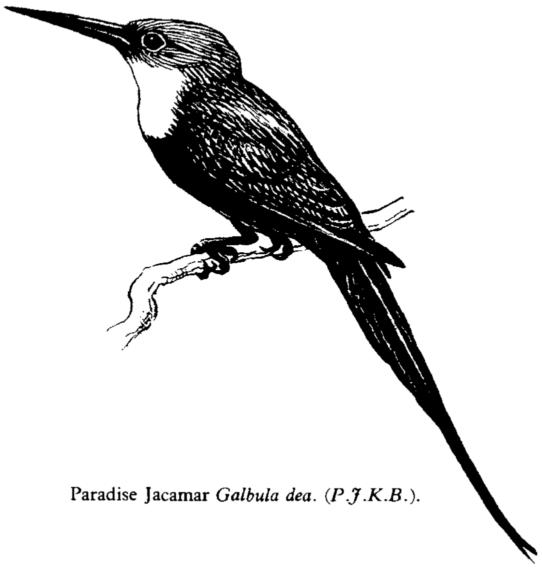
JACAMAR: substantive name of species of Galbulidae (Piciformes, suborder Galbulae): in the plural, general term for the family. This consists of 5 genera and 15 species of small or middle-sized birds (15–31 cm long).

Characteristics, distribution and habitat. Jacamars are confined to the wooded regions of continental tropical America, chiefly at low altitudes. Jacamars have long, pointed, usually slender bills. Their legs are short, and in the 4-toed species 2 toes are directed backward. The inner hind toe of the Three-toed Jacamar *Jacamaralcyon tridactyla* has been lost. The more typical species have glittering metallic plumage and, with their long, thin bills, are reminiscent of overgrown hummingbirds. Perhaps even more than hummingbirds, they seem charged with vitality and intensely alive. They are among the most exciting of all birds to meet.

One of the most widespread and familiar members of the family is the Rufous-tailed Jacamar *Galbula ruficauda*, which ranges from southern Mexico to north-eastern Argentina. Its upper plumage, including the wings and central feathers of the long tail, is glittering metallic green, over which play golden, coppery, and bronzy glints. A broad green band across the chest separates the white throat from the rufous-chestnut of the posterior underparts and the outer tail feathers. The female differs from the male only in having the throat pale buff instead of white. In both sexes, the long, sharp bill is black. *Galbula*, the largest genus, contains 7 other species, including the lovely Paradise Jacamar *G. dea*, distinguished by narrow, greatly elongated central tail feathers.

The stoutest member of the family is the Great Jacamar *Jacamerops aurea*, a long-tailed bird (in all 30 cm in length) that ranges from Costa Rica to the Amazon valley. The top of the male's head is bright metallic green, which merges into rich metallic golden or reddish-bronze on the back and shoulders; this in turn becomes bright golden-green on the rump and central tail feathers. The outer tail feathers are violet–blue. The sides of the head and upper throat are metallic green, the lower throat is white, and the remaining under plumage is rufous-tawny. The female is like the male, except that her throat is tawny instead of white. The black bill is only moderately long and slightly curved.

A less graceful and glittering member of the family is the Chestnut Jacamar *Galbalcyrhynchus leucotis* of Amazonia. Its plumage is largely dark chestnut, with white or chestnut ear coverts. A long, thick, pink or whitish bill and short tail give it a topheavy aspect. Plainest and smallest of the jacamars are the 4 species of *Brachygalba*, which have largely brown or dusky plumage with white on the under parts, short tails, and long, sharp, usually black bills.



Paradise Jacamar *Galbula dea*. (*P.J.K.B.*).

Food. Jacamars appear to be wholly insectivorous and, at least in the best-known genera, *Galbula* and *Brachygalba*, their prey is captured on the wing. They rest on an exposed perch, turning their heads from side to side, until they spy a suitable flying insect, which they overtake by means of a rapid sally. Morphos and large swallow-tails *Papilio*, which most flycatching birds eschew, are often captured by jacamars. With the victim fluttering in its slender bill, the captor returns to its perch, against which it beats the insect long and loudly until the brilliant wings flutter earthward, after which the body is swallowed. Skipper butterflies (Hesperiidae), dragonflies (Odonata), wasps and bees (Hymenoptera), beetles (Coleoptera), and other insects are also captured in large numbers; heliconian butterflies (Heliconiinae) are avoided. The feeding habits of jacamars have been compared to those of Old World bee-eaters.

Voice. The Rufous-tailed Jacamar is a voluble bird whose sharp calls, sounding afar through the woodland, suggest that it lives at a high pitch of excitement. When mated birds are together, and especially when two males compete for a female, their animated vocal performances include an accelerated series of high-pitched notes that may merge into a prolonged, clear, soft trill. The Pale-headed Jacamar *Brachygalba goeringi* has a similarly elaborate song, but in a weaker voice. At their best, jacamars' songs are delightfully melodious.

Behaviour and breeding. Solitary rather than colonial, jacamars nest chiefly in burrows, which they dig in roadside or streamside banks, in steep wooded hillsides, or in the wall-like root-plate of a great fallen tree. Breeding in cavities in termites' nests has been observed in the Great Jacamar and several species of *Galbula*, including the Rufous-tailed Jacamar, which usually nests in earthen burrows. Both sexes of this species loosen the soil with fine-pointed bills, and remove it from the tunnel by kicking vigorously backwards as they enter. The Rufous-tailed Jacamars' burrows range from about 28–50 cm in length. At the inner end, they dilate into a chamber that is not lined. The same burrow may be occupied in successive years.

The Rufous-tailed Jacamar lays 2–4 white, glossy eggs. Few records are available for other species. The Rufous-tailed female incubates through the night, and by day she and her mate sit alternately. Intervals of neglect are short, and the eggs are almost constantly attended. While sitting, the parents regurgitate many shards of beetles and other chitinous parts of insects, which accumulate on the floor of the chamber. The incubation period is 20–23 days.

In contrast to the perfectly naked nestlings of most piciform birds, newly hatched jacamars bear copious, long, whitish down. Their heels are covered with prominent callous pads that are nearly smooth instead of strongly papillate like those of woodpeckers, toucans and other birds that breed in unlined holes in trees. Both parents bring the young a variety of insects, but they fail to clean the nest. As they grow older, the loquacious nestlings repeat weak-voiced versions of their parents' calls, including pleasant little trills.They leave the burrow when from 19 to (in wet weather) 26 days of age, wearing plumage much like that of adults of the same sex. Fledgling Rufous-tailed Jacamars seem never to return to their natal burrow; but 4 juvenile Pale-headed Jacamars continued for several months to return each evening to sleep with both parents in their 79 cm-long burrow in a vertical bank. A.F.S.

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Skutch, A.F. 1937. Life history of the Black-chinned Jacamar. Auk 54: 135–146.

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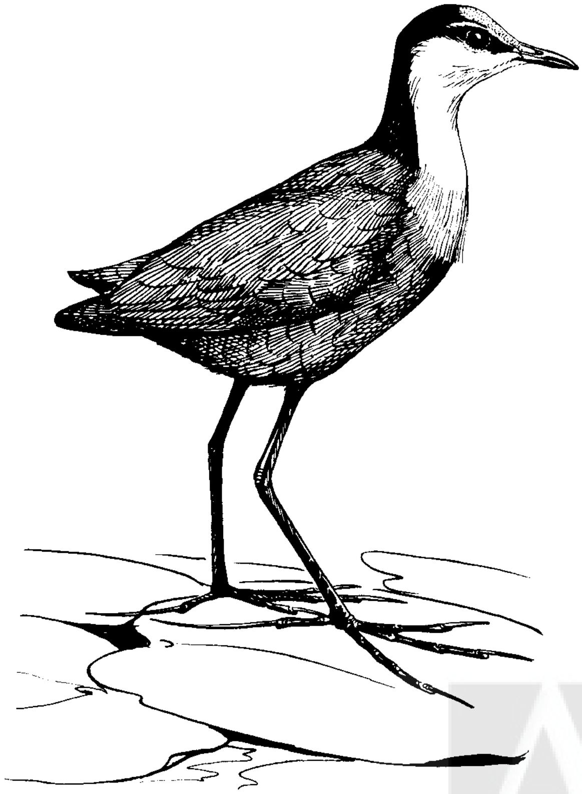
Skutch, A.F. 1968. The nesting of some Venezuelan birds. Condor 70: 66–82.

JACANA: name applied to species of the Jacanidae (Charadriiformes, suborder Charadrii). African and Australian forms are also called lily-trotters or lotus-birds. The name Jacana is an Anglicized form of the Portuguese name 'jaçaná' a transliteration of a native Brazilian name for the bird. The precise systematic relationship of the Jacanidae to the other Charadrii is not clear. Superficial resemblances to the Rallidae are due to convergence.



African Jacana *Actophilornis africanus.* (*C.E.T.K.*).

Characteristics. Conspicuous adaptations for walking on floating vegetation include long, mostly bare tibia and extremely elongated toes and nails. Jacanas are of moderate size (16.5–53 cm). Adult Northern Jacanas (*Jacana spinosa*) weigh only 80–170 g, but their feet cover an area as large as 12 × 14 cm. In the Northern Jacana sharp spurs on the wrist commonly reach 16 mm; other jacanas also have carpal spurs or knobs. In breeding populations Northern Jacana females average 161 g while males average only 91 g. Sexes are monochromatic in all species. The plumage is basically dark reddish or blackish-brown. Five species have white or pale yellow on lower neck, throat and head. Several have pale yellowish primaries and secondaries. The African Jacana *Actophilornis africanus* reportedly moults its flight feathers simultaneously, but the Northern Jacana has a gradual moult and is never flightless. Several species have fleshy frontal shields and/or lappets. The downy chicks are striped.

Habitat. Jacanas are never found on salt water. All species establish territories and breed on floating, low profile, aquatic vegetation in swamps, marshes, and along streams. In addition to feeding in their territories they may feed in dense emergent aquatic vegetation, wet meadows and short-grass uplands. Outside the breeding season jacanas may form flocks of up to several hundred birds that feed in meadows, irrigated farmland or other wet areas.

Distribution. This circum-tropical family occasionally extends into the sub-tropics (Houston, Texas; Peking). Jacanas are found from sea-level to 2,400 m in Kenya, 3,600 m in outer Himalayas. The African Jacana occurs throughout sub-Saharan Africa; *A. albinucha* is found only on Madagascar. The Lesser Jacana *Microparra capensis* is found in eastern Africa. The Bronze-winged Jacana *Metopidius indicus* occurs from India through south-eastern Asia, while the Pheasant-tailed Jacana *Hydrophasianus chirurgus* is found from Pakistan east into south-east Asia, southern China, Taiwan, and the Philippine Islands. The Comb-crested Jacana or Lotus-bird *Irediparra gallinacea* occurs in Indonesia and Australia. The Northern or American Jacana, which occurs from western Panama northward into Mexico, southern Texas and the Caribbean Islands, is regarded by some as conspecific with the Southern or Wattled Jacana *Jacana jacana* found from western Panama south to northern Argentina.

Populations. Local breeding populations vary from one pair to several hundred. Territory sizes vary depending on the quality and shape of habitat. Territories along streams tend to be linear. Territories of the Northern Jacana average 0.15 ha for males and 0.35 ha for females.

Movements. No regular migrations or patterns of movement have been reported. In some areas jacanas occupy territories year-round and breed in any month. In areas with prolonged dry seasons movement to permanent wet lands must occur but no detailed reports are available. In western Costa Rica flocks of 200 to 300 jacanas arrive on the breeding marshes at the beginning of the season; absence of reports of regular movements suggest these are local birds.

Food. Jacanas feed primarily by gleaning insects from floating vegetation. They also take small frogs, fish and invertebrates from just beneath the surface. Sometimes they turn rooted, floating plants upside down and remove invertebrate prey from amongst the roots. Stomach contents often include plant matter. Northern Jacanas occasionally feed on the ovules of water-lilies.

Behaviour. Four species of jacanas are polyandrous. Mating systems in the other species remain unknown. In the Northern Jacana, the best-known species, males defend small territories from which they exclude all other males. Females defend the territories of one to four adjacent males (polyandrous populations average 1.8–2.4 males per female). The pair co-operates in excluding intruders of both sexes, but the small males cannot exclude persistent females without help. Where jacanas breed year-round, both sexes are replaced by new birds on an individual basis. Deserted territories are promptly occupied by new, previously non-breeding birds. Neighbouring females sometimes take over an abandoned male and his territory. A new female that attacks and drives a territory owner from her territory is invariably larger than the female she replaces. Where Northern Jacanas breed seasonally, courtship and territory establishment occur simultaneously. Initial bonding occasionally occurs between one female and two adjacent males; additional males settle next to existing pairs or interpolate themselves between existing territories and become bonded to the already established females. In continuously breeding populations young sometimes stay on parental territory for more than a year. Where the marsh dries, young and adults leave when the chicks are 4–5 months old.

Over short distances the flight appears slow and laboured, with the feet dangling. Sustained flight is stronger and smoother with the legs extending out behind. Although capable of swimming, adult African and Northern Jacanas climb out of water as soon as possible. Small chicks of the Lotus-bird regularly dive beneath the surface to hide from predators.

Voice. Northern Jacana chicks give simple peeps similar to domestic chicks. Adults produce a relatively soft call consisting of very short, wide-frequency notes clustered in repeated groups of 3 to 4 notes. This call is used in non-threatening situations. In response to intruders or predators, adults produce a wide variety of squawks and calls that vary greatly in duration and inter-note interval.

Breeding. Breeding continues throughout the rainy season and may be year-round under uniformly wet conditions. Where they occupy territories, year-round bonds between females and their one to four males persist. Where suitable breeding sites are occupied only during the rainy season, new bonds are established each year. Courtship consists primarily of female aggression and male submission and is relatively subtle. Pre-copulatory displays include calling, posturing, nest building, wing raising and other conspicuous acts. Nests are built on floating vegetation, and construction by the Northern Jacana is primarily by the male. He grasps aquatic vegetation in his bill and either tosses it over his shoulder or backs up over the nest site where he drops it. Material is packed in place with the feet. Nests vary but are usually flimsy. Incubation is by the male and lasts 28 days in Northern Jacana. The clutch of 4 eggs is laid on consecutive days in the nest of one male. The eggs are glossy with dark markings on a brownish or bronze background, unmarked in Pheasant-tailed Jacana. The female may start laying a replacement clutch or a clutch for one of her other males 7 days after completing the first clutch. A polyandrous female Northern Jacana may copulate with all her mates in less than half an hour, but she does not copulate with a male who is incubating or caring for young chicks. Although females feed in and help defend the territories of all their males they do not necessarily visit every male every day. In the Pheasant-tailed Jacana similar interactions occur between the sexes and they are probably also simultaneously polyandrous. Bronze-winged and African Jacanas are less well known, but polyandrous mating groups have been reported. Mating systems in other species are not known, but the larger female size suggests polyandry.

Male Northern Jacanas usually provide all direct care for chicks. Male African, Northern and Comb-crested Jacanas all pick up young chicks

between the wings and body to shelter them from heavy rains. African and Comb-crested males also carry chicks under their wings. In the Northern Jacana the female occasionally broods the young. While the male is away feeding, females often stay near chicks where they can detect potential predators. The precocial chicks develop slowly and are dependent on the male for 3–4 months. Young chicks feed when accompanied by their male parent and may actually starve in his absence.
D.A.J.

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Jenni, D.A. & Betts, B.J. 1978. Sex differences in nest construction, incubation and parental behavior in the polyandrous American Jacana (*Jacana spinosa*). Anim. Beh. 26: 207–218.
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JACANIDAE: see under CHARADRIIFORMES; JACANA.

JACKASS, LAUGHING: alternative name of the Kookaburra *Dacelo novaeguineae*, while the Blue-winged Kookaburra *D. leachii* is sometimes called the 'Howling Jackass' (see KINGFISHER).

JACKDAW: *Corvus monedula*; also applied to one related species (see CROW (1)). See photos CARE OF SICK, INJURED AND ORPHANED BIRDS.

JACOBIN: substantive name of *Florisuga mellivora* and *Melanotrochilus fuscus* (for family see HUMMINGBIRD).

JAEGER: substantive name, in American usage, for skuas of the genus *Stercorarius* (as contrasted with *Catharacta*—not separated by all authors)—see SKUA.

JAW: see BILL; SKULL.

JAY: substantive name of many species of Corvidae, in various genera; used without qualification, in Britain, for *Garrulus glandarius* (see CROW (1)). 'Blue Jay' is a misnomer in India for *Coracias benghalensis* (see ROLLER). For 'jay-thrushes' (*Garrulax*) see BABBLER. See photo BROODING.

JERY: substantive name of *Neomixis* spp. (see BABBLER).

JESS: term (plural 'jesses') used in FALCONRY.

JEWELFRONT: substantive name of the HUMMINGBIRD *Polyplancta aurescens*.

JIZZ: combination of characters which identify a living creature in the field, but which may not be distinguished individually. A word coined by T.A. Coward (1922. Bird Haunts and Nature Memories. London).

JOURNALS: see ORNITHOLOGICAL SOCIETIES.

JUGAL: a paired bone of the SKULL.

JUGGING: sleeping place of Partridge *Perdix perdix*, where they jug or nestle together; also used of their call when jugging (Oxford English Dictionary).

JUGULUM: the foreneck (see TOPOGRAPHY).

JUNCO: substantive name of *Junco* spp. (see BUNTING).

JUNGLE BABBLER: substantive name of the tribe Pellorneini (see PASSERIFORMES; BABBLER).

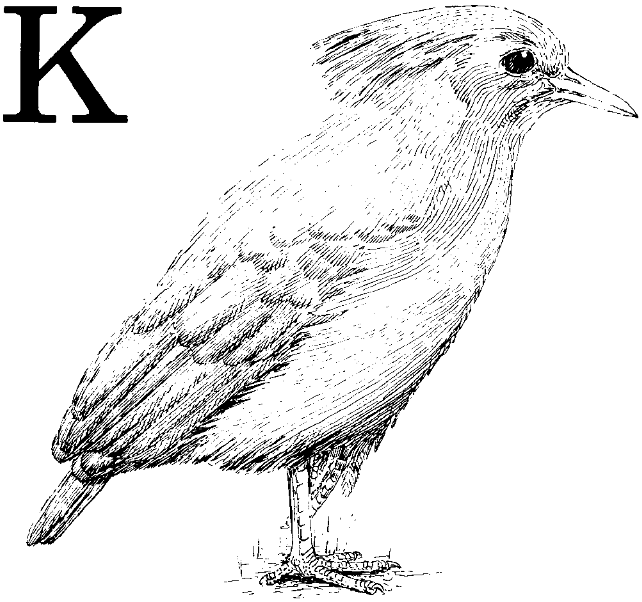
JUNGLEFOWL (1): substantive name of *Gallus* spp. (see PHEASANT; DOMESTICATION).

JUNGLEFOWL (2): name used in Australia for *Megapodius freycinet*; in the plural, serves as a general term for this and allied genera (some also called 'scrubfowl')—see MEGAPODE.

JUVENAL; JUVENILE: term of which the first spelling is usual in America, the second in Britain (see under YOUNG BIRD).

JYNGINAE: see under WOODPECKER.

K



Kagu *Rhynochetus jubatus*. (*C.J.F.C.*).

KAGU: native name, adopted as English, for the monotypic species *Rhynochetos jubatus* endemic to New Caledonia and sole member of the Rhynochetidae (Gruiformes, suborder Rhynocheti). Although some have considered it close to the Ardeidae, it is probably more closely allied to the Eurypygidae (see SUNBITTERN) or to some other gruiform group (Sibley 1972).

Characteristics. The overall colour is slate grey but there is a conspicuous pattern of white, reddish and black bars on the broad, rounded wings (length 29 cm) which is visible when they are spread. The head has a long loose crest which is raised during threat displays. The powerful bill (length 6.3 cm) is slightly decurved and reddish-orange. The reddish-orange legs and feet are strong, enabling it to run fast. Although flightless, the bird is able to glide down slopes. The sexes are alike but females weigh less than males. The total length is about 60 cm.

Habitat. The few hundred remaining birds survive in forests which have well developed undergrowth. These are found mainly in the central mountains on the eastern (wetter) side of the island, between 400 and 1,000 m, often close to rivulets. Only occasionally is the Kagu found in primary forest and in savanna.

Food. The Kagu eats invertebrates, particularly earthworms. It searches for food by tapping the surface of the ground. When a food item is located under the soil, the Kagu digs it up using its strong bill.

Behaviour. Birds move in loose flocks in search of food. Prior to breeding, prs move to higher altitudes. Contrary to earlier reports, the Kagu is active during the day and is only nocturnal when incubating. It has a characteristic habit of running rapidly and then standing motionless; captive birds have been observed whirling round holding the tip of the tail or wing in the bill, but the significance of these antics is unknown.

Voice. The Kagu has a variety of harsh, rattling call notes and, in addition, a powerful and solemn predawn 'song' which is a beautiful, melodious succession of notes and pauses; the female answers the male's song.

Breeding. The nest consists of a thin layer (10 mm) of dead leaves carefully placed on the ground. Occasionally 3 or 4 active nests per ha have been ocated. The single egg has red-brown and grey blotches on a yellow or creamy ground colour. Eggs are laid in the drier months (May to December); the incubation period is 35 days. The downy young is cryptically marked with black and yellow streaks. The young bird is strong enough at 15 days of age to run rapidly for short distances, and shows some independence in about the 10th week of life when it has half the body weight of an adult (about 900 gm); but the semi-dependent phase lasts until the 14th week or even later. At this age young birds compete partially with the parents for food and the latter begin to be aggressive towards their progeny. Family units break up when the young Kagu is between 6 and 12 months old. Young Kagus defend a territory and seek a mate when they are about 2 years of age.

J.-N.N. and R. de N.

Greenway, J.C., Jr. 1967. Extinct and Vanishing Birds of the World. New York.
Sibley, C.G. 1972. A comparative study of the egg white proteins of non-passerine birds. Bulletin 39, Peabody Museum of Natural History, Yale.

KAKA: Maori name used for *Nestor meridionalis* (see PARROT).

KAKAPO: alternative name (Maori) of the Owl Parrot *Strigops habroptilus* (see PARROT).

KAKARIKI: substantive name used for the *Cyanoramphus* spp. (Psittacinae, Platycercini) (see PARROT).

KAKELAAR: alternative name of *Phoeniculus purpureus* (see WOODHOOPOE).

KALIJ: substantive name of some *Lophura* spp. (see PHEASANT).

KEA: Maori name used for *Nestor notabilis* (see PARROT).

KEEL: the carina of the sternum (see SKELETON, POST-CRANIAL; and CARINATE).

KERATIN: the main structural protein found in the horny parts of the skin, scales, beaks and feathers of birds. It is also found in the skin and epidermal structures of mammals, reptiles and to a lesser extent lower vertebrates. There are two main types of avian keratin: hard keratin, found in claws, beaks and feathers, and soft keratin, found in the skin. Most research into avian keratin has used hard keratin, especially feathers.

Structure. Keratin is a generic name for several groups of closely related proteins which are characterized by their strength, flexibility and resistance to most common solvents and proteolytic enzymes. Avian hard keratins are extremely small and light; they comprise chains of about 100 amino acids, and have molecular weights (MWs) of *c.* 10,500 daltons (feather keratins) or 14,500 daltons (beak and claw keratins). By comparison, mammalian hard keratins are larger and much more variable; they are usually divided into two main groups, one with a high sulphur content and MWs of 10,500–28,000 daltons and the other with a low sulphur content and MWs of 45,000–50,000+ daltons. Reptile scales appear to be made up of two layers, one mammal-like and the other avian-like, with MWs in the range 10,000–85,000 daltons. All hard keratins are unusually rich in the di-amino acid cystine, which comprises two molecules of the amino acid cysteine. The strength and relative insolubility of keratin structures are due to the formation of strong disulphide bonds between the cysteine molecules in adjacent keratin chains. Sections of feathers studied using the electron microscope show an ultrastructure of parallel rod-like microfibrils in an amorphous matrix. The best model for the molecular structure of feather keratin suggests that the central third of each keratin molecule is folded into a pleated sheet, and that two chains of these pleated sheets are wound helically around a central axis, forming the microfibrils seen with the electron microscope. The ends of the keratin molecules (the other two-thirds) contain most of the cysteine amino acids and are believed both to form the amorphous matrix of the feather structure and to be the sites of the inter-molecular disulphide bonds.

Development and keratinization. Keratin is not detectable in chicken embryonic feathers until about the 12th day of incubation, by which stage the feathers are nearing completion of their morphological development. Keratins rapidly then become more abundant and account for most protein synthesis in the feather at 14 days. By 19 days nearly all the protein present in the feather is keratin. The onset of keratinization and the rate of its progress appear to be limited by the amount of keratin messenger-RNA (mRNA) in the embryonic feather cells. Keratinization begins within the cell cytoplasm with the formation of bundles of microfibrils which increase in size until they start to coalesce. Other cellular materials are then reabsorbed from the cells and the bundles finally pack together, trapping a certain amount of cellular debris in the matrix as the cell shrinks and dehydrates. The fully keratinized cell is a totally dead, solid structure.

Heterogeneity. Feather keratins are usually made soluble for chemical analysis by reducing (breaking) the disulphide bonds with thioglycollic acid and preventing them reforming with iodoacetic acid, giving *S*-carboxymethyl keratin (*S*CMK). Using electrophoretic techniques the *S*CMK produces a pattern with many bands showing it to be a complex mixture of many different *S*CMK molecules (monomers). There is good evidence that each *S*CMK monomer is a separate gene product; up to 35 different types have been found in many of the feather keratin electrophoretic patterns examined. This agrees well with an experimental estimate of 25–35 keratin mRNAs in chick embryonic feathers. There are believed to be 100–240 keratin genes in the whole chick genome. Such a multiplicity of genes probably arose following repeated duplication of an ancestral keratin gene and a subsequent slight divergence in the sequence of the coding nucleotides in the original DNA and the resulting copies. This has given rise to a large family of slightly different genes, each producing a slightly different protein. Some of the protein amino acid sequences within a species differ by only one in the hundred or so amino acids that make up the keratin monomers. Different parts of each feather (e.g., rachis, barbs) contain different subsets of the complete pool of keratin monomers and therefore give different electrophoretic patterns, but the way these monomers combine to produce the complex structure of a feather is unknown. Corresponding parts of different feathers of the same main type (e.g., flight, contour) from the same bird share the same subsets of *S*CMK monomers, and there is little or no intra-specific variation in electrophoretic patterns of *S*CMK from comparable feather parts from different individuals. However, using techniques of adequate resolution, differences have been found between all the species and some of the subspecies examined so far. These differences are of use in taxonomic studies. For example, analysis of *S*CMK electrophoretic patterns has been used to investigate the relationships of the African *Halcyon* kingfishers, suggesting, among other things, that the morphological similarity between *H. chelicuti* and *H. pyrrhopygia* is probably due to convergence and that the former is more closely related to the *H. albiventris–leucocephala–pileata* subgenus. Other studies have shown that *Bonasa bonasia* and *B. umbellus* (Tetraonidae) are not at all closely related despite being treated as congeneric, and that the Palm Cockatoo *Probosciger aterrimus* is an extremely aberrant member of the subfamily Cacatuinae. The technique has also been used to show that a unique museum skin of a cotinga belonged to a new species and to suggest affinities with other taxa.

The availability in museums of feather samples of practically all the extant and many extinct species of birds of the world, together with the refined analytical techniques now available, has made feather keratin a potentially important source of taxonomic information. A.G.K.

Brush, A.H. 1978. Feather keratins. *In* Brush, A.H. (ed.). Chemical Zoology 10. New York.

Knox, A.G. 1980. Feather protein as a source of avian taxonomic information. Comp. Biochem. Physiol. 65B: 45–54.

KESTREL: substantive name of certain *Falco* spp.; used without qualification, in Britain, for *F. tinnunculus* (see FALCON). See photo FLIGHT.

KIDNEY: see EXCRETORY SYSTEM.

KILLDEER: *Charadrius vociferus* (see PLOVER (1)).

KINESIS (1): movement of the upper mandible in relation to the SKULL (see BILL).

KINESIS (2): 'locomotory behaviour not involving a steering reaction but in which there may be turning, random in direction' (Thorpe)—compare TAXIS.

KINGBIRD: substantive name of *Tyrannus* spp. (see FLYCATCHER (2)).

KING-CROW: *Dicrurus macrocercus* (see DRONGO).

KINGFISHER: substantive name of all species (except kookaburras *Dacelo*) of Alcedinidae (Coraciiformes, suborder Alcedines); in the plural, general name for the family; applied without qualification in Britain to *Alcedo atthis*. A diverse family of 86 species, almost cosmopolitan, but with most species in the Paleotropics and only a few in the Palearctic and the New World. Most are generalized predators of arthropods, small lizards and fish, and inhabit rainforests and woodlands, usually near but often far from water. Three subfamilies are customarily recognized on the basis of morphological (Miller 1912) and biological (Fry 1982) characteristics: Daceloninae (tree-kingfishers, 55 species), Alcedininae (22 small species of insect- and fish-eaters), and Cerylinae (9 species, most large and piscivorous). Generic boundaries have been controversial, but the following genera and numbers of species are now recognized.

Daceloninae: *Tanysiptera*, 6, Papuan subregion; *Actenoides* (formerly *Halcyon*), 6, Malaysia to Solomon Is.; the monotypic *Cittura* (Sulawesi), *Lacedo* (Thailand to Wallace's Line), *Melidora* and *Clytoceyx* (both New Guinea); *Dacelo*, 4, New Guinea and Australia; and *Halcyon* (including *Pelargopsis*), 35, Paleotropics.

Alcedininae: *Ceyx*, 8, Paleotropics; *Corythornis*, 3, Afrotropics; and *Alcedo*, 11, Old World.

Cerylinae: *Chloroceryle*, 4, Neotropics; *Megaceryle*, 4—one Oriental, one African, one Neotropical and one Nearctic; and the monotypic *Ceryle* of the Paleotropics.

Characteristics. Kingfishers range from 10 cm in length and 8 g in weight (*Ceyx lecontei*) to 46 cm and 500 g (*Dacelo gigas*), but the majority of species weigh between 20 g and 100 g. They are large-headed birds with long, strong beaks, the maxilla straight and pointed (hooked in some) and the mandible straight and narrow or deep, wide, and recurved. They are short-necked, short-tailed, and round-winged; the legs are short and the feet weak and syndactyl—the second, third and fourth toes being united basally and the third and fourth for much of their length. The second toe is vestigial in *Ceyx fallax* and absent in some species of *Ceyx* and *Alcedo*. The Alcedinidae is rather a distinctive family, and all of the members show an unmistakable general similarity. The most aberrant is *Clytoceyx rex*, a large drab bird probably distantly allied with kookaburras (and like them having a shining azure rump); it eats earthworms and the beak is short, broad and deep with scoop-shaped mandibles. Plumages are generally striking and colourful, dominantly non-iridescent dark blue and rufous, with shining azure rumps, and black or scarlet beaks and legs. Cerylines have no blue, but are pied or rufous with grey or oily green. The sexes are alike or nearly so, but in cerylines and a few dacelonines they differ recognizably in the field. Juveniles are generally like adults, but duskier. Kingfishers are territorial, and only 3 are at all gregarious. Dacelonines have loud songs and conspicuous territorial displays; otherwise many kingfishers are rather quiet and inconspicuous birds,, seen mainly in fast, direct and non-undulatory flight.

Habitat. The interior of tropical rainforest in all strata, its canopy and edges; mangroves; lowland forests with a few species as high as 2,000 m; tropical savanna woodlands, farms and gardens; swamps, paddyfields, wooded or grassy margins of rivers and lakes; arid thorn-bush; seashores in tropical and temperate zones, from wooded estuaries to treeless beaches and coral islands. The few species in the Palearctic and Nearctic can be found by almost any waters, particularly in winter (*Megaceryle alcyon*, *M. lugubris*, *Alcedo atthis*) or in any open countryside and woodland (*Halcyon pileata*, *H. coromanda*). They perch freely in vegetation, often concealed from view, but also on treetops and any open vantage points from which they can scan the ground or water for prey. A few species regularly forage on the ground, rooting in litter and topsoil for invertebrates, but most perch on the ground only transiently when feeding or nesting. Fishing species use such man-made vantage points as posts, boats and quays.

Distribution. The greatest number and diversity of dacelonine species is in the Papuan subregion, and of alcedinine species in that subregion with the adjoining part of the Oriental region. The Papuan subregion has 16 dacelonines of which 13 are endemic there, including some of the most remarkable kingfishers, such as *Clytoceyx rex* and *Melidora macrorhina* which have unusual feeding habits (see below). Both subfamilies extend north to Japan and south to Tasmania; alcedinines do not occur east of the Solomon Is. but several dacelonines are endemic to Pacific islands, from the Caroline Is. to the Marquesas Is. To the west alcedinines range to the Atlantic seaboards of Europe and Africa and dacelonines to the Near East and Africa including the Cape Verde Is. Of the cerylines, the 4 green kingfishers *Chloroceryle* are sympatric in the Neotropics, and *Ceryle rudis* is widespread in Africa and the Orient (for the range of *Megaceryle*, see above). Several species are endemic to a small island; for instance *Halcyon gambieri* is restricted to Niau Is. in the Tuamotu Archipelago and numbers only 400–600 birds. The most widespread kingfisher is *Alcedo atthis*, breeding from the Baltic to the Cape (treating *A. semitorquata* as conspecific) and from Morocco to Japan and the Solomon Is.

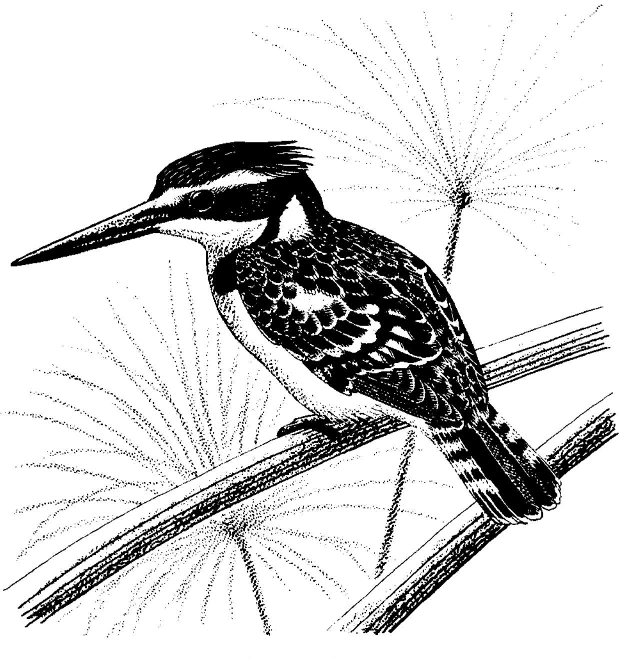
Movements. Most kingfisher species are sedentary, but the temperate-zone ones are migratory at least from more northerly latitudes, and several insectivorous species are intra-tropical migrants. *Halcyon leucocephala* is migratory throughout its African range and in Nigeria has a two-stage vernal movement northwards (pre-breeding and post-breeding), and one return migration after the rains. Its allospecies *H. pileata* in the Orient migrates from Korea to equatorial latitudes.

Food. The dacelonines are all sit-and-wait predators on a variety of arthropods and small vertebrates taken from the ground, tree-trunks and foliage and the surface of water. They eat insects, spiders, centipedes, scorpions, shrimps, frogs, lizards and, among *Halcyon* species, some fish, occasionally taking insects by flycatching, and in some cases evidently specializing on crabs (*Halcyon (Pelargopsis) capensis*) and snails (*H. coromanda*). *Clytoceyx rex* subsists largely on earthworms and other invertebrates caught at the surface of the forest floor by foraging in leaf-litter, worms being extracted in the manner of thrushes. *Melidora macrorhina*, which is evidently nocturnal or at least crepuscular, and at least 2 species of *Halcyon* sometimes feed on worms likewise, ploughing loose soil with their beaks. These kingfishers, and in particular the largest 2 of the 4 kookaburras, are formidable predators of vertebrates and catch snakes and some birds.

Among the Alcedininae, *Ceyx* species are dry-land insectivores but also take some prey from water. *Corythornis* (a genus of 1 forest and 2 savanna species intermediate between *Ceyx* and *Alcedo*) eat small dry-land and aquatic arthropods and vertebrates; and *Alcedo* feed almost entirely from water, on arthropods nearly as much as on fish. In the Cerylinae, *Chloroceryle* and *Ceryle* are almost exclusively piscivorous, *Megaceryle maxima* subsists largely on river crabs and *M. alcyon* takes fish and in addition mussels, clams, oysters, salamanders, young landbirds, mice, a variety of insects (including butterflies taken on the wing) and even, exceptionally, plant matter.

Dacelonines capture land prey by swooping down to seize it in the beak and alighting on the ground or a perch to immobilize it by beating. They usually take aquatic prey in much the same way, a splash-and-grab at the surface with subsequent beating at a perch. Species of alcedinines and cerylines (closely related subfamilies) can be arranged in a sequence suggesting evolutionary change from such swooping to more proficient diving and ultimately to reliance on more specialized diving. Evident correlates are a shift from forest floor to forest waterway to open-water habitats and from insectivory to piscivory. Moreover, those species which hunt farthest from the shore are the ones which eat the most fish, and the fish are caught in dives not only from perches but also from hovering flight: *Alcedo atthis*, *A. semitorquata*, *Chloroceryle amazona*, *C. americana*, *Megaceryle alcyon*, the marine *Halcyon saurophaga*, and—the extreme case—*Ceryle rudis*. No kingfisher other than these 7 is known to hover; and no other species regularly fishes open waters. *M. alcyon* and *C. rudis* are spectacular fishers; they scan the water by hovering as high as 12 m and make a straight or spiral dive directly downward, but how far they can submerge is not known. *Ceryle rudis* fishes up to 3 km offshore and in choppy conditions it makes 4 times as many dives from hovering flight as from perches. It can catch 2 fish at once, and swallow a small fish without having to return to a perch to beat it.

Voice and behaviour. Detailed accounts have been published for some dozen species; little is known about most others and nests of a few have not yet been described. Breeding biology is apparently rather uniform. Kingfishers are monogamous and territorial. A group of African and Asian *Halcyon* species maintain their territories by the frequent repetition of a far-carrying song delivered from a tree-top—a loud initial note and a series of evenly-spaced notes on the same or a falling pitch—accompanied by a highly conspicuous display. The bird perches erect with cocked tail, and flicks the wings to show a bold ventral pattern of chestnut, black and white. *H. senegalensis* pivots rapidly from side to side, holding the wings fully outstretched and vibrating. Mates may display and call together, and duetting occurs in *H. chelicuti*, an African arid-zone bird in which 20% of territories are occupied and defended by a mated pair with a helper. Helpers occur also in *Ceryle rudis* and *Dacelo gigas*. Nearly all other kingfishers live in pairs or, after dependent fledglings have dispersed, solitarily; but *C. rudis*, with up to 5 adult helpers at a nest, is quite gregarious and *D. gigas*, with helpers at more than half the nests, lives in pairs or perennial groups of 3–6. Kookaburras are obtrusive on account of their permanent occupancy of a socially defended territory and of their infectious 'laughing jackass' song. Alcedinines and cerylines are much less conspicuous in defence of their territories; cerylines are vocal, but songs and displays among alcedinines are weak or non-existent.



Pied Kingfisher *Ceryle rudis*. (*N.A.*).

Breeding. All kingfishers are hole-nesters, lay sub-spherical white eggs and have no nest sanitation. Dacelonines nest in tree-holes, often expropriated from other birds, remodelling the chamber, and they commonly use holes in termitaria on the ground or high in trees; some, notably the African and Asiatic halcyons, regularly nest also in earth banks, excavating the tunnel themselves. Alcedinines excavate their own nest holes in earth banks by water. Soil is loosened by the beak and kicked out backwards by the legs. The tunnel is horizontal, straight or a little curved, 0.75–1.5 m long, and ends in an oval egg-chamber.

Kingfishers never line the nest chamber. Incubation begins with the first egg laid, so the brood is staggered in size. The sexes incubate alternately in a cycle varying from 3–24 hours (*Chloroceryle amazona*, with the female incubating all night) and even 48 hours (*Megaceryle torquata*, with each sex taking 24-hour spells of incubation). During incubation the egg chamber becomes fouled with the pungent, watery excrement and with trodden-down pellets of regurgitated insect sclerites or fish bones. Clutches vary from one egg (rarely in *Dacelo gigas*) to 10 (rarely in *Alcedo atthis*), with specific means of about 3 to 4 eggs in the tropics and 6 to 7 in the temperate zone. Many species lay second and replacement clutches. The hatchling is naked and prognathous, the mandible projecting up to 2.5 mm beyond the maxilla. Nestlings stand on the heel, not the toes, and have rugose heel-pads. In most species fledglings have the same plumage as their adults, and they continue to be fed by adults for 10 weeks or more. Incubation and nestling periods are not known; incubation has been estimated as 14–16 days for *Corythornis*; 10–21 days for *Alcedo*; and about 14 days for *Halcyon*. The nestling period for *Corythornis* is at least 25 days.

See photo COMFORT BEHAVIOUR. C.H.F.

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KINGLET: in American usage, substantive name of *Regulus* spp. (see WARBLER (1)).

KINKIMAVO: substantive name of the Madagascar endemic *Tylas eduardi* (for family see BULBUL).

KIN SELECTION: the operation of natural selection, not directly on the individual under consideration but indirectly, on related individuals who share a proportion of his genes. Kin selection is one of the mechanisms that have been invoked to explain the evolution of ALTRUISM (see also SOCIOBIOLOGY).

KIOEA: the Hawaiian HONEYEATER *Chaetoptila angustipluma.*

KIRITIKA: substantive name of the endemic Madagascar warbler *Thamnornis chloropetoides* (for family see WARBLER (1)).

KISKADEE: substantive name of *Pitangus* spp. (see FLYCATCHER (2)).

KITE: substantive name of species of Milvinae, and used also for members of the Elaninae (for both these subfamilies of the Accipitridae see HAWK).

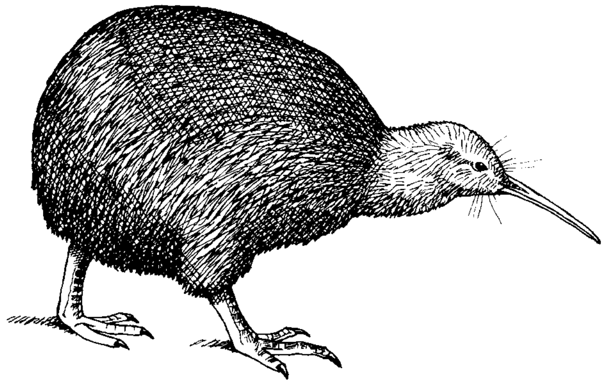
KITTIWAKE: substantive name of 2 species of Laridae; used without qualification in Britain for *Rissa tridactyla* (alternatively, Black-legged Kittiwake), the other species being the Red-legged Kittiwake *R. brevirostris* of the Bering Sea (see GULL).

KIWIS: the smallest and most aberrant of the RATITES and endemic to New Zealand. They are generally regarded as being most closely related to the MOAS (also endemic to New Zealand), each group being given the status of an order, or—as here—together making up the suborder Apteryges, one of the 4 suborders of the Struthioniformes. There are yet other alternative schemes for classifying the ratites, perhaps the most common recent ground for agreement being that they are monophyletic in origin. Both kiwis and MOAS are regarded as being descendants of the Gondwanaland fauna and thus the most ancient elements of New Zealand's recent avifauna. There are 3 species: *Apteryx australis* the Brown—or Common—Kiwi (subspecies, *A. a. australis* South Island, *A. a. mantelli* North Island and *A. a. lawryi* Stewart Island); *Apteryx oweni* the Little Spotted Kiwi (North and South Islands, no subspecies); *Apteryx haasti* the Great Spotted Kiwi (South Island only, no subspecies). No recently exinct species are known and the earliest fossil kiwi (*Pseudapteryx gracilis*) dates from the Quaternary. However, footprints attributed to the family have been found in Upper Miocene mudstone.

Characteristics. Kiwis are 35–55 cm long. Distinctive features include a long and slightly decurved bill with nostrils near the tip, a cone-shaped body tapering markedly to a strong neck and comparatively small head, small eyes, large ear apertures and many long tactile bristle-like feathers about the face and base of the bill, powerful muscular legs (which make up about one-third of the body weight), large feet with stout claws, and very small virtually bare wings (4–5 cm in length) which end in a claw and are hidden in the plumage. There is no external tail. The plumage is brown or grey, loose and hair-like, and does not change in form throughout life. Its neotenous characteristic of having weak barbs and lacking aftershafts gives the birds a shaggy appearance. The largest kiwis (the Stewart Island race) have females weighing at least 3.5 kg, the smallest (Little Spotted) about 1.2 kg. Females are about 20% heavier than males and their bills 25–30% longer.

With the exception of the Stewart Island race (which is also active during the early morning and evening) kiwis are nocturnal and uncomfortable in broad daylight.

Habitat. Though primarily birds of the indigenous forests (kauri, podocarp or southern beech), kiwis may also occur in scrub, native grasslands and even in exotic forests and pastures. Among critical environmental factors may be soil texture, its humus content, atmospheric humidity and dense vegetation overhead; certain combinations of which may be essential for kiwis to burrow and feed in and for the development of a suitable soil fauna for food. Nothing reliable is known about differences in habitat requirements that separate the 3 species.



Brown Kiwi *Apteryx australis.* (*N.W.C.*).

Distribution and populations. Originally Brown and Little Spotted Kiwis had a wide distribution on both main islands and D'Urville Island (which is separated from the South Island by a shallow strait only about 1 km wide and of post-glacial origin). Apart from the Stewart Island race of *A. australis*, they are not known to have occurred on any other islands. Now, they have gone from the east coast of the South Island (subfossil records only) and the southern and south-eastern parts of the North Island. The Little Spotted Kiwi has apparently been extinct in the North Island for about a century and is thought to be extinct in the South Island and survives only on Kapiti I. where it was introduced in 1913. The Great Spotted Kiwi is now found, apparently in good numbers, on the western side of the Southern Alps, mainly north of 43°S. More detailed information is needed on the distribution of all kiwis, especially to determine the extent to which overlap, spatial as well as ecological, occurs.

Kiwis have been successfully introduced to offshore islands and will readily breed in captivity, so the ultimate survival of all species and subspecies seems assured. They have no native predators, and do not seem to be unduly sensitive to predation by the various introduced mammals (rats, mustelids and cats), though the Little Spotted Kiwi may be an exception. However, many are maimed or killed by being caught in traps set for the introduced Australian possum or by being burnt or crushed in forestry or land-clearing operations. Nevertheless, kiwis have long been fully protected by law and have added protection where they occur in national parks or similar reserves.

Food. All 3 species have the same general food habits but little is known in detail. Earthworms are the principal item of diet, though woodlice, millipedes, centipedes, slugs, snails, spiders, a wide range of insects, seeds and berries are also taken. The highly developed sense of smell is apparently important in finding food.

Voice. Although each species and subspecies has contact calls of characteristic quality, all are essentially similar—males utter a shrill and prolonged whistle with a slightly ascending and then brief descending pitch (from which the species' name is derived); females have a hoarser and lower cry. These are heard at dusk, during the night and near dawn. When alarmed or aggressive, kiwis growl, hiss and loudly snap their mandibles. The other common noise is a loud snuffling made by expelling air forcibly through the nostrils while feeding.

Breeding. It is not known what stimulates breeding—the egg-laying period extends from July (late winter) to February (late summer). A functional right ovary is always present but only the left oviduct. The age of sexual maturity is unknown, but is likely to be at least 2 years. Studies of captive kiwis have shown that after about 2 months of burrowing or otherwise preparing a nest site, mainly by the male, the first egg is laid. Captive females may lay up to 5 eggs in a continuous series with a mean interval of 33 days between each; but in the wild clutches contain 1, 2 or rarely 3 eggs (each 18–25% of the female's body weight, depending on the species). The heavily yolked (61%) white-shelled egg is incubated almost entirely by the male for some 74–84 days before the chick hatches active, open-eyed and fully feathered. G.R.W.

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KLEPTOPARASITISM: see FEEDING HABITS; PIRACY.

KNEE: for both the true knee and for a popular misconception on the subject see LEG.

KNOT: substantive name of *Calidris canutus* and one congener (see SANDPIPER).

KOEL: *Eudynamys scolopacea* (see CUCKOO).

KOKAKO: *Callaeas cinerea* (see WATTLEBIRD (2)).

KOKLASS: *Pucrasia macrolopha* (see PHEASANT).

KOLOA: alternative name (indigenous) for the Hawaiian Duck *Anas wyvilliana* (for family see DUCK).

KOOKABURRA: substantive name of *Dacelo* spp. (see KINGFISHER).

KORHAAN: substantive name of some South African species of *Eupodotis* (see BUSTARD).

KORI: *Ardeotis kori* (see BUSTARD).

KRONISM: see CRONISM.

K-SELECTION AND r-SELECTION: see ECOLOGY (final paragraph).

L

L. LINN. LINNAEUS: see NOMENCLATURE.

LABYRINTH: part of the ear (semicircular canals)—see HEARING AND BALANCE.

LAGENA: part of the cochlea, in the inner ear (see HEARING AND BALANCE).

LAGGAR: *Falco jugger* (see FALCON).

LAMELLAE: in birds, fine hair-like structures lining the bills of some species, enabling them to filter small food particles (see BILL; FEEDING HABITS).

LAMINIPLANTAR: having the horny sheath of the tarsus undivided on its posterior surface, although scutellate on the anterior surface (see LEG); compare BOOTED.

LÄMMERGEIER: name, alternatively 'Bearded Vulture', of *Gypaetus barbatus* (see VULTURE (1)).

LANCEBILL: substantive name of *Doryfera* spp. (for family see HUMMINGBIRD).

LANCEOLATE(D): spear shaped.

LAND-BRIDGES: see GEOLOGICAL FACTORS.

LANDRAIL: alternative name (probably obsolescent) for the Corncrake *Crex crex* (see RAIL).

LANGERHANS, ISLETS OF: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

LANIIDAE: a family of the PASSERIFORMES; suborder Oscines; SHRIKE.

LANNER: *Falco biarmicus* (see FALCON).

LAPAROTOMY: the minor surgical process used to assess the state of the internal organs of an animal. Typically involves making a small opening (1–2 mm) between the ribs and then using a powerful light source to look into the body cavity. General or sometimes a local anaesthetic is used. Valuable in sexing birds.

LAPPET: a wattle, particularly one at the gape (see INTEGUMENTARY STRUCTURES).

LAPWING: substantive name of some *Vanellus* spp., others being called 'plover'; used without qualification for *V. vanellus*; in the plural, general term for plovers of this genus (split by some authors into several genera constituting a subfamily Vanellinae)—see PLOVER (1).

LARDER: a collection of prey items impaled on thorns or barbed wire by shrikes (Laniidae) and some other birds.

LARI: see under CHARADRIIFORMES.

LARIDAE: see under CHARADRIIFORMES; GULL.

LARK: substantive name of the species of the family Alaudidae (Passeriformes, suborder Oscines).

Characteristics. Larks are small (11–19 cm) ground-feeding birds of open spaces. They rarely perch on vegetation to feed although some species do so regularly to sing. Like pipits and some buntings which also spend much time on the ground, larks have long, generally straight claws on their hind toes. Larks differ structurally from other Passeriformes in lacking an ossified pessulus in the syrinx and in having the posterior surface of the tarsus covered by scutes rather than an unbroken lamina. Most larks have cryptic brown or buff plumage with dark streaks. The sexes are usually similar in appearance though in a few cases (e.g., *Melanocorypha yeltoniensis*, some *Eremopterix*) they differ, with the male being more strikingly marked though not in bright colours. Many species have a marked size dimorphism, the males being larger than females.

Habitat. Larks live in open country including hot and cold deserts, tundra, moors, grasslands, steppe, savanna and farmland. Nests are always on the ground so the abundance of trees and bushes is not important in determining the availability of nesting cover. However, sympatric species often differ in the preferred density of trees and bushes in the habitat. Skylarks *Alauda arvensis* tend not to feed near tall hedges or woodland even when food is abundant there. Woodlarks *Lullula arborea* are superficially similar but are less averse to feeding near cover and live in areas with scattered trees or by woodland edges.

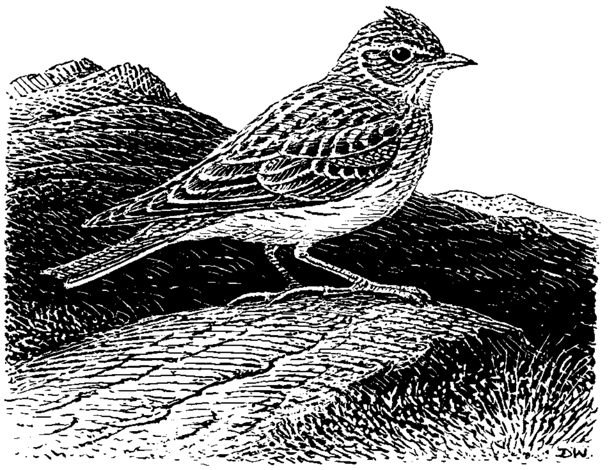
The colour of the soil is an important habitat feature for some desert-dwelling larks (*Ammomanes*, *Mirafra*, *Certhilauda*, *Eremopterix*) which tend to live in areas with soil similarly coloured to their plumage. In some species birds avoid landing on ground with contrasting soil colour even when driven over it. This matching is presumably an adaptation providing concealment from avian predators (see COLORATION, ADAPTIVE).

Distribution. A predominantly Old World family with one species, the Shore Lark *Eremophila alpestris*, in the Americas. Three-quarters of the 76 species occur in Africa and over half are only found there. Only one species (*Mirafra javanica*) occurs in Australia and New Guinea.

Populations. Larks generally occur at lower population densities than are typical of similarly sized woodland or scrub-dwelling passerines, which is probably due to the simple vegetation structure and low productivity of their preferred habitats. However, suitable habitat often covers vast tracts of land (e.g., deserts, tundra, arable farmland) so total populations may be very large. For example, the tundra dwelling Shore Lark is one of the world's most numerous birds. Population densities of Skylarks are 10–50 pairs/km^2 on arable farmland in England and up to 70 pairs/km^2 on coastal dunes. Woodlarks also occur at fairly low densities with territories 5 ha or more in extent. Population densities of desert-dwelling larks are very variable in space and time, since many species are nomadic, and are also usually low, though pockets with densities up to 1,250 pairs/km^2 can occur in *Eremopterix* spp. where rain has fallen. The average annual mortality rate for adult Skylarks is about 33% which is low for a temperate small passerine.

Movements. The family includes long distance and partial migrants and sedentary species. All North Temperate larks are at least partially migratory. Some species living in arid areas are nomadic, moving between areas of localized rainfall and abundant food. In the Kalahari desert granivorous species such as *Calandrella conirostris* and *Eremopterix* spp. are nomadic, while larks which include more arthropods in their diet are mainly sedentary. In the short term, frequent movements are made by some larks (e.g., *Eremopterix*) to waterholes to drink while other desert species appear to derive sufficient water from dew and food. There may be a correlation with diet; species feeding on arthropods and green vegetation being less likely to need to fly to water than those taking dry seeds.

Food. As a family, larks feed on a great variety of foods including seeds, flowers, buds, leaves, seedling cotyledons, molluscs and arthropods. A large proportion of species take a broad range of foods but some are specialized in feeding on insects or seeds. Omnivorous species have a conical, straight bill (e.g., *Alauda*, *Galerida*) while seed-eating specialists such as *Eremopterix*, *Melanocorypha* and *Calandrella* have deeper, finch-like bills. The Hoopoe Lark *Alaemon alaudipes* and some other species have thin decurved bills which they use to dig for soil arthropods. All larks search for food by walking. The Skylark is an omnivorous species with an unspecialized bill. On arable farmland it feeds on grain, weed seeds, leaves and cotyledons and insects, particularly beetles. Grain and seeds are not hulled as they are by finches and buntings since the bill lacks the grooves within the upper mandible used to hold the seed by these groups. Although Skylarks may feed almost entirely on leaves of cereals in midwinter, they have a short intestine and lack the large caeca of larger



Skylark *Alauda arvensis*. (*D.W.*).

herbivorous birds. Larks which take green leaves probably select plant species and growth stages rich in nutrients. Skylarks feed on weed and crop seedlings with high-protein levels. Stark's Lark *Spizocorys starki* in the Namib desert feeds on grass seedlings soon after germination. Gray's Lark *Ammomanes grayi* and Stark's Lark also select the tender basal node of grasses, discarding less digestible parts. Most larks feed their young on insects though some feed seeds by regurgitation (e.g., *Eremopterix leucotis*). On arable farmland Skylarks collect weevils, click beetles, grasshoppers, caterpillars and sawfly larvae for their young from rough grass and weeds at field edges. Desert-dwelling larks in southern Africa exploit ant and termite colonies, particularly when these are producing sexuals, and also locust nymphs.

Behaviour. Most larks breed on dispersed territories and are monogamous. Breeding territories are defended by song and chasing. Skylarks sing and visit the territory for much of the year in England as do some *Mirafra* larks in southern Africa. Nomadic desert species such as Stark's Lark may only be territorial and sing when breeding. Song and territory may function more to attract a mate than to maintain a feeding area which may be more important in sedentary species. Skylarks tend to remain faithful to a breeding site from year to year. In the Namib desert Gray's Lark lives in small groups throughout the year; territoriality is not strongly developed, with courtship and mating sometimes taking place within the group. Many lark species associate in flocks when not breeding. In southern Africa nomadic species form the largest and most cohesive flocks. Skylarks and Shore Larks migrate in flocks.

In hot deserts larks show behavioural adaptations to avoid overheating. Karroo Larks *Certhilauda albescens* and Stark's Larks become inactive and sit in shade during the hottest part of the day while Spike-heeled Larks *Certhilauda albofasciata* and Gray's Larks, foraging partly in the shade around the entrance of rodent burrows, are able to remain active. Larks roost on the ground and do not roost communally.

Voice. Song is well developed and long in many species, often delivered during a song flight or from a prominent perch. The song flight incorporates a rapid dive to the ground in several species. The wings and sometimes the tail are used in sound production in some larks, especially *Mirafra*, though these also sing. Flight calls are uttered by single and flocking birds. In the Skylark single birds usually call *chir-r-rup* while those in cohesive flocks call *seep*.

Breeding. All larks nest on the ground. Often the nest is a scraped cup but on hard substrates a foundation may be built to support the sides of the cup. The cup is often lined with grass or grass fibre. Sand larks (*Ammomanes*) and finch-larks (*Eremopterix*) build a rampart of pebbles on the windward side of the nest. This may act as a windbreak and prevent the nest filling with sand. Shore Larks also collect pebbles and other objects around the nest. In hot deserts lark nests are often built close to a stone or tuft of grass which shades the nest during the hottest part of the day. Nest ramparts may also contribute to shading the nest as well as perhaps partly concealing the nest from predators at ground level. The eggs are usually cryptically streaked or spotted. Clutch-sizes are larger in arctic and temperate larks (average about 4 eggs) than in tropical Africa (2–3 eggs). In Africa clutch-size tends to be larger in species living in more arid, less wooded habitat. Skylarks in England show a seasonal variation in clutch-size with mid-season clutches being larger than those at the beginning and end. Incubation is for 10–12 days by the female alone or by both sexes in some species. The young are fed by both parents and leave the nest well before they can fly, usually at about 10 days old. The down of the nestlings is cryptically coloured. Leaving the nest early is probably an anti-predator adaptation, reducing the risk of loss of a whole brood collected at one place, although movement of the young may also be beneficial in reducing the distance the adults have to carry food; the feeding areas are sometimes far from the nest. Losses of nests and young to predators are often high, 80% of eggs failing to produce fledglings for 7 species in the Kalahari and 90% of eggs failing to give rise to independent young for Skylarks on coastal dunes in England. Breeding is annual in temperate and arctic larks but is initiated after rainfall in many desert species. Skylarks begin to breed in the year after hatching.

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LARK, MAGPIE: see MAGPIE–LARK.

LARK, MEADOW: see MEADOWLARK; ORIOLE (2).

LARK-QUAIL: name, alternatively 'quail-plover' (misnomer), of *Ortyxelos meiffrenii* (see BUTTONQUAIL).

LARK, SONG-: see SONGLARK.

LARO-LIMICOLAE: Stresemann's order equivalent, in the classification here followed, to the order Charadriiformes less the families Jacanidae, Thinocoridae, and Alcidae.

LARYNX: see RESPIRATORY SYSTEM; SYRINX; TRACHEA.

LATEBRA: core of fluid white yolk at the centre of an EGG.

LATENT LEARNING: see LEARNING.

LATEROSPHENOID: a paired bone of the SKULL.

LATIN NAME: see NOMENCLATURE.

LATIPLANTAR: having the hinder aspect of the tarsus flat (applied to oscine Passeriformes); opposite of ACUTIPLANTAR (in general, see LEG).

LAVEROCK: archaic name for the Skylark *Alauda arvensis* (see LARK).

LAYING: the deposition of the egg; the act of oviposition.

Oviposition. At ovulation the ovary releases a yolk (ovum) into the body cavity. Within half-an-hour it is engulfed by the upper end of the oviduct, the infundibulum, and it then passes through three further regions of the oviduct (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM). In the 'magnum', the chalazae and the thick albumen are added; in the 'isthmus', inner and outer shell membranes are formed; and in the 'uterus' or shell-gland, where the egg remains for 20–24 hours, it undergoes a 25% osmotic increase in volume, the chalky shell is deposited, and (mainly in the last hour before laying) pigment and the cuticle may be formed (see EGG). The times given apply to the domestic hen, in which the whole process from ovulation till laying takes about 24–27 hours.

The method by which the egg is carried through the oviduct has not been demonstrated conclusively. Some maintain that it is moved entirely by ciliary action, and others that it is propelled by peristaltic movements of the oviduct (Gilbert 1971). In the oviduct the egg lies with its pointed end towards the cloaca and in many species, e.g., domestic pigeon, eggs are correspondingly laid pointed pole first. In other species, e.g., Black-headed Gull *Larus ridibundus*, domestic hens and ducks, eggs are quite often laid blunt end first; this happens in 29% of the eggs of Khaki–Campbell domestic ducks. By using X-rays, it has been shown that such eggs undergo a quick 180° rotation (in a horizontal plane) an hour before they are laid. On rare occasions this rotation precedes the formation of pigment spots; the latter then collect round the pointed pole of the egg. Rotation is more frequent in some individuals than in others, and its incidence increases with age, presumably because the uterus wall becomes more stretched with repeated layings.

How the egg is actually released from the body has for long been a matter of controversy. Some maintained that the whole uterus (with contained egg) prolapses through vagina and cloaca to the exterior, where the uterine wall everts, thus unwrapping the egg and leaving it outside. Sykes (1953), however, observed, in laparotomized hens, that the uterus is not everted during oviposition; instead, the egg passes from the uterus into the vagina and is then pushed out by peristaltic action of the vaginal muscles. In intact birds he showed, also, that the distension of the vagina by the egg evokes a ventroflexion of the legs and erection of the feathers surrounding the vent, as well as 'bearing down' contractions of the abdominal muscles and increased respiratory movements causing a rise in the abdominal pressure. The egg may be expelled after a period of bearing down lasting 1–3 minutes. In social parasites, e.g., cowbirds *Molothrus* spp. and cuckoos (Cuculinae), the process is a matter of seconds. A Bobwhite Quail *Colinus virginianus* needs from 3–10 minutes at the nest to lay an egg, whereas Turkeys *Meleagris gallopavo* and geese *Anser* spp. are reported to labour for 1–2 hours. A bird that cannot lay its egg is called egg-bound; this condition may be caused by inflammation, stricture, or tumour in the oviduct; sometimes a malformed, oversized, or soft-shelled egg may be responsible.

An egg that is ready for laying can be held back; a Cuckoo *Cuculus canorus* is thus able to wait until the nest-owner has left the nest (see BROOD-PARASITISM). Many song-birds postpone laying while quickly constructing a new nest when the old one has been damaged or removed. For review of the hormone and neural control of oviposition, see Gilbert (1971), Sturkie and Mueller (1976).

Age of bird. Captive Quail *Coturnix coturnix* reproduce at 6 weeks of age, some individuals laying as early as 38 days (*Science* 129: 267). Most breeds of domestic hen begin laying at 5–7 months; most passerines, pigeons (Columbidae), and ducks *Anas* spp., etc., many gallinaceous birds, and some owls (Strigiformes) at one year; geese, many gulls (Laridae), and birds-of-prey, some waders (Charadriidae), and a few passerines at 2 years; cormorants (Phalacrocoracidae), divers (Gaviidae), and the larger gulls at 3 years; the large birds-of-prey and storks (Ciconiidae) when 4–6 years old, and the Royal Albatross *Diomedea epomophora* not until it is at least 8 years old. In many of these species the age at which breeding first occurs may vary with the individual. These differences are often explained by stating that larger birds require longer to mature than those of smaller size. More convincing is Lack's suggestion that breeding imposes a strain on the parents that may have been too great for the young individuals in some species, thus leading to adaptive retardation of the breeding age (Lack 1968). This is particularly the case for species with specialist feeding techniques, for themselves or for their young. For example, neither Arctic Tern *Sterna paradisaea* nor the Puffin *Fratercula arctica* breed before 3 years, rather later than do land birds of equivalent size. Breeding also takes place earlier in low-density populations with little adult competition than it does in more crowded ones, as expected if inexperienced females find it easier to collect enough food for egg formation when fewer birds are present.

Time of year. Like other reproductive activities, egg-laying is restricted to particular seasons of the year in most birds (see BREEDING SEASON). In general it is so timed that the young grow up when their food is most abundant, or when the female can find enough food to form eggs (Perrins 1970). In temperate and cold climates, the proximate factors controlling the time of egg-laying are increase in day-length in late winter and warm temperatures in early spring. In the tropics the rainy season determines the onset of breeding in many passerines. In special cases other factors and adaptations may be involved; thus the Great Crested Grebe *Podiceps cristatus* does not normally breed until the vegetation supporting its floating nest has grown up. Eiders *Somateria mollissima*, Common Gulls *Larus canus*, and Herring Gulls *L. argentatus* in the Arctic are reported to postpone breeding on islets until the surrounding ice has melted, which may be an adaptation against robbing by Arctic Foxes *Alopex lagopus*. The date of laying of the first egg varies somewhat from year to year and between individuals; in many species, birds laying for the first time tend to do so a few days later than older ones. According to one view, birds of a colony influence one another's reproductive activities in such a way that bigger colonies lay earlier in the season and within fewer days, i.e., are more closely synchronized, than small ones. Other studies do not support either statement, but it appears that small colonies may lay later in the season because they include a larger proportion of young birds than bigger colonies.

Time of day. Some birds lay only at a particular time of day; many song-birds such as finches (Fringillidae), wrens (Troglodytidae), tanagers (Thraupinae), wood-warblers (Parulidae), and hummingbirds (Trochilidae) around sunrise; pigeons (Columbidae) early in the afternoon; pheasants (Phasianidae) in the evening. In a flock of domestic hens, 56% of the eggs were laid between 9 am and 1 pm.

Successive eggs may not be laid at the same time of day; in the domestic pigeon the second egg appears 44–46 h after the first and is thus laid earlier in the day. The laying pattern, i.e., the time interval between the laying of successive eggs, is characteristic for a species. This interval is 20–24 h for most but not all passerines and for many ducks; 24–28 h for the domestic hen; 24–72 h, with an average of 40 h, for the Black-headed Gull; 2 days for the Raven *Corvus corax*, Ostrich *Struthio camelus*, and Rhea *Rhea americana*; 3 days for cassowaries *Casuarius* spp; 5 days for the Condor *Vultur gryphus*; and for the Masked ('Blue-faced') Booby *Sula dactylatra* a 6–7 day interval has been reported.The interval probably corresponds to the time necessary for the formation of the various layers of the egg. It is known that in the domestic hen ovulation usually follows the laying of the previous egg within about 30 minutes, except when the previous egg is laid late in the afternoon—in which case ovulation is delayed until the next morning.

Number of eggs. Most birds lay eggs in a clutch—they lay a few eggs in sequence, then stop and incubate. The domestic hen is a notable exception, laying continuously for a large part of the year. Here cycles of 3, 4 or more days of uninterrupted laying are separated from one another by one or a few days of non-laying. The annual output declines steadily with increasing age and so does the length of the laying season; 351 eggs in one year and 1,515 eggs laid within 8 years by a single hen have been recorded.

The number of eggs in a clutch (clutch-size) varies with the species. Some lay only 1 egg; others regularly have clutches of 2, 3, or 4; others show more variability, especially where the number is large (such as 10–20 for the Partridge *Perdix perdix*). In many species clutch-size varies between populations, with the individuals of a population, and even for one individual in different years. The average clutch-size of a population has been shown to be delicately adjusted to yield the maximal number of successfully reared young (Lack 1968). It is influenced by such factors as the age of the parents, seasonal influences responsible for the availability of food later in the year, and population density (see EGG; CLUTCH-SIZE).

Determinate and indeterminate layers. Little is known about how the regulation takes place—what are the climatic (or other) indicators of abundance of food later in the season, and by what means they affect the activity of the ovary. A further complication arises from the fact that 2 types of egg-laying mechanism may have to be distinguished; in some birds (indeterminate layers) the number of eggs laid can be changed by adding or removing eggs during or just before the time of laying; in other birds (determinate layers) this has no influence. In the latter case, presumably, the ovary produces only as many yolks as eggs will be laid. Experimental addition of eggs to the first egg of the clutch may reduce the number of eggs laid subsequently, e.g. in the Tricolored Blackbird *Agelaius tricolor* of North America. In many other species, e.g., Swallow *Hirundo rustica*, pigeons, gulls, and the Lapwing *Vanellus vanellus*, this has no effect; but if eggs are presented a few days earlier in some of these, egg-laying may be suppressed fully or partially—thus a Black-headed Gull sitting on model eggs for 2–8 days before laying its first egg may lay only 2 or 1. Removal of eggs, so as to leave only one or a few in the nest, increases the number to be laid in many species. Such protracted laying occurs, e.g., in the Yellow-shafted Flicker *Colaptes auratus* (where one female laid 71 eggs within 73 days) and in other woodpeckers (Picidae); a Mallard *Anas platyrhynchos* is reported to have laid 80–100 eggs when one was removed daily, and a House Sparrow *Passer domesticus* laid up to 50 eggs in succession (of which 12–19 were laid on consecutive days) instead of the usual clutch of 4–5. These and many other birds thus qualify as indeterminate layers. In a few others, e.g., Swallow, Magpie *Pica pica*, Gentoo Penguin *Pygoscelis papua*, Lapwing, and gulls, this procedure has no influence on the number of eggs laid. Nevertheless some of these have been shown to be indeterminate layers; they will lay additional eggs at normal intervals if the first egg is taken as well, i.e., if all eggs are removed as soon as they are laid. In these circumstances the Lapwing and Gentoo Penguin will lay one and gulls 3 more additional eggs. In pigeons, egg-laying could not be protracted in this way (Poulsen 1953).

In the ovary of an indeterminate layer more oocytes may enter the final phase of growth than are normally laid, and tactile or visual stimuli from the eggs in the nest are responsible for the cessation of laying. In some species, e.g., gulls, the end of laying is determined not by a definite number of eggs in the nest but by the opportunity for the bird to incubate. Only a limited number of eggs are laid after the onset of incubation, which causes all oocytes under a critical size in the ovary to degenerate. In species that do not incubate before the clutch is complete this explanation cannot apply. Here it is the critical number of eggs in the nest that stops the growth or causes the degeneration of superfluous oocytes. In neither case can laying be protracted once the reserve follicles have started to degenerate, i.e., one or more days after the onset of incubation.

Number of clutches. Many wild birds normally lay only one clutch in each year, but there are others that have two or more broods in a season. The domestic pigeon may lay up to 10 clutches a year. In most species (but not the domestic pigeon) the number of eggs tends to decrease with each successive clutch.

In Megapodiidae there may be no clutch in the ordinary sense; the eggs, often very numerous, are laid at intervals throughout several months, and there is no synchronization of incubation and hatching (see MEGAPODE).

Most birds with only one brood annually, and all of those with more than one, are able to replace the clutch when it is lost (repeat laying); a Black-headed Gull will lay again 8–12 days after the loss. Exceptions are some big vultures (Aegypiinae) and most Procellariiformes. Repeat clutches tend to be smaller than the first one. (U.W.) S.G.T.

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LEADING LINE: see MIGRATION.

LEAD POISONING: see DISEASE.

LEAFBIRD: substantive name of the species of the genus *Chloropsis* of the Chloropseidae (Passeriformes, suborder Oscines). Members of a second genus, *Aegithina*, are called ioras. There is no accepted collective in English.

Characteristics. Small to medium-sized, wholly arboreal passerines 12–19 cm long in the weight-range 10–40 g, with small toes, tarsi slender in ioras, short and thick (similar to bulbuls) in leafbirds; bill medium to fairly long and slender, terminally decurved to hooked and finely notched; wing and tail of moderate length. All have ample, fluffy body plumage, long on the rump. Leafbirds resemble fairy-bluebirds (Irenidae) and bulbuls (Pycnonotidae) in profusely shedding feathers when handled. During flight the white flank feathers of some ioras conspicuously overlay the rump, and all except *A. lafresnayei* also have two white wing-bars.

All chloropseids are predominantly green or green and yellow (or orange). Most male leafbirds combine intense black and glossy blue on the throat and a proportion of the males of some ioras (not *A. viridissima*) tend to be black rather than green above, which character often varies clinally. Black is lacking in the body plumage of most females and apart from some south-east Asian island leafbirds most chloropseids show well-marked sexual dichromatism. Juveniles resemble females, and some populations of non-forest ioras acquire a brighter breeding plumage by moult.

Leafbirds superficially resemble and behave like some bulbuls, with which all chloropseids have at times been merged. A possible link with Meliphagidae has also been suggested.

Distribution and habitat. The 12 species constitute 1 of only 2 bird families endemic in the Oriental biogeographical region, chloropseids being found to its full limits. Northern congeners tend to be segregated by biotope and maximum co-occurrent diversity is reached in Sundaic dipterocarp forests where up to 5 species in both genera can be found together. Philippine congeners are allopatric by island.

Only *Aegithina* has non-forest representatives. The familiar *A. tiphia* everywhere inhabits thinly wooded environments (locally also mangrove), its range being almost that of the family. In evergreen forests of the Sunda and Indochinese subregions it is replaced respectively by *viridissima* and the larger *lafresnayei* (which also occurs in the Malay Peninsula but is scarce there away from forest-edge). A close relative, *nigrolutea*, replaces it in the driest scrub of north-west India and Pakistan.

Leafbirds are purely forest dwellers. *C. aurifrons* inhabits northern deciduous forest, others evergreen forest though *C. cochinchinensis* comes to quite open edge. The continental montane species is nearly everywhere the colourful *C. hardwickii*. Its place in the mountains of Sumatra is taken by an isolated form of *aurifrons* (possibly with the little insular endemic, *venusta*), and in Borneo by an upland subspecies of *cochinchinensis*.

Movements. Non-migratory, but in its Himalayan range *C. hardwickii* makes seasonal shifts of altitude.

Food. Ioras are mostly insectivorous. Leafbirds have mixed insect/fruit diets and some at times visit flowers, reputedly for nectar. A role in the pollination biology of certain forest trees is conceivable. The main foraging mode of both genera is leaf-searching, often acrobatic and frequently in dense foliage. Non-forest and forest-edge species hunt at all levels, forest species largely in the continuous canopy (from which *A. viridissima* regularly visits the crowns of tall emergents).

Behaviour. Ioras and leafbirds forage alone, in pairs or small, loose groups, and in forest frequently attend mixed-species gatherings. At flowerings or fruitings in extensive forest the northern leafbirds congregate in considerable numbers but show no flock cohesion, such gatherings being strictly temporary.

Voice. *A. tiphia* has numerous sharp or drawn-out and repeated whistles, loud and with spectacular shifts of pitch. Leafbirds have liquid, whistling songs, most sustained and melodious in *C. hardwickii* and *C. aurifrons*. Some are also considerable mimics of other birds.

Breeding. Some ioras have elaborate courtship displays involving vertical leaps and parachuting flight by males. *A. tiphia* builds a neat compact cup of fine grass and plant fibre felted into a branch fork with cobweb. The few known leafbird nests are loose cups of fine twigs variously mixed with grass and bryophytes, felted with cobweb and suspended by the rim from outer branchlets.

A. tiphia eggs are pale pinkish with purple–brown blotches zoned in some populations round the longest circumference. Known leafbird eggs are pale buff–cream to pinkish-white speckled, or speckled and hairlined, reddish or purple–black. Chloropseid clutches average 2 eggs, rising to 3 only in some outer tropical forms. *A. tiphia* fosters the cuckoo *Cacomantis sonneratii* (see BROOD-PARASITISM). D.R.W.

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LEAFLOVE: used as a substantive name for some species of Pycnonotidae (see BULBUL).

LEAFSCRAPER: substantive name of *Sclerurus* spp. (see OVENBIRD (1)).

LEAF WARBLER: see WARBLER (1).

LEAP-FROG MIGRATION: migration by a northern breeding population to winter quarters which lie further to the south than those occupied by a southern breeding population of the same species; or the corresponding return migration to the breeding quarters.

LEARNING: best defined as 'the production of adaptive changes in individual behaviour as a result of experience'. There has been considerable difference of opinion as to whether the term 'adaptive' should be included in the definition (Thorpe 1956); the word is used here to prevent the term 'learning' from including such changes in behaviour as those resulting from fatigue, sensory adaptation, and the effects of injury (surgical or otherwise). This is important, because it is generally agreed that learned behaviour is to be carefully distinguished from changes in behaviour caused by physiological or structural damage to the system.

Many workers have considered that a more or less frequent repetition of a stimulus or of a changed situation is necessary for learning, but so many examples are now known of learning as a result of a single experience that this contention can no longer be maintained. There are 6 different categories of learning that are found to be useful in describing behaviour of birds and the higher vertebrates generally, one of which is discussed in a separate article (see IMPRINTING; see also BEHAVIOUR, DEVELOPMENT OF).

Habituation. This is, in some respects, the simplest type of learning found in the Animal Kingdom. It consists of 'the waning of a pre-existing response as a result of repeated stimulation when this is not followed by any kind of reward or punishment' (*reinforcement*). It is most evident in nature in relation to avoiding action to more generalized and simple stimuli such as loud sounds, sudden movements, any stimulus or situation that is strange, and any familiar stimulus at an unusually high intensity. Many species of birds, also, have the inborn ability to recognize, and immediately take appropriate avoiding action or other response in regard to certain types of predator, such as hawks and owls that are particularly dangerous to their species; but such an inherited response is hardly likely to have been evolved except in response to dangers that are of primary significance to the particular species. To have such an instinctive response to every kind of predator, and to every and any danger, would be out of the question. Therefore instead of, or in addition to, such specific responses, practically all animals show this ability to become habituated to stimuli that experience shows to be harmless. Obviously, if the response to such stimuli as sudden movements and sounds were completely automatic and unvarying, the life of the animal would become impossible since it would be continually taking cover from the flicker of a leaf and from every passing shadow. Habituation is thus that very simple form of learning which saves an animal from wasting its energies in response to stimuli that experience shows to be of no significance. Habituation is obviously of prime importance in the process of taming birds and other animals, constituting as it does the first step in accepting the abnormal conditions of captivity. The term 'habituation' is used in a general way for any type of response decrement shown by animals.

It is, however, important to distinguish between habituation and the alternative processes, *sensory adaptation* and *muscular fatigue*. An example of how these can be distinguished refers to the withdrawal response of the marine worm *Nereis pelagica*. This animal, which lives in a burrow, withdraws into its home in response to a stimulus such as a shadow or a touch from a small rod, but repeated presentations of such stimulus lead to a waning of the withdrawal response. The worm's muscles are not fatigued, because a change in stimulus immediately elicits complete withdrawal. Nor have the worm's sense organs adapted to the stimulus (in much the same way as we adapt to bright light after emerging from a dark room), because the worm, even though it does not withdraw when prodded, shows other responses such as turning towards the rod. Therefore the change in the withdrawal response is due to habituation. In vertebrates, habituation is probably a result of a process in the central nervous system, although not many examples have been studied at the neurophysiological level.

Associative learning. The great majority of studies of animal learning by experimental psychologists have focused on two kinds of associative learning, in which the animal learns an association between a reward or *reinforcement* and another event. Two main categories of associative learning are recognized.

(a) *Classical or Pavlovian conditioning* (named after the great Russian scientist I. Pavlov) in which the animal learns an association between two *stimuli*. One stimulus is motivationally significant, such as the sight of food (this acts as the reinforcer) and the other is a neutral arbitrary stimulus such as light or a buzzer. In Pavlov's classic experiment a dog learned to associate the light or buzzer with food, so that eventually it would respond by salivating whenever the light or buzzer was presented.

(b) *Operant or instrumental* conditioning, in which the animal learns an association between a *reward* and a *response*. In a typical experiment an animal has to perform a response (e.g., pecking at a key), to get a reward in the form of food. In both kinds of associative learning, then, the experimenter arranges a set of contingencies—in classical conditioning between a stimulus and reward, in operant conditioning between a response and reward.

Adaptive value of operant and classical conditioning. The two kinds of associative learning obviously play a major adaptive role in the life of birds. The ability of birds to learn to go to good feeding sites and to stay away from places where predators are likely to attack are examples of operant conditioning. An adaptive advantage of classical conditioning is that it allows an animal to anticipate the onset of a biologically significant event: by learning to associate the start of a rain shower with the emergence of worms birds might get to the feeding site ahead of competitors.

The role of associative learning can also readily be seen in the process of DEVELOPMENT OF BEHAVIOUR. For example, pecking movements of young chicks, or the ability of young Great Tits *Parus major* to deal with food items held under the feet are both examples of feeding skills that improve with performance. A chick's first pecks are poorly co-ordinated and inaccurate, but within a few days precision and control has improved greatly; the young Great Tit is clumsy and inept when it first handles food with its feet, but it soon learns to do the job skilfully and without errors. In these cases the process of instrumental conditioning is serving to modify the animal's natural behaviour to improve efficiency at obtaining rewards. In this kind of learning the animal gradually selects successful (in terms of reward-getting efficiency) manoeuvres and rejects less successful ones, suggesting an analogy between natural selection over many generations and learning within the lifetime of an individual. Both processes involve the selection of successful variants and discarding others. A similar point is made by K. Lorenz who has dubbed instrumental associative learning 'trial-and-success' (as opposed to the more usual term 'trial-and-error').

Although animals in the laboratory can be taught rather arbitrary responses to obtain food (e.g., raising a leg, pressing a lever, putting a coin in a slot), such instrumental conditioning proceeds more readily if there is some natural association between the response and the reinforcer. In fact what appears to be an arbitrary response to get food may be based on a natural feeding movement: rats 'pressing a bar' to get a food reward may often, on closer inspection, be gnawing at the bar as though engaged in normal appetitive behaviour for feeding.

Latent learning and perceptual learning. In the types of learning so far described the performance is established or stereotyped as a result of the attainment of some kind of reward, e.g., food, drink, effective nest building, or control of flight movements. It has long been recognized that in some animals another type of learning can be discerned which is independent of reward in the ordinary, physiological sense of the term. The classical experiment is as follows: a litter of young rats is divided into two groups, one of which is placed for a period every day for 10 days in a particular maze of a particular pattern and allowed to explore this maze at random; the others are given no such experience. If, then, both groups of rats are given identical training in such a maze by being rewarded in the normal manner by finding food in the food box on completion of the run, it will be found that those rats which had had the chance to explore the maze previously (but without being rewarded in it) had, in fact, learnt a great deal about its layout and showed a striking decrease both in errors and time of running as compared with the control group. A simple maze may in this way be entirely mastered through random exploration, but this learning is latent in that it cannot be demonstrated until the introduction of a reward. Latent learning can thus be defined as 'the association of indifferent stimuli or situations (i.e. situations without reward)'. One cannot conveniently train pigeons in mazes, but there is little doubt that latent learning is a laboratory version of what is a very general feature of animals that in nature have to find their way about. There is no doubt that a great deal of the learning displayed by birds in getting to know territory, individual habitat, migration routes, and so on, resembles latent learning in that the learning achieved is not immediately rewarded in the ordinary physiological sense. Also, like latent learning, it implies a tendency to explore the environment and to learn as a result the characteristic features and their special relation to one another.

Perceptual learning is essentially similar to latent learning: prior exposure to a stimulus improves later learning abilities. For example, rats reared with circles and triangles on the walls of their cages may subsequently be able to learn to discriminate these stimuli more rapidly than control animals. Perceptual learning, therefore, involves building up a set of descriptions of the critical features of a stimulus situation. Song learning in birds (see VOCALIZATION) and IMPRINTING are examples of perceptual learning.

Insight and other complex forms of learning. There are some examples of learning which at least at first sight appear to go beyond the processes of habituation and associative learning. In the early part of this century the psychologist W. Köhler made the classic observations of *insight learning* in Chimpanzees *Pan troglodytes*. He saw that they could pile boxes on top of one another to make a 'ladder' to reach bananas hanging from the ceiling, and piece together sections of bamboo pole to make a 'rake' which they used to collect food outside their cage. According to Köhler the chimpanzees were perceiving objects in their environment in a new way—in a flash of *insight* the animals saw that sticks could be used as a rake, boxes as a ladder. An analogous form of learning is the ability of some animals to work out a short-cut through a maze, having been taught only a devious route.

The extent to which these examples of learning should be viewed as qualitatively different from associative learning is not clear. For example, during the course of their normal play behaviour Chimpanzees will manipulate sticks and even fit them together or pile boxes up and climb on them without using the behaviours to obtain food. What Köhler saw as a flash of insight may in fact have simply been a reflection of the Chimpanzees' normal behaviour patterns. Among birds there are examples, along the same lines, of tool using in the normal process of food acquisition (see TOOLS, USE OF).

Imitation is another class of learning which has sometimes been viewed as being more complex than associative learning. In birds a famous example is the ability of titmice Paridae to peck open milk-bottle tops to drink the cream. It is likely that relatively few individuals learned the trick *de novo* and that others acquired the novel feeding method by watching those that had already learnt it. In this way milk-bottle opening spread as a cultural behaviour tradition. The ability of birds to learn by watching others seems widespread. Experiments have shown that an individual can learn to avoid certain distasteful foods, to obtain food from a novel hiding place, and to mob an artificial 'predator' stimulus simply by observing another bird doing the same thing.

It is sometimes suggested that the various learning abilities of animals can be expressed in terms of a single dimension of *intelligence*. However, as yet this term is not very useful to the student of animal behaviour since it is hard to define precisely and as we have seen, learning phenomena are diverse in nature. It is also becoming increasingly apparent that different species may have different specialized learning abilities to cope with their particular way of life. W.H.T. and J.R.K.

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LEATHERHEAD: substantive name, alternatively 'friar-bird', of *Philemon* spp. (see HONEYEATER).

LECTOTYPE: see TYPE SPECIMEN.

LEG: the paired hind limb; but the term 'leg' is variously used, in different contexts, for the whole limb or for the ordinarily visible part of it and to include or exclude the 'foot', itself an inexact term for the extremity. The main components are the thigh, the lower leg (equivalent to shin), the so-called tarsus, and the toes—corresponding osteologically with the femur, the tibiotarsus plus fibula, the fused tarsometatarsus (with one free metatarsal where there are four toes), and the digit phalanges (see SKELETON, POST-CRANIAL). The joints between these components are the knee, the inter-tarsal joint or ankle, and the joints of the toes; as most birds stand on their toes, the raised ankle is often popularly mistaken for a knee (the real knee being concealed in the plumage) although it bends in the reverse direction.

Birds are dependent upon their limbs for locomotion on land or on water, and there are a number of adaptations to meet these varying conditions. When the bird is standing, the leg is situated just behind the bird's centre of gravity, balance being maintained by the toes. The legs are set farther back in swimming species; this is particularly true of the divers (Gaviidae), in which walking becomes almost impossible, so that on land they rest on their tarsi and wriggle on their stomachs—as sometimes do penguins (Spheniscidae), although these can also walk or hop in the upright position; the grebes (Podicipedidae) can run on their toes in emergency.

The thigh, knee, and upper part of the lower leg are completely hidden by the flank feathers and it is only the lower part of the lower leg, the ankle joint, the tarsus, and the toes that are visible. The relative length of the limb is extremely variable. Birds that walk or run, such as the Ostrich *Struthio camelus*, have long legs, whereas most small birds hop and have relatively shorter legs (see LOCOMOTION, TERRESTRIAL). In passerine birds that run, e.g., larks and wagtails, the young initially hop. Similarly, wading birds, particularly flamingos and the Stilt *Himantopus himantopus*, have long legs and can thus go far into the water without wetting their plumage. The Secretary-bird *Sagittarius serpentarius* is an example of a long-legged hawk-like bird that both evades snakes and preys on them by springing in the air and killing them by striking. The shortest legs are seen in those species that seldom walk, such as the swifts and the kingfishers; but such short legs are capable of digging—the Bee-eater *Merops apiaster* leans on its wings while it digs with its feet.

Relative strength depends upon function. Birds-of-prey possess powerful limbs for striking and holding their quarry; swimming species, particularly those that are not assisted in the water by their wings, possess massive thighs (see SWIMMING AND DIVING); whereas those that scratch the ground for food, such as the gallinaceous birds, have heavy tarsi and toes. See also CARRYING; HOLDING; PERCHING.

Covering of tarsi and toes. In some birds, the tarsi and even the toes are covered with feathers or bristles. This may be protective against the cold, e.g., Pallas's Sandgrouse *Syrrhaptes paradoxus*, in which the feathers extend to the upper surface of the toes only, and the Ptarmigan *Lagopus mutus*, in which the under surface of the toes is also feathered. Feathering in other species, including the owls (Strigiformes) and the House Martin *Delichon urbica*, cannot be accounted for in this way. Feathering may therefore be primitive, a scaly covering being a secondary transformation of feathers. These scales may be shed annually (see MOULT), and occasional variants of the Buzzard *Buteo buteo* possess feathered tarsi, similar to those of the Rough-legged Buzzard *Buteo lagopus*. Man has produced feathered tarsi by selective breeding in domestic pigeons and fowls.

The part of the limb lacking feathers is covered with a thickened, hardened structure, the podotheca. This may be corneous (horny) as in land birds or softer and more 'leathery' as in water birds. The surface may be scutellate (scaly), reticulate (covered with polygonal plates), granulate (covered with small tubercles), cancellate (covered with cross lines, as on the webs of water birds). If the podotheca is undivided or has only a few scales close to the toes, the bird is said to be 'booted' or holothecal, a condition found in most passerines (but when young these have scutellae that disappear by fusion). The young of certain Piciformes, Coraciiformes, and Trogonidae possess 'heel' pads, at the back of the intertarsal joint, that are shed when the birds leave the nest. These pads are in most cases strongly papillate, but smooth in Galbulidae. In some grouse (Tetraonidae) with unfeathered toes these are laterally pectinated (for pectinate claws see below). (See also FOOT PAPILLAE AND PADS.)

Tarsal shape. In most species the tarsus is rounded in cross section, but in many swimming species it is compressed laterally to reduce water friction when the leg is brought forward, the foot folding neatly to the same shape. This is most highly developed in divers and grebes, where the tarsus resembles a knife blade.

Spurs. These consist of a bony core covered with a pointed horny sheath and are situated on the posterior and inner surface of the tarsus. They are used with skill in battles that can well prove fatal, and are possessed by cock birds of polygamous species such as pheasants and peacocks and turkeys. The peacock-pheasants *Polyplectron* spp. have up to 4 full-sized spurs on each leg (see also COCK-FIGHTING).

Number and arrangement of toes. No bird has more than 4 toes; some have only 3, the hallux having been lost (vestigial in some others), and one species has only 2, as noted below. Their arrangement depends upon function. The majority have 3 forward toes and one, the 1st toe or hallux, behind (anisodactyl). This was the position in *Archaeopteryx* of the Jurassic period (see ARCHAEOPTERYX). Exceptions are as follows:

(*a*) All 4 toes may point forwards, as in the swifts.

(*b*) The 1st toe may be capable of turning backwards or forwards, as in

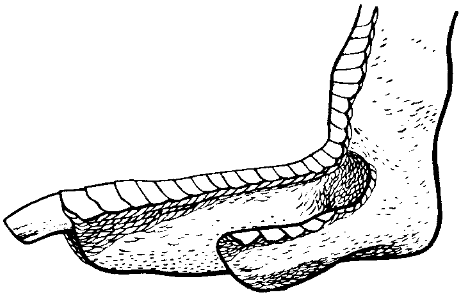

Fig. 1. Foot (right) of Ostrich *Struthio camelus*, with toes uniquely reduced to two. One-fifth natural size. (*M. Yule*).

the mousebirds (Coliidae); this and the preceding case have been termed the pamprodactyl foot.

(*c*) The outer forward toe (4th) may be capable of turning backwards or forwards, as in most owls (Strigiformes) and the Osprey *Pandion haliaetus*.

(*d*) The toes may be permanently in pairs, 2 in front and 2 behind—the zygodactyl or 'yoke-toed' foot. This occurs in woodpeckers, toucans, cuckoos, parrots, and others. These have the 1st and 4th toes pointing backwards, but in the trogons it is the 1st and 2nd that do so (sometimes called 'heterodactyl'). In some Picidae, e.g. the Three-toed Woodpecker *Picoides tridactylus*, the 1st toe has been lost; in a few others (*Campephilus* etc.) the 1st and 4th toes are, during climbing, rotated into an external lateral position (ectropodactyl).

(*e*) The 3rd and 4th toes may be partly united, with a single broad sole—the syndactyl foot of the kingfishers, hornbills, and the Cock-of-the-rock *Rupicola rupicola*.

In swift-running species it may be advantageous to lessen the surface of contact with the ground. Thus the 1st toe becomes raised and tends to disappear, as in some plovers (Charadriidae). The extreme is seen in the Ostrich, which has only 2 forward toes, one poorly developed and both possessing a soft elastic cushion on the sole to prevent sinking into soft sand. In sandgrouse the 3 forward toes are united by a membrane holding them close together.

Claws. Claws are specialized scales, and in ptarmigan *Lagopus* spp. are moulted in winter. Their shape is variable; sharp, well-curved claws are used for gripping firmly and are seen in such birds as the treecreepers (Certhiidae), the Wallcreeper *Tichodroma muraria*, woodpeckers, and the birds-of-prey (excepting the carrion-feeding vultures (Aegypiinae) and the Honey-buzzard *Pernis apivorus*, in which the claws are weaker and straighter). The claws of oxpeckers *Buphagus* spp. are extremely sharp. Strong, blunt claws are associated with species that scratch the ground in search of food, while exceptionally long claws, such as the hind claws of some larks and pipits *Anthus* spp., and the long 2nd claw of the One-wattled Cassowary *Casuarius unappendiculatus*, may be concerned with balance when running. In the jacanas all 4 claws are long, in association with long thin toes; this remarkable adaptation enables the birds to walk over floating vegetation. In grebes the claw is flattened and is incorporated into the paddle.

The herons, nightjars, and pratincoles *Glareola* spp., have a serrated edge or 'comb' on the inner border of the 3rd claw, which, in the herons at least, has a special function in plumage-maintenance (see COMFORT BEHAVIOUR).

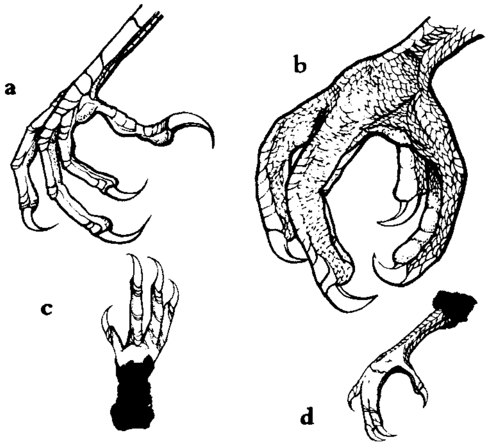

Fig. 2. Some perching and clinging feet (right): (a) Starling *Sturnus vulgaris*, anisodactyl; (b) Senegal Parrot *Poicephalus senegalensis*, zygodactyl; (c) Swift *Apus apus*, with all 4 toes directed forwards; (d) Kingfisher *Alcedo atthis*, syndactyl. Natural size. (*M. Yule*.)

Types of foot. Although there are many transitional forms, three main functional patterns have been evolved.

1. *Perching*

(*a*) In the passerine foot all the toes are free and mobile, the hind toe being highly developed and 'opposable' to produce a firm grip. (For an exception see PARROTBILL (1).)

(*b*) The zygodactyl foot with 2 'opposable' toes provides an even surer grip. Parrots use the foot like a hand in feeding. The 'semi-zygodactyl' variant, typified in *Turacus fischeri*, has been defined by R.E. Moreau 'as having a fourth (outside) toe that can be brought back to form an angle of about 70° with the first toe, and forward until it almost touches the third toe, but normally is held at right angles to the main axis of the foot'.

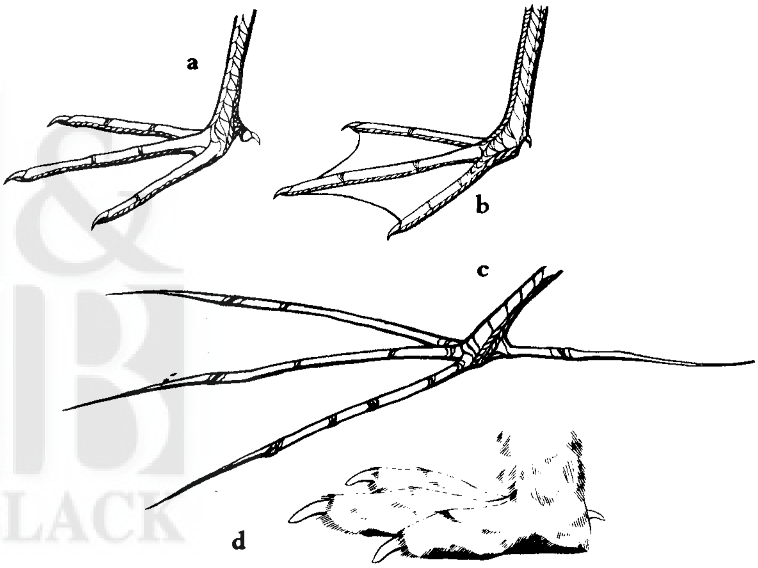

Fig. 3. Some walking and wading feet (right); (a) Lapwing *Vanellus vanellus*; (b) Avocet *Recurvirostra avosetta*, webbed; (c) Lesser Lily-trotter or Jacana *Microparra capensis*; (d) Ptarmigan *Lagopus mutus*, in winter plumage with feathered toes ('snowshoes'). Two-thirds natural size. (*M. Yule*).

(*c*) In the raptorial foot the toes are widely spread and possess sharp, highly curved claws. The under surface of the toes has bulbous and roughened pads, which in the Osprey carry spines to fix the slippery fish. This type of foot has great grasping and holding powers.

2. *Walking and wading*. In general the foot has tended to lose its power of gripping. The hind toe may become elevated to lose contact with the ground and has become reduced in size—or it may be lost, as in the Kittiwake *Rissa tridactyla*. In some wading birds the toes are partially or completely webbed, for example the flamingos, storks, and avocets *Recurvirostra* spp.; walking over soft ground is thus facilitated, and such species can swim well on occasion.

The rails have developed long toes and claws as an adaptation for walking over soft ground; this type reaches its extreme form, as already mentioned, in the jacanas, which are thus able to distribute their weight over a large surface area.

The feathered foot of the Ptarmigan increases the weight-bearing surface when walking on snow in winter. The American Ruffed Grouse *Bonasa umbellus* in winter develops 'snow shoes' in the form of a row of scales along each side of the toes.

3. *Swimming*. Many unrelated birds such as the petrels, gulls, auks, ducks and geese, have developed along similar lines to transform the foot into a paddle.

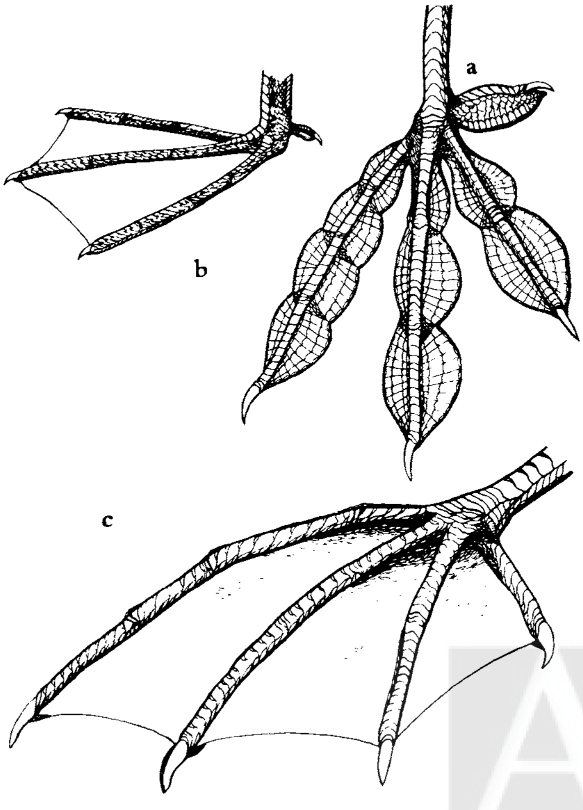

Fig. 4. Some swimming feet (right): (a) Coot *Fulica atra*, lobate; (b) Mallard *Anas platyrhynchos*, palmate; (c) Cormorant *Phalacrocorax carbo*, totipalmate. Half natural size. (*M. Yule*).

In the lobate variation, each toe carries independent webs, examples being the coots *Fulica* spp., phalaropes, the grebes, and the three remarkably grebe-like species of finfoot, thought to be of gruiform affinity. In grebes, the tibiotarsus is held in extreme external rotation when the bird is swimming; the foot is pale on its inner surface and dark on its outer surface, so that, as the latter is uppermost in swimming, the normal countershading is maintained.

In the palmate variation the 3 forward toes are united by a web, typical examples being the gulls, petrels, and ducks. The hind toe is free, poorly developed, and unmodified except in diving ducks, in which it is lobulate. The Hawaiian Goose *Branta sandvicensis* possesses a partially palmate foot and is an example of a goose that has reverted to a more terrestrial life.

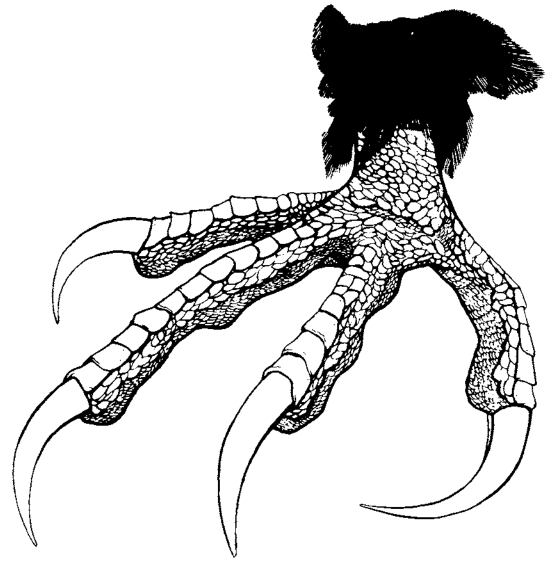

Fig. 5. Foot (right) of Golden Eagle *Aquila chrysaetos*, adapted for grasping. Half natural size. (*M. Yule*).

In the totipalmate variation characteristic of the Pelecaniformes, all 4 toes are webbed to provide the perfect swimming foot, the outer toe being the longest and the hind toe pointing slightly forward.

Unfeathered legs and feet, particularly webbed feet, are a potential source of heat loss. Irvine and Krog have shown in gulls *Larus* spp., however, that there is not only a reduced blood flow at low external temperatures but also some kind of vascular heat exchange, so that blood flowing into the unfeathered part of the leg does so at a very low temperature. This can be appreciated by feeling the cold web of any water bird. Serious heat loss is thus eliminated; and, in extremes, loss can be further reduced if the bird sits on its legs, covering them with its feathers (see also HEAT REGULATION).

Abnormalities. Supernumerary limbs and toes occur as genetic variants (except in domestication, the Dorking Fowl possessing a constant supernumerary toe on each foot). Very rarely a toe may be missing due to a congenital defect; frequently the toes are crooked, in association with inbreeding. Survival has been recorded in a wild Pheasant *Phasianus colchicus* after both feet had been accidentally amputated through the tarsi. Partial or total loss of one or both feet is not uncommon in water or wading birds and there is evidence that this is caused by fishes and molluscs. Loss of toes in a Moorhen *Gallinula chloropus* has followed a tuberculous arthritis. Normal embryonic development may be altered by radiation or drug administration. J.G.H.

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LEITLINIE: original German term, best translated as ‘leading line’ (see MIGRATION).

LEK: a communal display ground (sometimes called ‘arena’) where males congregate for the sole purpose of attracting and courting females and to which females come for mating. The term is sometimes applied to the group of males congregating at such an area, and seems to be derived from Swedish ‘leka’, ‘to play’, which can have a sexual connotation. In resident species leks are usually traditional, their location remaining unaltered year after year; but in some migratory species the position of leks may change yearly, and even within seasons.

Lek displays constitute one of several categories of polygynous mating systems (see MATING SYSTEM; POLYGYNY), their most important distinguishing feature being that the males do not defend any resource needed by the female (nest-site or food) but compete directly among themselves for the attention of females, those of the highest status doing most of the mating. It is the rule for each male to occupy and defend his own display area (a cleared or trampled area, usually known as a ‘court’ if it is on the ground, or a special perch or group of perches if it is in a tree) within the lek. Mating normally takes place at the lek, on the successful male’s court or display perch, after a stereotyped display sequence. Detailed studies of lek displays have shown that some males, usually those whose courts are centrally placed within the lek, attract most females and do most of the mating, while peripheral males are relatively or completely unsuccessful. It is assumed that even peripheral males nevertheless have a better chance of mating than they would have if they attempted to court females away from the lek, and that this is so for two reasons. First, because the males stimulate and enhance each other’s displays, a group of *n* males will be more than *n* times as effective in attracting females as a single male displaying alone, and secondly, peripheral males have a chance to succeed to central positions in a lek when these fall vacant. Evidence for the first of these assumptions, which are crucial to explaining the evolution of lek displays, is very difficult to obtain; but there is a considerable amount of evidence that peripheral males in a lek take every opportunity to claim more central positions and regularly succeed in doing so.

It is not always possible to draw a clear distinction between true leks (in the sense used above) and those in which males display in a looser group within a circumscribed area, often out of sight but within earshot of one another. The term 'dispersed lek' or 'exploded lek' has been used for such cases. In some species the spatial organization of displaying males probably varies according to population density. Closely related species within the same genus (e.g. manakins of the genus *Pipra*) may show examples of different degrees of spacing.

In many species with lek displays the intense inter-male competition has led to the evolution of striking male ornamentation; display postures and movements are typically both striking and highly stereotyped. In some groups of lek birds, however, most notably the hermit hummingbirds, male and female differ hardly at all in plumage. It is noteworthy that the most refined elaborations of plumage, as in the Great Argus Pheasant *Argusianus argus*, Peacock *Pavo cristatus* and Lyrebird *Menura novaehollandiae*, are found in species in which the males display solitarily or in 'dispersed leks'. There is generally a clear distinction between displays which serve to attract females from a distance (loud calls, and very striking visual displays, especially flight displays) and those that presumably stimulate females at close quarters (the more elaborate and refined, often static, visual displays).

Lek displays, being performed by birds belonging to several different families in which monogamy is probably the primitive condition, exemplify evolutionary convergence in behaviour. An important predisposing condition is that the male is emancipated from nest-attendance and parental care. This probably explains why lek displays have evolved only in birds with precocial young and, among birds with altricial young, only in some fruit-eating, nectar-eating and seed-eating groups (for further explanation, see MATING SYSTEM). The following is a systematic summary of the main known cases of lek behaviour.

Male Ruffs *Philomachus pugnax* displaying and fighting at a lek with (lower photo) females, 'reeves', in attendance. (*Photos: A. Christiansen*).

Game-birds. The grouse family (Tetraonidae) includes several species with highly developed lek displays, the Black Grouse *Tetrao tetrix* and Sage Grouse *Centrocercus urophasianus* being well-studied examples. True lek displays apparently do not occur in the largest of the game-bird families, the Phasianidae, but males of the Great Argus and some other species occupy isolated display areas within earshot but not within sight of one another ('dispersed leks').

Bustards. The Great Bustard *Otis tarda* has a lek display; in other species, so far as known, the males display solitarily.

Waders. The Ruff *Philomachus pugnax* is one of the most outstanding and best known of lek birds. Ruffs are unique in having highly polymorphic male display plumage, no two individuals being exactly alike. There are two main types of male: independent males, with mainly dark display plumage, which occupy and defend courts within the display grounds (known, in this species, as 'hills'); and satellite males, with largely white display plumage, which lack aggressive behaviour and are tolerated at the courts of the independent males. The Ruff is exceptional among lek birds in being silent at the 'hill', but the courts may be only *c.* 0.5 m from each other, the area is open and frequented year after year, and conspicuousness is increased by corporate flights. Two other waders, the Buff-breasted Sandpiper *Tryngites subruficollis* and the Great Snipe *Gallinago media*, have lek displays. Unlike the Ruff, they show little sexual dimorphism in plumage. The display of the Great Snipe, which takes place mostly at night, is accompanied by loud vocalizations; the Buff-breasted Sandpiper's displays are made conspicuous by showing off the satin-white underside of the raised wings.

Parrots. It is reliably reported that the little-known, and gravely endangered, Kakapo or Owl Parrot *Strigops habroptilus* of New Zealand is a lek species. The males congregate in restricted display areas, where each bird advertises itself with a booming call.

Hummingbirds. Many, perhaps all, of the hermit hummingbirds of the genus *Phaethornis* display in leks. They are dull-coloured for hummingbirds, and the sexes are nearly or quite alike in plumage. The males advertise themselves on their display perches by constant singing; displays directed towards intruding males and females are similar, mating being elicited by appropriate behaviour on the part of receptive females. Singing assemblies of some other tropical hummingbirds, which may qualify as leks, have been less studied. It seems that the evolution of lek behaviour in the hermit hummingbirds is connected with the fact that they are 'trap-lining' hummingbirds and do not defend their nectar sources (see HUMMINGBIRD). A 'resource-based' mating system, such as is found in some other hummingbirds, is therefore not possible, and males establish their status by direct competitive interaction.

Manakins (Pipridae). This Neotropical family of small forest-living birds contains a number of species with highly developed lek displays, notably the White-bearded Manakin *Manacus manacus* (and its near relatives), several species of *Pipra*, and the 4 species of *Chiroxiphia*. *Manacus* species display on cleared courts on the forest floor, *Pipra* species on perches in under-storey trees, and *Chiroxiphia* on low, more or less horizontal vines and other stems within a few metres of the ground. The display behaviour of *Chiroxiphia* is unique in that 2, or in one species 3, males take part in a perfectly coordinated joint dance in front of a female but only one, apparently the dominant male of the group, mates with her. In one closely related group of *Pipra* species, including the Wire-tailed Manakin *P. filicauda*, the owning (or dominant) male on a display perch is regularly joined by a visiting (or subordinate) male in the absence of a female, and the two birds carry out an elaborate series of coordinated display flights and other movements.

Cotingas. This family, closely related to the manakins but containing mainly larger forest birds and, like the manakins, largely frugivorous, contains many species with extravagantly ornamented males which have elaborate displays, but only a few of them are known to display at leks, most notably the 2 cocks-of-the-rock *Rupicola* spp. Several species, including the bellbirds *Procnias*, have dispersed leks. The Screaming Piha *Lipaugus vociferans* parallels the hermit hummingbirds in that the sexes are alike and dull-coloured, and the males advertise themselves by persistent calling from their display perches within a well-defined lek.

Jackson's Whydah *Euplectes jacksoni* male displaying at a lek, showing development of 'ornamental' features often found in birds with this type of behaviour. (*Photo: J.F. Reynolds*).

Weavers. Among weavers, Jackson's Whydah *Euplectes jacksoni* is unique in having a lek display, the females nesting away from the display area (not within the male's display territory, as in the typical polygynous weavers).

Birds-of-paradise. Several of the birds-of-paradise, notably the species of *Paradisaea*, display at leks; in others the males have a system of dispersed leks or display solitarily. In all these, the males are extravagantly ornamented. Other species are monogamous, and show much less sexual dimorphism. As in the manakins and cotingas, the evolution of lek displays seems to be related to frugivory. D.W.S. (1)

Bradbury, J.W. 1981. Evolution of leks. *In* Alexander, R.D. & Tinkle, D. (eds.). Natural Selection of Social Behavior: 138–169. New York.

Hogan-Warburg, A.J. 1966. Social behavior of the Ruff, *Philomachus pugnax* (L.). Ardea 54: 109–229.

Kruijt, J.P. & Hogan, J.A. 1967. Social behavior on the lek in the Black Grouse, *Lyrurus tetrix tetrix* (L.). Ardea 55: 203–240.

Lemmell, P.A. 1978. Social behaviour of the Great Snipe *Capella media* at the arena display. Orn. Scand. 9: 146–163.

Lill, A. 1974. Sexual behavior of the lek-forming White-bearded Manakin (*Manacus manacus trinitatis* Hartert). Z. Tierpsychol. 36: 1–36.

Snow, B.K. & Snow, D.W. 1979. The Ochre-bellied Flycatcher and the evolution of lek behavior. Condor 81: 286–292.

Snow, D.W. 1981. The Cotingas. London.

Stiles, F.G. & Wolf, L.L. 1979. Ecology and evolution of lek mating in the Long-tailed Hermit Hummingbird. Orn. Monogr. (A.O.U.), no. 27.

Wiley, R.H. 1978. The lek mating system of the Sage Grouse. Sci. American 238: 114–125.

LENS: part of the eye (see VISION).

LEPTOSOMATIDAE: see CORACIIFORMES; CUCKOO-ROLLER.

LESSER COVERTS: see TOPOGRAPHY.

LEUCISM: see PLUMAGE, ABNORMAL.

LEUCOCYTE: see BLOOD.

LEYDIG CELLS: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

LICE: see ECTOPARASITE.

LIFE, EXPECTATION OF: see AGE.

LIFE ZONE: an area defined, for ecological purposes, in terms of temperature and humidity rather than of nature of ground and vegetation (contrast BIOME).

LIGAMENT: band of connective tissue, tough and flexible, uniting two bones (see SKELETON, POST-CRANIAL) or supporting an organ.

LIGHT: considered as an environmental factor—see PHOTOPERIODISM; also under BREEDING SEASON; MIGRATION; NOCTURNAL HABITS; RHYTHMS AND TIME MEASUREMENT; ROOSTING; VISION.

LILY-TROTTER: substantive name most commonly used for African species of Jacanidae (see JACANA).

LIME, BIRD: a viscous substance (made from holly bark, etc.) used for smearing on twigs or other perches in order to catch small birds. The term is sometimes popularly misapplied to the residual excrement adhering to trees, rocks, buildings, and the like much frequented by birds.

LIMICOLAE: formerly used as the name of an order equivalent to the suborder Charadrii of the Charadriiformes (see also LARO-LIMICOLAE).

Limpkin *Aramus guarauna*. (*C.J.F.C.*).

LIMPKIN: *Aramus guarauna*, sole species in the New World family Aramidae (Gruiformes, suborder Grues). It has certain osteological and pterylographical characters that are crane-like (i.e. as in Gruidae) and a digestive system like that of the rails.

Characteristics. In general appearance the Limpkin is like a very large rail (length 58–71 cm). The sexes are similar in size and appearance. The bill is long, laterally compressed, and slightly decurved. The neck is long and slender; the wings are very broad and rounded; the tail is short and broad; the legs are long, with tibiae partly bare. The general coloration is glossy brownish olive, quite finely streaked with white on the neck and with broader broken streaks on the body. Fledged young closely resemble adults, but have shorter bills. Nestlings are dark brownish, evenly coloured. The feet are not webbed, but it is an efficient swimmer. It is seldom seen in flight. It stands on the ground or perches at any height, including the tops of tall trees.

Habitat. Although it is a wading bird, usually occurring in wooded swamps or shaded places where there is a lush growth of woody or herbaceous vegetation, it has been found in areas of arid brush in the West Indies.

Distribution and movements. The Limpkin is a sedentary species. It occurs from Georgia and Florida through Central America and on various islands, south in South America east of the Andes to central Argentina. Four subspecies are recognized.

Food. The Limpkin feeds almost exclusively on large snails, mainly *Pomacea* (*'Ampullaria'*), obtained in water of wading depth. The bird walks ashore or to very shallow water with its prey, extracts the snail, and discards the undamaged shell; a perching place is sometimes littered with these.

Behaviour. Although, where not protected, it is considered to be crepuscular and nocturnal in its habits, it is notably unwary and diurnal (as well as nocturnal) at certain localities in Florida where it is responding to full protection.

Voice. The Limpkin is best known for its voice and is often called 'wailing bird' or 'crying bird'. Its varied wailing, screaming, and assorted clucking notes are heard most frequently at night.

Breeding. Relatively little is known about its breeding habits. The rather flimsy shallow nest, of sticks and dry vegetation, is built in a shaded spot on the ground near water or even as high as a few metres up in a bush or tree. The 4–8 eggs are pale buff, spotted or blotched with various light browns. Incubation is by the sexes in turn for an unknown period. Both parents tend the precocial young for an unknown length of time. Either the nesting season (in Florida) is very prolonged or else the species is double-brooded. The young out of the nest, even for some weeks after they have attained flight, approach from behind and reach forward between a parent's legs for food; the snail (in shell) is taken from the bill of the parent and swallowed whole. R.S.P.

Nesbitt, S.A. *et al.* 1976. Capturing and banding Limpkins in Florida. Bird Banding 47(2): 164–165.

Snyder, N. & H. 1969. A comparative study of mollusc predation by Limpkins, Everglade Kites and Boat-tailed Grackles. Living Bird 8: 177–223.

LINCOLN INDEX: the formula of a sampling method used in population studies (and see PREDATION), viz.:

$$\text{Population} = \frac{\text{M} \times \text{S}}{\text{m}}$$

where 'M' is the number of marked animals released in a given area; 'S' is the number of animals captured in a sample taken after the dispersal of the marked animals from the release point; and 'm' is the number of marked animals in the sample S.

Lincoln, F.C. 1930. Calculating waterfowl abundance on the basis of banding returns. Circ. U.S. Dept. Agric. no. 118: 1–4.

LINE TRANSECT: see CENSUS.

LINKAGE: see GENETICS.

LINNET: *Carduelis cannabina* (see FINCH).

LIOCICHLA: substantive name sometimes used for laughing thrushes of the genus *Liocichla* (for family see BABBLER).

LIVER: a large unpaired organ associated with the digestive tract (see ALIMENTARY SYSTEM). In addition to secreting bile into the duodenum by way of the hepatic duct or ducts (gall-bladder present or absent), it is the site of important metabolic changes in substances brought to it by the portal vessels (see VASCULAR SYSTEM) and also to some extent a storage depot, e.g., of glycogen (see METABOLISM).

LIVER (with long 'i' as in 'diver'): name derived from that of the city of Liverpool and applied since the 17th century to a bird imaginatively portrayed in the municipal coat-of-arms, originally intended to be the eagle of St John the Ecclesiastic but now changed out of recognition (see, in general, HERALDIC BIRDS).

LLANO: an environment of savanna type characteristic of parts of tropical South America (see SAVANNA).

LOAFING: see ROOSTING.

LOBATE; LOBED: having the toes separately fringed by lobes, as distinct from webs connecting the toes (see LEG).

LOCAL ENHANCEMENT: see FACILITATION, SOCIAL.

LOCOMOTION, TERRESTRIAL: birds use three gaits, the walk and run in which the feet move alternately and the hop in which they move together. In walking, each foot is on the ground for more than half the stride so there are times when both are on the ground. In running, each foot is on the ground for less than half the stride so there are times when both are off the ground.

Gait and energy cost. Turkeys, ducks, rheas and probably many other birds use the gait known as the stiff walk, which is also used by man. In it, energy is saved by the principle of the pendulum. The potential energy of a pendulum increases and decreases as the bob rises and falls, and its kinetic energy increases and decreases as the bob accelerates and decelerates. Very little work is needed to keep the pendulum swinging because kinetic energy increases as potential energy decreases and vice versa: energy is shuttled back and forth between the two forms. In the stiff walk, the leg is kept rather stiff while the foot is on the ground so the bird's centre of mass rises as it goes from position (a) to position (b) (Fig. 1). At the same time the force exerted by the ground on the foot, acting along the leg, slows the bird down a little. Thus potential energy increases and kinetic energy decreases as the bird goes from (a) to (b). The reverse changes occur between (b) and (c). There is a maximum speed which depends on the length of the leg, above which it is impossible to make the potential energy changes compensate for the kinetic energy changes, and the stiff walk loses its advantage. The Wild Turkey *Meleagris gallopavo* uses the stiff walk at speeds below 1.5 m/s but runs to go faster.

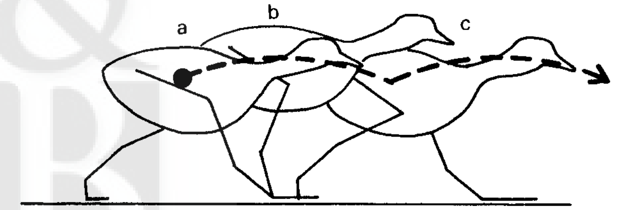


Fig. 1. Successive positions of a bird performing the stiff walk. The broken line represents the path of the centre of mass.

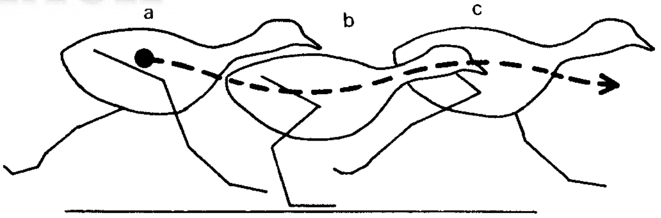


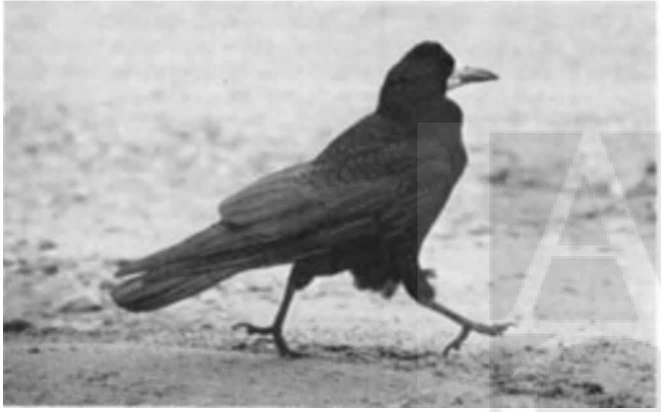
Fig. 2. Successive positions of a running bird. The broken line represents the path of the centre of mass.

In running, energy may be saved by the principle of the bouncing ball. The centre of mass is lowest when the bird is moving most slowly (Fig. 2b) so kinetic and potential energy have their lowest values at the same time. However, the force on the foot is largest at this time and tendons in the leg are stretched, storing elastic strain energy. Kinetic and potential energy are converted to elastic strain energy between (a) and (b), and restored by elastic recoil between (b) and (c). This mechanism is most effective at high speeds, when the feet are on the ground for only a small fraction of the stride and the forces on them are correspondingly large. Calculations based on films and dissections seem to show that tendon elasticity saves a lot of energy in the fast running of Ostriches *Struthio camelus*, but it is not certain that it is important in smaller birds. It may also save energy in hopping.

Most small passerines and some other birds hop. Most of those that do are small or arboreal in habits or both. Hopping seems a particularly

Sanderling *Calidris alba* in winter plumage, running. (*Photo: J.B. & S. Bottomley*).

Large Pied Wagtail *Motacilla maderaspatensis* walking. (*Photo: T. Shiota*).



Rook *Corvus frugilegus* walking. (*Photo: H.E. Grenfell*).

Lesser Yellowlegs *Tringa flavipes* wading. (*Photo: J.B. & S. Bottomley*).

useful gait in trees where supports for the feet are sparse (in comparison with solid ground) but where the feet can always be placed side-by-side on the branch. Some families (for instance, the Corvidae) include species which hop and others which walk or run. Some species (for instance the Blackbird and American Robin, both species of *Turdus*) sometimes hop and sometimes run. The Magpie *Pica pica* walks to travel slowly and hops to go faster, but its hop is a peculiar asymmetrical gait with the left and right feet out of phase. Vultures use a similar asymmetrical hop.

Birds have been trained to run on a conveyor belt, so that they remain stationary while the belt moves under them. This technique has made it possible to measure the rate at which they use oxygen as they run, and so to estimate their energy consumption. Ostriches use oxygen at about the same rate as ponies of the same weight, running at the same speed. Similarly roadrunners *Geococcyx* use oxygen at about the same rate as ground squirrels of similar weight at the same speed. However, birds whose style of walking looks clumsy (for instance, geese and penguins) use oxygen up to three times as fast as more graceful species of similar weight at the same speed. Ostriches seem to run a little faster than typical antelopes but most birds are slow runners, compared to mammals of similar size. Ostriches have a much larger proportion of leg muscle in the body than flying birds.

Measurements of oxygen consumption of kangaroos have shown that their hopping uses more energy than the running gaits of other mammals of similar size, except at high speeds. Measurements on smaller hopping mammals (for instance, kangaroo rats) show that they use oxygen about as fast as similar-sized running mammals, at all speeds. There is no evidence that hopping can give any energetic advantage, for any size of mammal, and no measurements seem to have been made on birds.

Penguins slide down slopes on their bellies and presumably save energy that way, but this technique of locomotion seems not to have been closely studied. The mechanics of wading have also been neglected by zoologists.

Balance. The hips of birds are far posterior to the centre of mass of the body, but standing and walking without overbalancing are only possible if the average position of the feet is directly below the centre of mass. Most birds stand and walk with the thighs nearly horizontal, so that the knees are alongside the centre of mass. They move their thighs only a little as they walk or run, and swing the legs mainly from the knees. Penguins and auks have thighs too short for this, and bring the centre of mass over the feet by standing with the trunk erect.

Head bobbing. A bobbing movement of the head is characteristic of the gaits of many birds, including pigeons. The head moves backwards and forwards relative to the body in every step. There is a stage in the step when the head is moving backwards relative to the body and is more or less stationary relative to the ground. It is believed that having the head even briefly stationary relative to the surroundings may make it easier for the bird to detect moving objects visually. In support of this idea, pigeons do not bob their heads when walking on a conveyor belt so as to be stationary relative to their surroundings. R.McN.A.

Alexander, R.McN. & Goldspink, G. (eds.). 1977. Mechanics and Energetics of Animal Locomotion. London.

Alexander, R.McN., Maloiy, G.M.O., Njau, R. & Jayes, A.S. 1979. Mechanics of running of the ostrich (*Struthio camelus*). J. Zool., Lond. 187: 169–178.

Cavagna, G.A., Heglund, N.C. & Taylor, C.R. 1977. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. Am. J. Physiol. 233: R243–R261.

Dagg, A.I. 1977. The walk of the Silver Gull (*Larus novaehollandiae*) and of other birds. J. Zool., Lond. 182: 529–540.

Fedak, M.A. & Seeherman, H.J. 1979. Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. Nature, Lond. 282: 713–6.

Frost, B.J. 1978. The optokinetic basis of head-bobbing in the pigeon. J. exp. Biol. 74: 187–195.

LOCUS: of a gene (plural 'loci')—see GENETICS.

LOCUST-BIRD: name applied in parts of Africa to various species of birds that congregate to feed on locust swarms, e.g. the Black-winged Pratincole *Glareola nordmanni* as an off-season visitor to South Africa.

LOGGERHEAD: name applied in the Falkland Islands to steamer ducks *Tachyeres* spp.; and in North America to the Loggerhead Shrike *Lanius ludovicianus*.

LOGRUNNER: substantive name of *Orthonyx* spp. (see RAIL-BABBLER).

LONGBILL: substantive name of the 2 New Guinea HONEYEATERS of the genus *Toxorhamphus*.

LONGCLAW: substantive name of *Macronyx* spp. (see under WAGTAIL).

LONGEVITY: see AGE.

LONGSPUR: substantive name, in North America, of *Calcarius* spp., including the Lapland Bunting *C. lapponicus* (see BUNTING).

LONGTAIL: substantive name of *Urolais epichlora*, and an alternative substantive name for prinias *Prinia* spp. (see WARBLER (1)).

LOOMERY: term which has been applied to breeding colonies of guillemots (*Uria*)—see AUK.

LOON: substantive name used in North America for all the species of Gaviidae (see DIVER).

LOOP MIGRATION: see MIGRATION.

LORE: the area between the base of the upper mandible and the eye, on each side (plural 'lores'; adjective 'loral')—see TOPOGRAPHY.

LORICULINAE: see PARROT.

LORIINAE: see PARROT.

LORIKEET: substantive name used sometimes for the smaller species of lories (Loriinae) (see PARROT).

LORY: substantive name of the species of the Loriinae; in the plural (lories), general term for the subfamily (see PARROT).

LOTUS-BIRD: name in Australia for *Irediparra gallinacea* (see JACANA).

LOURIE: alternative substantive name of some species of Musophagidae (see TURACO).

LOUSE-FLIES: see ECTOPARASITE.

LOVEBIRD: substantive name of the African *Agapornis* spp. (Psittacinae, Psittaculini); sometimes applied to the Budgerigar *Melopsittacus undulatus* (Psittacinae, Platycercini) (see PARROT).

LOWAN: name, alternatively 'Mallee Fowl', of *Leipoa ocellata* (see MEGAPODE).

LUMPER: a taxonomist who prefers a nomenclature that recognizes broad groupings, and hence emphasizes relationships—in contrast to a SPLITTER, who prefers a nomenclature that recognizes fine distinctions. Workers interested primarily in wider evolutionary problems tend to be lumpers, while specialists in narrower fields of research tend to be splitters; but this distinction should not be pushed too far.

LUNG: see RESPIRATORY SYSTEM.

LURE: instrument used in imitating bird-calls to attract birds of the particular species within range; also a form of bait used by falconers to recover their charges (see FALCONRY).

LUTEIN: a yellow, fat-soluble, carotenoid pigment ($C_{40}H_{56}O_2$) found in many plant and animal materials; for example, in yolk of eggs, fat cells, corpus luteum, and feathers.

LYMPHATIC SYSTEM: much of the fluid part of blood, with its protein, that escapes from the blood capillaries into the tissue spaces is retrieved by lymphatic capillaries, collected in lymphatic vessels and ultimately returned to the venous system. Thus the lymphatic vessels function in the maintenance of the fluid balance of the body. Throughout the body are accumulations of lymphoid tissue, the cells of which provide immunity to antigens such as microorganisms, toxins, foreign cells and tissues. Embryologically, lymphoid tissue and lymphatic vessels originate independently.

Lymphatic vessels. The lymphatic capillaries are blind endothelial tubules forming plexuses which drain into collecting vessels that are tributaries of the main transporting lymphatic vessels. Lymphatic vessels accompany blood vessels, usually veins. Generally the lymphatics are paired and flank their veins. Most of the lymph flow of the body converges on the 'venous angles' at the confluence of the jugular and subclavian veins where the major transporting trunks (thoracoabdominal, jugular, and subclavian) empty individually, their orifices guarded by valves.

Dual thoracoabdominal trunks (thoracic ducts) are tightly applied to each side of the descending aorta, and communicate extensively with one another. The jugular trunks, usually two on each side, descend the neck adherent to the jugular veins. Lymph is propelled by compression of the vessels brought about by muscle contraction and body movements, backflow prevented by the valves interspersed along the vessels. In most mature birds lymph hearts are absent. A pair of contractile hearts have been reported in some ratites, anseriforms, storks, and grebes, located in the pelvic region. In birds lymph vessels, especially cutaneous vessels, and their valves are more sparse than in mammals. Most of the lymph is produced by the alimentary canal and the liver.

Lymphoid tissue. Most of the lymphoid tissue is found in the wall of the alimentary canal, cloacal bursa, thymus, spleen as well as in numerous small nodules and foci scattered throughout many organs and tissues, including the lymphatic vessels themselves. The lymphoid tissue is in the form of solitary or aggregated nodules, consisting largely of lymphocytes and organized into diffuse masses with germinal centres.

Birds generally lack lymph nodes which function as filters of lymph. Avian lymph nodes somewhat resembling those of mammals are reported to occur in adults of some anseriforms, the Coot *Fulica atra* and the Herring Gull *Larus argentatus*. In these forms only 4 nodes are present: a pair of cervicothoracic nodes located on the jugular lymphatic trunks and a pair of lumbar nodes located on the thoracoabdominal trunks in the pelvic region. The avian node is a fusiform structure grafted on to the vessel with an irregular central sinus, a central zone of lymphoid tissue, and a peripheral meshwork of reticular fibres into which the sinus spaces open, allowing some filtration of the lymph. The main sinus space is central rather than peripheral as in mammalian nodes.

Accumulations of lymphoid tissue occur abundantly on the lymphatic vessels of all species examined so far. These are the mural lymphoid nodules which are embedded in one side of the vessel, protruding into the lumen. Nodules apparently have no filtration capacity.

Birds, especially the chicken, have been important research subjects in the elucidation of much basic information on adaptive immunity since it was discovered that the cloacal bursa possesses an immunological function. The bursa and the thymus are intimately connected with the development of immunity. In the early life of these organs are found the primary sources of immunologically competent cells which are seeded to other connective and epithelial tissues, where they form secondary centres of lymphoid tissue. The bursa and thymus programme the cells, which are sent elsewhere to proliferate and respond to antigens.

The *cloacal bursa* (of Fabricius) is unique to birds. A diverticulum of the proctodeal part of the cloaca, it rests on the dorsal wall of the cloaca. The bursa has a central space; its walls contain numerous lobules (follicles) of lymphoid tissue. The bursa begins to regress with onset of sexual maturity, diminishing in size and undergoing fibrosis. The bursa-dependent line of cells is represented morphologically by larger lymphocytes of the germinal centres and by plasma cells. These cells bear surface immunoglobulins which appear to function as antibody receptors for various antigens.

The *thymus* consists of a series of lobes stretched out along each jugular vein. Each lobe contains lobules of lymphoid tissue which also regress at onset of sexual maturity. The thymus-dependent line of cells is represented morphologically by the smaller lymphocytes of the circulation and the diffuse type of lymphoid tissue. These cells which carry no antibodies on their surfaces are concerned with the development of cellular immunity such as graft-versus-host, homograft, and delayed hypersensitivity reactions.

The *spleen* is a small, brownish-red organ located near the junction of proventriculus and gizzard. The spleen of birds has little or no function as a blood reservoir. It produces red blood cells only in foetal life and lymphocytes throughout adult life. As a lymphoid organ the spleen contains both thymus-dependent (diffuse) lymphocytes and bursa-dependent (germinal centres and plasma cells) lymphocytes in the white pulp and loose lymphocytes in the red pulp. The main functions of the adult spleen are destruction of red blood cells in the red pulp, production of lymphocytes in the white pulp, and uptake of antigens and antibody production by lymphocytes in both types of splenic pulp. J.J.B.

King, A.S. 1975. Aves. Lymphatic System. *In* Getty, R. (ed.). Sisson and Grossman's The Anatomy of the Domestic Animals. Vol. 2. 5th ed. Philadelphia.
Payne, L. N. 1971. The Lymphoid System. *In* Bell, D.J. & Freeman, B.M. (eds.). Physiology and Biochemistry of the Domestic Fowl. Vol. 2. London.

LYREBIRD: name applied to the 2 species of Menuridae (Passeriformes, suborder Oscines). The name stems from the supposed close resemblance of the male Superb Lyrebird's tail to a Greek lyre. Lyrebirds rank among the largest passerines and are renowned for their spectacular courtship display and vocal mimicry.

The origin, affinities and even the specific name of one of the species are controversial. On the basis of their simple syringeal musculature, the aberrant lyrebirds and their distant relatives the SCRUB-BIRDS, Atrichornithidae, have long been considered suboscine and grouped together in the suborder Menurae. Lyrebirds and scrub-birds have 3 pairs of intrinsic syringeal muscles whereas the suborder Oscines usually have 4. This suboscine classification has naturally led some authors (e.g. Cracraft 1973) to propose a southern, Gondwanaland origin for the Menurae, even though most of the extant Australian avifauna, except possibly the ratites, is probably of northern origin.

Recently, C.G. Sibley proposed on the basis of a review of anatomical and egg white protein comparisons that lyrebirds and scrub-birds are oscine and allied to the bird-of-paradise–bowerbird assemblage. He advocates dropping the suborder Menurae and placing lyrebirds and scrub-birds next to Ptilonorhynchidae in Passeres. He thus considers lyrebirds part of the 'corvine assemblage' and probably of Asian origin. While the morphology of the stapes (see SKULL) also supports the affinities with the oscines (Feduccia 1975), the alleged close relationship with bowerbirds and birds-of-paradise is not reflected in the appendicular myology (Raikow 1978). Nonetheless a more distant sister-group relationship with this assemblage remains possible.

Characteristics. Lyrebirds have weak powers of flight but run swiftly. Flying is limited to downhill gliding and short, clumsy flights of a few metres between tree branches. Despite this, they roost high in the forest canopy (especially males), ascending by jumping from branch to branch and gliding. They are very 'shy' and difficult to approach and observe.

The Superb Lyrebird *Menura novaehollandiae* is mainly dark brown dorsally and grey-brown ventrally. The Albert Lyrebird *Menura alberti* is more rufous-brown above and has rufous rather than grey undertail coverts. Both species have long legs and large feet equipped with big claws, and are sexually dimorphic in size and tail plumage. Male Superb Lyrebirds (80–90 cm long) have highly modified rectrices comprising 2 outer lyrates, 2 medians and 12 filamentaries. The lyrates are 's'-shaped with one vane greatly reduced; their upper surfaces are dark brown edged with black, their under surfaces white (except in the race *edwardi*). The broad vane has a black tip and many transparent notches edged with rufous on the underside. The medians have very narrow vanes, while the filamentaries, black above and white below, have widely spaced distal barbs which lack barbules. The smaller female has unspecialized rectrices, except for the outermost 2 which have transparent notches like male lyrates. Male Albert Lyrebirds also have unspecialized lyrates but their tails are otherwise like those of male Superb Lyrebirds.

Superb Lyrebird *Menura novaehollandiae*. (*N.W.C.*).

Distribution and habitat. Lyrebirds are endemic to Australia and restricted to the mountains and foothills of the south-eastern seaboard. The Superb Lyrebird ranges from southern Victoria to south-eastern Queensland, inhabiting mainly wet sclerophyll eucalypt forest and temperate rainforest dominated by beeches *Nothofagus*. However, it also occurs in sub-tropical rainforest and the *edwardi* race is restricted to drier, open forest in the granite country of southern Queensland. The Albert Lyrebird has a much more restricted range, occurring only in subtropical rainforests in a narrow belt in north-eastern New South Wales and southern Queensland. In 1934 the Superb Lyrebird was introduced to Tasmania where it now has a restricted range in wet sclerophyll and temperate rainforest.

Food. Lyrebirds eat mainly soil-dwelling invertebrates which they expose by digging with powerful feet capable of removing large obstructions such as stones and roots with comparative ease. In southern Victoria, Superb Lyrebirds typically catch about 13–17 prey per minute of foraging and dig to a maximum depth of approximately 12 cm. Invertebrates living in fallen, rotting logs are also secured by ripping away the covering bark and outer layers with the claws. The adult diet has not been quantitatively documented, but widely overlaps that of the nestling whose principal foods are earthworms, amphipods, spiders, millipedes, centipedes, isopods and fly and beetle larvae. Superb Lyrebirds regularly drink from streams and surface pools.

Behaviour and mating system. Both lyrebird species probably exhibit sexual bimaturism (deferred male maturity). Male Superb Lyrebirds gradually acquire adult-type rectrices from age 2–5, 6 or 7 years. They frequently associate in pairs or trios characterized by much mutual aggression and display during their early development. Shortly before or when the full adult tail has developed, they become territorial and begin to show courtship behaviour; females are thought to commence breeding at a much earlier age. Adult males occupy marginally overlapping territories averaging 2.5–3.5 ha throughout the year and defend them by displaying, chasing and singing. In southern Victoria, males are fairly evenly dispersed throughout suitable habitat. However, they often have a preferred singing area within the territory, and since those of some neighbours are commonly adjacent across a shared boundary, temporary clustering sometimes occurs during display and countersinging.

Lyrebirds exhibit arena behaviour. Male Superb Lyrebirds clear and maintain many earth mounds 1–1.5 m in diameter on their territories and spend up to 50% of daylight singing and displaying on them, as well as on the ground, on fallen trunks and in trees, during the mating season. Male Albert Lyrebirds display on well-concealed platforms of criss-crossing vines and/or fallen branches on scratched ground (Curtis 1972). Copulation is probably largely restricted to the mounds and platforms.

Male Superb Lyrebirds are polygamous, probably promiscuous, and take no part in caring for the young (see POLYGAMY). In southern Victoria, 2–3 female breeding territories lie within or partially overlap each male territory and some females visit more than one displaying male immediately prior to laying. Heterosexual association between adults is limited and typically brief (Lill 1979a), so that pair-bonding seems to be absent. However, some hens have been recorded copulating with the same male in successive seasons (see Reilly 1970 and Kenyon 1972 for other interpretations of the parental care and mating systems).

Voice. The territorial song of the Superb Lyrebird contains a loud, species-typical component lasting about 5–6 s, audible from 1 km under minimal wind conditions and exhibiting marked local dialects. But up to 80% of territorial song is composed of extended bouts of mimicry of the vocalizations of a wide range of co-habiting bird species (see MIMICRY, VOCAL). There is some evidence that these are learned in part from conspecifics rather than the models themselves. The mimicked sounds include the antiphonal duetting of whipbirds *Psophodes*, kookaburras *Dacelo* and magpies *Gymnorhina* and the wing-beats and calls of flying flocks of *Rosella* parrots. A quieter type of singing occurs during close pursuit and courtship of hens away from the mounds. This often contains mimicked bird calls rarely heard in territorial song, as well as mimicry of dogs barking and, reputedly, occasionally sounds made by inanimate objects. Females can produce full territorial song including mimicry but do so infrequently. Superb Lyrebirds also give 3 distinct species-typical calls during courtship display and emit loud whistles when alarmed. The Albert Lyrebird also has a loud territorial song and a softer courtship song, but its mimicry is restricted largely to only 4 or 5 avian models (Smith 1976).

Display. In full courtship display, the singing male Superb Lyrebird holds the rectrices horizontally over the back so that they form a fan spread over and in front of the bird. The white undersurfaces of the lyrates and filamentaries are thus strikingly exposed. When a female visits the mound, however, the rectrices are held forward but close together and rapidly quivered. Courtship climaxes in rapid circling and jumping displays. Away from the mounds and main display area, courtship involves quiet song, wing-lowering and tail-shaking. The display of the male Albert Lyrebird has been less well described but is broadly similar.

Breeding. Both species commence breeding in winter. The nest of the Superb Lyrebird is a large chamber with a side entrance and averages 14 kg. The base and sides are built of sticks, the interstices being packed with moss and bark strips. The chamber is lined and roofed with fine rootlets and sometimes a little green vegetation is placed on the roof. Immediately before laying, some body feathers are added to the chamber floor. Nests are constructed from ground level to 22 m, the preferred range being up to 2 m. The principal nest sites are on earth banks and rock faces, in trees and grass and sedge clumps, and on boulders. Nestbuilding is usually protracted over several months (Reilly 1970, Lill 1980).

The clutch-size is one and re-laying is uncommon. The egg is grey with dark brown markings and averages 62 g when fresh. The full incubation rhythm takes up to 18 days to develop and even then daytime attentiveness averages only 45%. Throughout incubation the egg is continuously deserted for 3–6 hours each morning, during which time embryonic temperature falls to and remains at the prevailing ambient level of less than 10°C and development is presumably interrupted. Consequently the incubation period is unusually long, averaging 50 days (Lill 1979b).

The newly-hatched chick with its incomplete dorsal cover of black down is brooded for a gradually diminishing percentage of daylight hours until it is effectively homeothermic at about 10 days old. However, it also chills appreciably during maternal absences in the first few days after hatching. In the post-brooding stage, the nestling is fed about 3 times per hour, the mother storing collected food in a gular sac. During the 47-day nestling period the chick's weight increases roughly 12-fold to an average fledging weight which is 63% of adult female body weight. Available nesting success estimates vary widely from 11–20% to 65–79% and introduced mammals and native birds have been implicated as the major nest predators (Lill 1980). Fledglings leave the nest in October and November and accompany and are partly fed by the mother for up to 8 months. Although the breeding biology of the Albert Lyrebird is less well known, the main features are similar.

Lyrebirds were slaughtered in great numbers in the 19th century for their tail plumage. Nowadays both species have protected status and are quite common in suitable habitat. The impact of introduced predators on recruitment is difficult to assess; probably the main threat to lyrebirds' survival is continuing large-scale clearance of wet forests for commercial purposes. A.L.

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M

MACAW: substantive name of the Neotropical *Ara* spp. and *Anodorhynchus* spp. (Psittacinae, Arini). (see PARROT).

MACHAERAMPHINAE: see HAWK.

MACHAIR: florally rich turf on leeward side of dunes on north-west Scottish coast and especially in the Hebridean islands.

MACROCHIRES: name formerly used for the order APODIFORMES; SWIFT.

MACROSMATIC: having a highly developed olfactory sense (see SMELL).

MADAGASCAR: see MALAGASY REGION.

MAGELLANIC PLOVER: *Pluvianellus socialis*, sole member of the Pluvianellidae (Charadriiformes, suborder Charadrii).

Characteristics. The superficially dove-like Magellanic Plover is a small grey wader, *c.* 20 cm long, with a white belly. It has a short straight bill, stout legs and feet, and a bright coral red iris. Though formerly classified with the plovers (Charadriidae), its closest relatives are the sheathbills (Chionididae).

Habitat and distribution. It breeds along gravel shores of small fresh-water ponds in Patagonia and northern Tierra del Fuego, and winters in sheltered bays and estuaries on the coast of Argentina north to Chubut Province. During the breeding season it is sparsely distributed and the entire population may not exceed several hundred individuals.

Food. Magellanic Plovers feed exclusively on invertebrates which they obtain by walking slowly along the shore or upper beach and pecking at the surface. In a unique behaviour, they also stand in one spot and spin, phalarope-like, using their feet to excavate shallow holes in areas of rotting vegetation where fly larvae are common.

Breeding. During the breeding season, they are invariably found in pairs, whereas in winter they form small flocks and often associate with Two-banded Plovers (*Charadrius falklandicus*) and other waders. Although at least 10 distinct vocalizations have been documented, the birds are quiet and inconspicuous at all seasons.

Nesting begins in September. Linear territories are established along the lake shore and are defended in a complicated display involving both members of the pair. The clutch consists of 2 relatively small unspotted eggs, laid in a nest-scrape lined with a few pebbles and incubated by both parents. Apparently only one chick is raised. Both parents feed the chick by regurgitation. The chick grows slowly and makes its first flight at 28 days of age. It remains with the parents, and is still being fed by them, at least until day 40.

See photo INCUBATION. J.R.J.Jr.

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MAGNETIC SENSE: see NAVIGATION.

MAGPIE (1): substantive name of the two species in several genera of Corvidae; used without qualification, in Britain, for *Pica pica* (the 'Black-billed Magpie' of North America)—see CROW (1).

MAGPIE (2): substantive name of the two *Gymnorhina* spp. in the family Cracticidae (Passeriformes, suborder Oscines).

Characteristics. These similar crow-like birds of upright stance, about 25 cm high, have boldly pied plumage, with black underparts, wings (with white flashes) and head; the tail is white with a terminal black band. In the Black-backed Magpie *Gymnorhina tibicen* the back is black and the male has a white nape and rump, which are variably greyish in the slightly smaller female. The males of the White-backed *G. t. hypoleuca* and Western *G. t. dorsalis* are pure white-backed and the females are mottled grey-backed, darker in *dorsalis*. In first-year birds the pied effect is reduced by grey or buff fringes to all the feathers; this varies in degree so that some individuals are much lighter and others darker than average. Most second-year plumages resemble the adult, but some lighter individuals are difficult to distinguish from darker one-year-olds. The bill of first-year birds is dark and the pale bluish base develops in the second year until only a dark tip remains in the fully adult bird. The Western Magpie is longer-billed than the others.

Habitat. The preferred habitat is open savanna woodland, with pasture for feeding and trees for nesting, roosting and shelter. Australian magpies are most abundant, and prominent visually and vocally, in settled areas, rural and urban.

Distribution. The Black-backed Magpie occurs throughout New South Wales (except the southern border) and Queensland, becoming sparse across the north into Western Australia and southern New Guinea. The White-backed Magpie covers Tasmania, South Australia into the centre of the continent, Victoria and across its northern border into New South Wales, with further penetration and increasing scarcity northward along the Great Dividing Range and Pacific coast, finally petering out in south-eastern Queensland. Black-backed and White-backed forms interbreed, producing plumage intergrades which breed successfully. The White-backed Magpie is well established by introduction to both islands of New Zealand, where variable dark-backed birds also occur. The Western Magpie is confined to the south of Western Australia.

Food. Magpies are versatile ground feeders, taking mainly beetles and other insects, earthworms, ants and spiders, and a few frogs and lizards; they hawk for adult scarabs and grasshoppers in season, and survive on grain during frost and drought.

Voice and behaviour. The loud melodious carolling throughout the year, with social groups calling in antiphonal chorus between neighbouring territories, especially at dawn, is one of the most popular Australian bird sounds. The birds often become quite tame, and the adult male can be embarrassingly aggressive to humans near the nest. By contrast, in the outback they are shy and distant.

The habitat is divided into permanent territories of about 8 ha strongly held all year by small social groups of Black-backed and White-backed Magpies; larger groups of Western Magpies hold larger areas. In the first two, non-territorial and therefore non-breeding birds form loose flocks, which feed in open treeless pasture by day and roost in denser woodland up to several km distant; in Western Magpies, all birds are in territorial groups. Top-quality habitat contains all requirements for survival and breeding within each territory, often in excess of needs; it is held most strongly and permanently, and birds so ensconced never leave their territory so long as the group remains intact to defend it. At all seasons there is intense competition by groups and individuals to improve their habitat and social status; groups pre-formed in the flock continually seek entry to breeding habitat, and familiarity with the voices of neighbouring birds enables vacancies to be exploited at once. In dry country, where food may be less abundant or seasonally unreliable, territories are enormous.

Breeding. In treeless country, magpies nest on telegraph poles, low bushes, and even the ground. The nest of twigs lined with grass or wool contains 3–5 mottled eggs during July to October, and is usually obvious in the outer canopy of a gum tree. The hen does all the building and incubation, and often alone rears the nestlings for 4 weeks, while their plaintive insistent food-begging calls can be heard for another 2 months or more. The males police the territory, and the females assist to repel invaders of their own sex. Polygamy is common, and a sex hierarchy of dominance within the group leads to subordinate hens breeding later or not at all. In exceptional cases, where older hens are unusually tolerant or the younger ones can escape their attention, one-year-old females have bred, but most are 2 or 3 years old at first breeding. They are single-brooded and productivity is low; only 1 young for every 2 adult hens in permanent territories survives to independence, and none at all in poorer territories. A detailed large-scale study of individually-marked Black-backed Magpies during 1955–1966 (Carrick 1972) showed that social groups of 2–10 birds consisted mainly of monogamous and bigamous adults plus immatures, but all ratios up to 3 adults of each sex occurred. Territory boundaries and size remain fairly constant despite wide fluctuations in the number of occupants. Individual advancement takes precedence over group loyalty. Birds established in good territories are long-lived, and the main mortality occurs in the slightly nomadic flocks. Australian magpies are aggressive capitalists, and very sedentary birds indeed; even non-breeding individuals move only a few km throughout life. R.C. (1)

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MAGPIE-LARK: substantive name of *Grallina cyanoleuca*, one of the 2 species in the family Grallinidae (Passeriformes, suborder Oscines), the other being the Torrentlark *G. bruijni* of New Guinea (see Schodde 1975 and CHOUGH (2)). Alternative English names for the group are 'mudlark' and 'mud nest-builders'.

Characteristics. The Australian Magpie-lark, 26–30 cm long, is a medium-sized boldly pied bird, showing conspicuous sexual dimorphism in head and throat patterning. The relatively long legs are black, the beak and iris creamy white. The male's crown and throat are black, with white eyebrow and cheek patches. The female's crown and breast are black, but a black vertical stripe runs through the eye and joins them; forehead, throat and sides of the head are white. Juveniles have the black forehead and white eyebrow of the male and the white throat and chin of the female. They moult into adult plumage after about 3 months.

Distribution and habitat. Widespread throughout mainland Australia, but rare in Tasmania. It prefers open areas such as water margins, open woodland and cleared paddocks and rarely penetrates closed forest or dense scrub. Agricultural development, with the provision of water in dams and bores, has led to considerable extension of the bird's original range. Its wide distribution, conspicuousness and the readiness with which it has adapted to city suburbs have made it among the best known Australian birds.

Food. Magpie-larks are ground-feeders, their varied diet consisting mainly of insects, but also spiders, pond snails, small frogs and seeds.

Behaviour. Adult Magpie-larks live in monogamous pairs in all-purpose territories of 4–8 ha. Both partners actively defend the territory and share nesting duties. The pair-bond and territory probably endure for the lifespan of the birds. Aggression is mostly confined to encounters between birds of the same sex, and is most intense against single intruders. This suggests that year-round territoriality not only protects resources but, with the persistent pair-bond, has adaptive advantage for a species so dependent on rainfall for opportunistic breeding.

Unlike the adults, young birds are relatively wide-ranging. After leaving the parental territory at about 3 months old, they join local flocks of their peers, moult into adult plumage, develop song and eventually form pairs. These leave the flock, which may number from 50–3,000 individuals, at the start of the next breeding season, and set up their own territories. Ringing studies have shown that adults are sedentary and that flocks are mainly composed of first-year birds.

Voice. Magpie-larks communicate through a large and varied repertoire of strident calls, often accompanied by striking displays. These are used for communicating with the mate, while a few universal calls are reserved for contact with the young, with rivals or to warn of predators. The most interesting feature of the vocal behaviour is antiphonal singing in exact alternation. This helps to keep the partners together and the territory intact.

Breeding. The local distribution of the Magpie-lark is related to the availability of fresh surface water, since breeding depends on a source of mud for nest-building. A typical bowl-shaped mud nest was 15 cm across, 9 cm deep, with walls 2 cm thick and weighed 950 g (Serventy and Whittell 1967). Nests are built far out on bare horizontal branches often over water. Wads of grass are collected with the mud to strengthen the construction and the finished nest is lined with dry grass, feathers or wool. Clutch-size ranges from 1–4, commonly 3 eggs, white with violet or purplish brown blotches. Breeding takes place during the wet season (summer in the north, winter in the south and at variable times inland) and its success seems to depend upon an adequate spell of favourable rainfall conditions. Breeding may be stopped or interrupted in dry or unusually wet years, but birds will rear 2, or rarely 3, broods if the wet season is consistent and long-lasting. Also, rainfall outside the normal nesting season can stimulate successful breeding (Serventy and Marshall 1957). Both parents incubate and tend the young, which are downy when hatched and fledge in *c.* 20 days.

Magpie-lark *Grallina cyanoleuca*, juvenile (top), adult female and male (bottom). (*N.W.C.*).

Torrentlark. The Torrentlark has a pied plumage like the Magpie-lark and also shows marked sexual dimorphism. The legs are blackish, the iris dark brown and the bill greyish white. The male has a black face, chin, throat and upper abdomen, with a white superciliary stripe. The female is distinguished by her white forehead and breast and a more pronounced eyebrow. The Torrentlark is restricted to montane habitats where it feeds on insects along fast-flowing streams. The cup-shaped nest is made of mud and rootlets. Little is known of the species' biology and behaviour. (A.K.) S.T.

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MAGPIE-ROBIN: substantive name of *Copsychus* spp. (see THRUSH).

MAINTENANCE ACTIVITY: see COMFORT BEHAVIOUR.

MAJOR MITCHELL: the Australian cockatoo *Cacatua leadbeateri*, formerly known as Leadbeater's Cockatoo (see PARROT).

MALACONOTINAE: see SHRIKE.

MALAGASH: alternative name of the Cape Gannet *Sula capensis* (see GANNET).

MALAGASY REGION: the faunal region formed by Madagascar (adjective Malagasy) and outlying islands, east to the Mascarenes, north to the granitic Seychelles. Although Madagascar, the putative main source of the avifauna of the outlying islands, is separated from Africa at the nearest point by only some 400 km, its fauna is so unique that it is now widely accepted as distinct from the AFROTROPICAL REGION. Madagascar was probably separated from Africa in the late Cretaceous. If the fossil remains found in Africa are correctly attributed to the Aepyornithidae, which is questionable (see ELEPHANT-BIRD; FOSSIL BIRDS), it would follow that their dispersal to Madagascar pre-dated this separation. Most of the remainder of the avifauna may have arrived later by flying and, as might be expected, has an African origin. Nevertheless, there is a distinct Asian element, including 3 genera unknown in Africa, viz. *Ninox*, *Hypsipetes* (=*Ixos*) and *Copsychus*.

Apart from the Aepyornithidae, which may have survived until 400 years ago, there are 3 families endemic to Madagascar, the Mesitornithidae (3 species in 2 genera), Brachypteraciidae (5 species in 3 genera) and the suboscine Philepittidae (4 species in 2 genera): see MESITE, GROUND-ROLLER and ASITY. The Leptosomatidae (1 species) are only otherwise known from the Comoros: see CUCKOO-ROLLER. The Vangidae (14 species in 11 genera, including the Coral-billed Nuthatch *Hypositta corallirostris*, formerly placed in its own family, the Hyposittidae) are only represented outside Madagascar by one of these species in the Comoros: see VANGA. Of the *c.* 180 breeding land birds (including 2 only discovered since 1970), 67% are endemic, even 94% in the passerines. Specific differentiation is so marked that the genera average less than 1.3 species each (in passerines as low as 1.1 as against 3.5 for the Afrotropical Region). Nevertheless, there is striking evidence of evolutionary radiation in the Vangidae and in the endemic genus *Coua* (see CUCKOO), with 10 species.

Ecological diversity is strongly marked. Eastern Madagascar is very wet (rainfall per annum up to 350 cm in the north-east); the original vegetation dense evergreen forest, much of it cleared for cultivation, but perhaps 3,000 km^2 still standing. A spine of highlands runs down the middle, mostly at 1,600 m, but rising in places to *c.* 3,000 m. This area, where habitat destruction has been worst, has largely degenerated into eroded grassland. The much drier west consists of more or less wooded savannas, with subdesert scrub in the south-west (rainfall less than 50 cm per annum). While some species range practically throughout (but often showing well-marked subspecific differentiation), others are very restricted. Thus, of the 10 *Coua* spp., 4 are only known from evergreen forest, one from subdesert scrub.

A figure of 180 breeding land birds is small in comparison to the Afrotropical Region. The comparable figure for Zambia exceeds 600. The water birds make up 30%, as against 16% Afrotropical (some not even subspecifically distinguishable between the two regions, but 1 in 3 in the former is endemic). Yet the Malagasy passerines account for 34% only, as against 48%. They are deficient in fruit eaters—only 1 starling (Sturnidae) and 1 bulbul (Pycnonotidae, but 6 others possibly wholly insectivorous)—and in seed-eaters, 1 lark (Alaudidae), 4 weavers (Ploceidae) and 1 mannikin (Estrildidae).

According to Cheke (1985), the volcanic Mascarenes developed a highly endemic and bizarre avifauna in the absence of any native mammalian ground predators. The Dodo and solitaires (see DODO), and the large rails *Aphanapteryx* spp. were flightless. There were also several endemic genera of parrots and starlings, and endemic species of ducks, raptors, pigeons, owls, swifts, and at least 8 families of passerines. The introduction of rats, monkeys, pigs, cats and other animals by man took their toll of the flightless birds soon after the islands were discovered and settled (16th and 17th centuries), and hunting followed by extensive habitat destruction has left only 16 survivors from the 40–45 known endemic species. The affinities of the Mascarene avifauna are with Madagascar and Asia, a pattern also shown by the native bats and reptiles.

The 4 Comoro Islands, also volcanic (Grand Comoro, still active, rising to 2,560 m), have an avifauna predominantly Malagasy, but with some Afrotropical transitional elements. The number of species of land birds (excluding water birds, few in number) is *c.* 30 per island. Endemism is considerable (1 genus, *c.* 8 species). North-eastward, towards the granitic Seychelles, there are many low-lying islets, some important for breeding sea birds, but few with more than 2 species of land bird. By far the largest and least disturbed is the elevated limestone atoll of Aldabra, rising 10 m above sea level, and 36 km long. The number of species of land (excluding water) birds attains the relatively high figure of 12, including 2 endemics, while even among the 7 water birds there are 2 endemic subspecies (6 among the land birds), one of the 2 being a flightless form of rail. The Aldabra avifauna is predominantly Malagasy-derived.

The Seychelles, possibly a continental relic, are nevertheless oceanic from the ornithological aspect. At the height of a glacial epoch *c.* 18,000 years ago, with sea levels *c.* 150 m lower than now, they would have formed a single land mass. There were at least 14 species of land bird, and 4 water birds (3 herons, Moorhen *Gallinula chloropus*) still breed. Endemic, very well marked, subspecies of parakeet *Psittacula eupatria* and white-eye *Zosterops mayottensis* apparently became extinct in the 1890s. Several of the 12 surviving land birds, under special protection, are on the upgrade from near extinction. There is no endemic genus, but 7 endemic species. As to be expected, the Asian element is more pronounced than in Madagascar and the Comoros. C.W.B.

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MALAR: pertaining to the area on the side of the throat immediately below the base of the lower mandible (see TOPOGRAPHY).

MALEO: Dutch name (sometimes used as English) in Indonesia for *Megacephalon maleo* (see MEGAPODE).

MALIA: *Malia grata*, an endemic BABBLER of Celebes (Sulawezi).

MALIMBE: sometimes used as substantive name of certain *Malimbus* spp. (see WEAVER).

MALKOHA: substantive name of *Rhopodytes* spp. (see CUCKOO).

MALLARD: *Anas platyrhynchos*, the common 'wild duck', but originally applied only to the male (a usage now obsolete)—see DUCK.

MALLEE: an environment, consisting of *Eucalyptus* scrub, characteristic of Australia.

MALLEE FOWL: name, alternatively 'Lowan', of *Leipoa ocellata* (see MEGAPODE).

MALPIGHIAN BODY: see EXCRETORY SYSTEM.

MALPIGHIAN LAYER: the basal layer of the epidermis (see SKIN).

MALURIDAE: family of PASSERIFORMES, suborder Oscines; WREN (2).

MAMMALS, ASSOCIATION WITH: occurs as a regular habit of various avian species, chiefly in relation to the quest for food (see FEEDING HABITS). The most frequent role of mammals, wild or domesticated, is that of a beater, disturbing insects or other prey for birds, as they move through the herbage or foliage. Cattle Egrets *Bubulcus ibis* find food more rapidly when they are associated with mammals than when they hunt alone. Similar associations are shown by such familiar birds as the Starling *Sturnus vulgaris* associating with cattle in Europe, or by the Piapiac *Philostomus afer* with domestic stock and wild grazing mammals in tropical Africa; its habit of perching on the Elephant *Loxodonta africana* is well known, and most remarkable, because elephants do not tolerate the attentions of oxpeckers *Buphagus* spp. Examples of such associations between birds and mammals of many species, in various parts of the world, are too numerous to cite at length.

Often, the attendant bird will perch on the mammal. Aquatic and wading birds of many species habitually perch on the backs of an almost submerged Hippopotamus *Hippopotamus amphibius*: cormorants (*Phalacrocorax* sp.) are characteristic in this role. Sometimes the animal provides the bird with a vantage point for fishing, as in the case of

Great Tit *Parus major* attacking field mouse *Apodemus*. (*Photo: M.S. Wood*).

White Wagtail *Motacilla alba* and pig. (*Photo: F. Pölking*).

Hamerkop *Scopus umbretta* on the lookout for frogs; in other instances, it may be no more than a convenient resting place.

Sometimes birds find some part of their food on the beast itself, as the Common Sandpiper *Actitis hypoleucos* on the hippo's hide. The 2 oxpeckers have a closer, rather symbiotic, relation with the mammals that they frequent, feeding upon the ticks in the hide (see OXPECKER). Another special case is the strange association on the part of HONEYGUIDES (Indicatoridae) with Ratels *Mellivora capensis* and man.

In tropical forests, association of mixed bird parties with squirrels is frequent, sometimes to mob a snake or an owl, more often to catch the insects which the mammal flushes out of the foliage. The same type of association exists with duikers *Cephalophus* and various rodents. The most remarkable case is the constant association of the Hornbill *Tropicranus albocristatus* with *Cercopithecus* monkeys in tropical Africa. *Tropicranus* apparently possesses anatomical and behavioural adaptations which have evolved in connection with its constant association with monkeys.

Nesting associations with mammals are rare. The only perfect case seems to be that the Miner *Geositta cunicularia* of South America, which nests only in the burrow of the Vizcacha *Lagostromus trichodactylus*.

All associations between birds and mammals are initiated by the birds, and are for their own benefit. Nevertheless, in some cases, the presence of the birds obviously favours the security of the mammals; for example, at the approach of a potential enemy, the roving troop of *Cercopithecus* is alerted by a special call of *Tropicranus*, which is followed by modification in the behaviour of the monkeys.

For associations with mankind, see also TAMENESS. A.B.

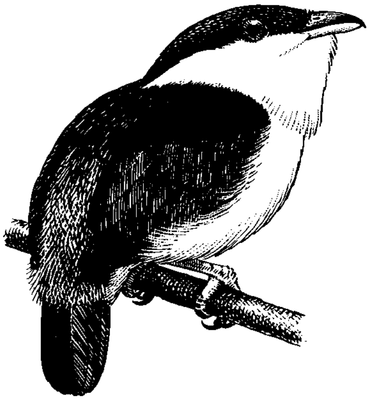
MAMMAL SIMULATION: also 'rodent run' (see DISTRACTION BEHAVIOUR).

MANAKIN: substantive name of species of Pipridae (Passeriformes, infraorder Tyranni)—not to be confused with MANNIKIN; in the plural, general term for the family. This Neotropical group of some 50 species is allied to the cotingas (Cotingidae) and, less closely, to the tyrant-flycatchers (Tyrannidae).

Characteristics. Manakins are small, stocky birds the size of tits (Paridae) 9–15 cm long, usually with short wings and tail, and with short bills rather broad at the base and slightly hooked at the tip. In most species the sexes are strikingly different, the males being predominantly black with patches of brilliant red, orange, blue and other colours, and the females greenish. In several species the males have some of the flight feathers modified for making mechanical sounds. In one species, the Wire-tailed Manakin *Pipra filicauda*, the tail feathers are prolonged into curved wire-like structures. In a few species, supposed to be primitive, the sexes are alike and mainly green or brown. It is, however, doubtful whether some of these, for example the Thrush-like Manakin *Schiffornis turdinus*, are really closely related to the typical manakins.

Habitat and distribution. Manakins are distributed throughout the lowland forests of South and Central America; few of them extend up into subtropical montane forests. Most are birds of primary forest, but some species are regular in secondary growth. They feed mainly on small fruits which they pluck on the wing; insects are also taken in small quantities by the adults, and form a major part of the food of the young. As far as known, all species are sedentary.

Behaviour. Manakins are especially notable for their elaborate courtship behaviour, which appears to have evolved under conditions of intense sexual selection. They are polygynous, the males taking no part in attending the nest. In the White-bearded Manakin *Manacus manacus* (a member of a widely distributed assemblage of forms, including Gould's Manakin which is sometimes treated as a separate species, *M. vitellinus*), the males display in LEKS. Each clears for itself a small 'court' on the floor of the forest, taking away all leaves and twigs that are small enough to be carried, and dropping them a few metres away. Each court contains a vertical sapling that serves as the main display perch, and one or more other saplings. On and around his court the male executes astonishing jumps and evolutions of a highly stereotyped nature. Various loud snapping and whirring noises are made with the wing feathers, the secondaries having much thickened shafts and a special musculature, while the outer primaries are thin, stiff and curved. The females visit the males at their courts and take part in a joint dance with them. Mating in



White-bearded Manakin *Manacus manacus*. (*R.G.*).

this genus, as in the other species studied, takes place on the main display perch.

Several *Pipra* species that have been studied display on horizontal perches between about 2 and 15 m up in trees or saplings, below the main forest canopy. Their displays consist of various elements: a swift flight to the perch from a distance, often accompanied by vocal or mechanical sounds; 'sliding' movements along the perch (in fact, very short and rapid steps); raising of the wings and spreading of the tail; rapid about-turns on the perch; and quick to-and-fro flights between the main perch and an adjacent perch, accompanied by mechanical wing-noises. Some *Pipra* species, e.g., the Golden-headed Manakin *P. erythrocephala*, display in typical leks, while in others the males are dispersed more widely, within sound but not in sight of one another. In a group of 3 closely related species that includes the Wire-tailed Manakin, the owner of a display perch is regularly joined by a visiting, or subordinate, male, and the two perform beautifully coordinated joint displays. The Wire-tailed Manakin has a unique display that makes use of its modified tail: the male faces away from his display partner, elevates his tail, and with a rapid twisting movement of his body brushes the other bird's throat with the wire-like tips of his tail-feathers. This display is little used in the joint displays of males (mentioned above), but is the main element of the male's display to a female.

The displays of several species are remarkable, but little known. In 2 species of *Machaeropterus* the male hangs head downwards on a vertical perch and rapidly turns the body from side to side while making a grasshopper-like reeling sound. It is noteworthy that, in *Machaeropterus* and some other species, observers have found it extremely difficult to determine whether certain sounds accompanying the displays are vocal or mechanical in origin. In *Corapipo gutturalis* the male is described as crouching on the ground and, with wings fully spread, moving towards the female in a laboured undulating crawl, an action strikingly like that described for the bowerbird *Archboldia sanfordi* (see BOWERBIRD).

The 4 species of *Chiroxiphia* have perhaps the most remarkable behaviour in that 2, or in *C. caudata* 3, males take equal parts in various joint displays that serve to attract and stimulate the female, after which one male only (apparently always the dominant male of the group) takes part in the final phase of courtship and copulation. The most striking of the joint displays is a 'catherine wheel' dance. When a female comes to the display perch the males face her; the front bird then jumps up and, hovering, moves backwards through the air while the other (in *C. caudata*, the next) bird hops up into his place and in his turn jumps as the first bird lands. The dance is accompanied by a rhythmic twanging, consisting of alternating calls uttered by each bird as it hovers.

Breeding. Except for *Schiffornis*, which builds a bulky cup nest composed chiefly of leaves (and may not be at all closely related to the typical manakins), all manakins whose nests are known build thinly woven cup nests slung in a horizontal fork of a tree branch, sapling or fern, at heights ranging from less than a metre to as much as 15 m above the ground. The clutch normally consists of 2 eggs. The eggs are pale grey, brown or beige in ground colour, mottled and spotted with darker brown. Recorded incubation periods are mostly 17–19 days, and fledging periods 13–15 days. The female alone builds, incubates, and cares for the young. D.W.S. (1)

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MANDARIN: substantive name, often used instead of Mandarin Duck, of *Aix galericulata*, a highly ornamental Chinese duck now naturalized in Britain (see DUCK).

MANDIBLE: term sometimes used without qualification for the lower jaw (compounded of several bones—see SKULL) and its horny covering (see BILL), and in this sense contrasted with 'maxilla'; in another usage applied to either jaw, with the adjective 'upper' or 'lower' (see also MAXILLA; MUSCULATURE).

MANGO: substantive name of *Anthracothorax* spp. (for family see HUMMINGBIRD).

MANGROVE SWAMP: a specialized type of environment widely distributed in tropical parts of the world and bordering areas of the sea, tidal rivers, or saline marshes; it consists of mangrove trees (several species) growing closely together out of water and liquid mud, presenting a most formidable obstacle to human ingress.

MANNIKIN: substantive name of various *Lonchura* spp.; in the plural, general term for a tribe (Amadini) of the Estrildidae (see ESTRILDID FINCH). Not to be confused with MANAKIN.

MAN O' WAR BIRD: sailors' name for *Fregata* spp. (see FRIGATE-BIRD).

MANTLE: see TOPOGRAPHY.

MANUBRIUM: forward process of the sternum (see SKELETON, POST-CRANIAL).

MANUCODE: substantive name of species of *Manucodia* and *Phonygammus* (see BIRD-OF-PARADISE).

MANUS: the 'hand' (see SKELETON, POST-CRANIAL; WING).

MAO: *Gymnomyza samoensis*, a HONEYEATER endemic to Samoa.

MAPPING: see CENSUS.

MARABOU: also 'Marabou Stork', *Leptoptilos crumeniferus* (see STORK).

MARGARORNITHINAE: see OVENBIRD (1).

MARGINAL COVERTS: see TOPOGRAPHY.

MARISMA: Spanish word applied to marshy country, notably in the delta of the Guadalquivir (an important bird habitat).

MARKING: a term initially confined in its application to what is now known as 'bird ringing' or 'banding', but conveniently extended as a comprehensive term for all techniques used to mark birds. All forms of

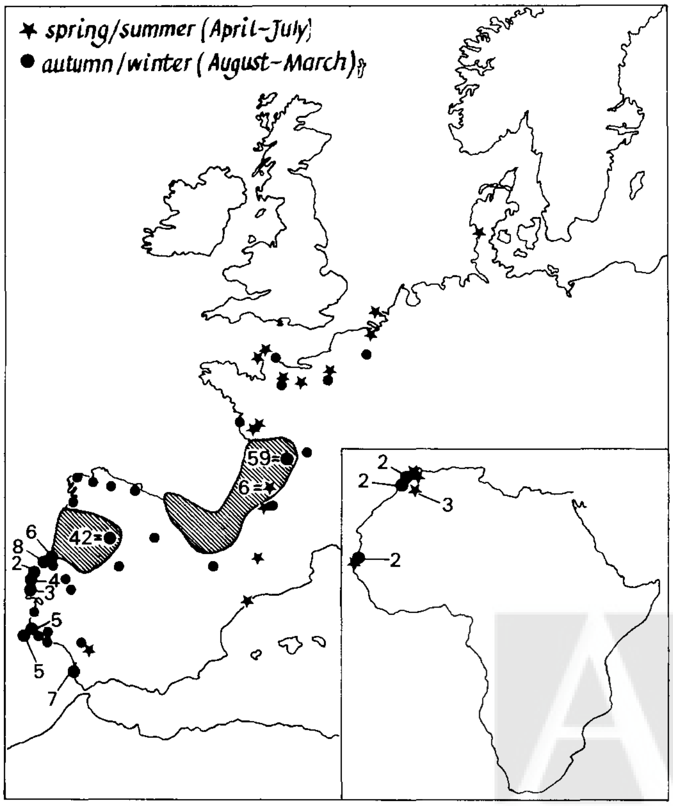

Fig. 1. Recovery localities of Common Whitethroat *Sylvia communis* ringed in Great Britain. The British population of this species migrates slightly west of south to its wintering area in West Africa. There is a major autumn stop-over area in northern Portugal.

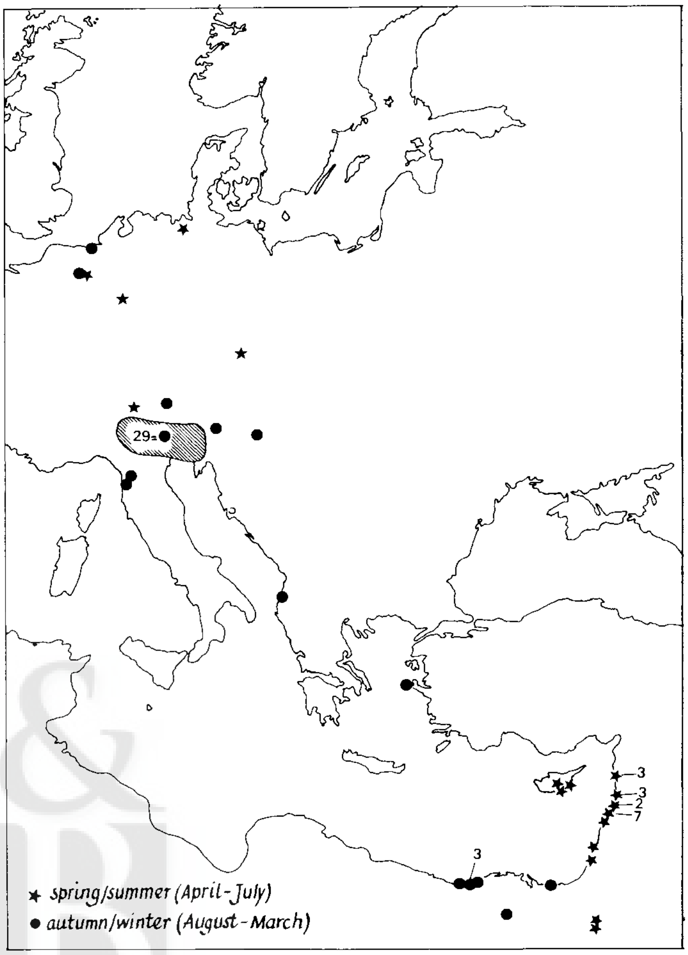

Fig. 2. Recovery localities of Lesser Whitethroat *Sylvia curruca* ringed in Great Britain. The British population migrates south east to winter in East Africa. The recoveries indicate staging posts in northern Italy and, probably, the Nile Delta in autumn and in Asia Minor during the spring.

marking have in common a basic purpose: to make a bird recognizable, either as an individual or else as a member of a class, e.g., a brood, a colony or an age group. The many techniques now in use may be divided into two categories: the extensive system, generally organized on a national or even Continental basis, in which public co-operation is normally important or essential, and the intensive or private systems, in which the marks are meaningful only to the operator, or to those he initiates.

The main—almost the only—extensive technique is known as bird ringing, the term 'banding' being preferred in North America and Australasia. The private or intensive techniques include colour ringing or marking in various forms, tagging, radiotelemetry, undertaken for reasons of research, and closed ringing for captive birds (see CAGE BIRD).

Bird ringing. The essential feature of bird ringing, as here defined, is that each ring carries, in addition to a unique serial number, a postal address to which any finder of the ring is invited to write. Usually both number and address appear on the outside of the ring, but in North America, on the smallest sizes, the return address may be on the inside.

The rings are bands of metal which are fixed around the tarsus (or, occasionally, tibia) of the bird. They range in size from an inside diameter of 1.8 mm to one of 30 mm. Aluminium or aluminium alloys are used for small sizes. Large sizes are frequently of modern alloys such as monel, incoloy or stainless steel. Most rings are supplied in the shape of a 'C', which is closed to form a circle round the leg. In some countries the largest rings are secured by having the two ends brought together and bent over to form a clip.

The rings may be fitted on nestlings, as soon as the legs and feet are sufficiently developed, or on fully-grown birds caught specially for ringing (see TRAPPING). As a part of their bird-ringing scheme, certain issuing authorities have also used wing-clips. These resemble small safety-pins, the pin being passed through the PATAGIUM and secured in the cap, upon which are marked the usual inscriptions of address and serial number. Wing clips are especially used for marking young Anatidae, which may be very difficult to catch by the time their legs have grown sufficiently to retain an ordinary ring (but see next paragraph). Their chief disadvantage is that they are inconspicuous when partly concealed by the feathers and hence produce proportionately fewer recoveries than do rings.

A technique developed in Latvia temporarily reduces the inside diameter of rings with soft plasticine or florist's wax, thus permitting ducklings to be marked at a much earlier age and obviating the need for wing tags. The growing tarsus squeezes out the plasticine or wax so that the inside diameter is automatically adjusted to the diameter of the tarsus.

The details of species, race, age, and sex (if ascertainable), date and locality are recorded for each ring used and the bird is released or returned to the nest. The ringing data are entered on schedules which are filed at the headquarters of each scheme for reference.

Objects. Two broad categories of study may be recognized, migration and vital statistics, including life histories. The more spectacular nature of migration studies attracted attention from the outset (see MIGRATION), whereas the use of ringing for population studies and similar investigations began rather later and new methods of interpretation are still being developed.

Results. Ringing data, based on the accumulation of individual case histories, provide generally more precise information than other migration study techniques. Limitations arise from the small proportion of birds recovered and the fact that the geographical distribution of these recoveries may not be fully representative. Effectiveness in determining the summer and winter distribution of migratory species tends to bear a close relationship to the density of the human populations in the areas concerned, their literacy, and their hunting traditions. Thus, for the Anatidae wintering in Britain, with a breeding range extending northwards and eastwards across Europe, the recovery rate may exceed 20% for some species and is generally over 10%. In contrast, small passerines wintering in Africa may show a recovery rate of less than 0.5%. Common British garden birds have recovery rates in the range 1–4%, although the figure for particular species may vary appreciably between rural and suburban areas. Because of the high human population and the high level of ringing activity, ringers operating in countries like Britain and the Netherlands tend to enjoy much higher recovery rates for non-quarry species than do ringers in other parts of the world. Furthermore, improved catching efficiency, associated especially with mist nets and cannon nets (see TRAPPING), is leading to further improvement. For many species, ringers can now rely on re-capturing far more of their ringed birds than will be reported by the public—a factor of obvious importance in the development of population studies.

For species with low recovery rates, there are generally still too few records to permit detailed analysis of summer and winter distribution. Recoveries providing data about migration are more numerous and may be used to determine such features as the direction and sometimes the speed of migration, and time of arrival of passage migrants in given areas. Only ringing can provide quantitative data for the study of partial migration and abmigration, and the presence of ringed birds in 'wrecks' and other weather movements is often a valuable guide to the origin of the populations involved. For species which may be at risk, as for example, auks from oiling, raptors from pesticides, terns from persecution, the policy of keeping a proportion of the population ringed at all times provides a sensitive monitoring system. Locally, ringing has proved effective as a means of studying the gathering area for communal roosts and the feeding ranges of colonial nesters.

In the study of population dynamics, ringing data have been used to establish the age at which breeding begins; age structures of populations; annual, seasonal, and regional variations in mortality; common causes of death. The value of such data depends on the fate of the recovered birds being representative of what happens to all birds. This may be almost impossible to prove, but allowance can be made for recognized sources of bias, and recovery data are generally regarded as valid (see ECOLOGY).

In long-lived species, including many seabirds, longevity studies were for a time handicapped by the weakness of the aluminium rings. The harder modern alloys, first introduced in the late 1950s, are beginning to produce more realistic survival figures (see AGE).

History. Although there had been sporadic attempts and a few schemes (in Great Britain from 1890) of limited scope, the first ornithologist to undertake systematic large-scale ringing was Christian Mortensen of Viborg (Denmark), who commenced his experiments in 1899. Germany was quick to take up the study (1903) and the pioneer 'Vogelwarte' at Rossitten, on the Baltic, did much to establish the value of ringing. The practice soon gathered impetus: Hungary (1908), Great Britain (1909), Yugoslavia (1910), Holland (1911), Sweden (1911), Denmark (1914) and Norway (1914) all had effective schemes before the 1914–1918 war. Between the two World Wars there was a rapid growth in the number of ringing schemes, especially in Europe, at least 15 being established between 1918 and 1930, and a further 8 by 1939. In North America the start was later, for although an American Bird Banding Association was founded in 1909 (and Jack Miner was marking wildfowl before 1914 with rings carrying Biblical quotations instead of serial numbers), the two main centres, at Washington and Ottawa, were not established until 1920 and 1922 respectively; but the growth of activities was rapid and the scale of ringing soon outpaced work of individual European centres. Outside Europe and North America, ringing has been on a small scale, and generally of recent development, as is shown by the following dates of commencement: Japan (1924), Egypt (1937), New Zealand (1947), Tasmania (1947), Union of South Africa (1948), Australia (1953), and Zaire (1954). Marking has also been done in the Antarctic (e.g., by the UK, USA, France, Australia and New Zealand) and from time to time on various oceanic islands.

In Britain, H.F. Witherby in London and A. Landsborough Thomson in Aberdeen both started comprehensive schemes in 1909. The latter scheme came to an end during the First World War, but the former developed steadily under the guidance of its founder until 1937, when responsibility for the organization was handed over to the British Trust for Ornithology, and a special Bird Ringing Committee was appointed to control activities, with headquarters at the British Museum (Natural History). Although the scheme was for many years financially self-supporting, since 1954 it has required a subsidy, currently from the Nature Conservancy Council. In 1963, the headquarters moved to Tring in Hertfordshire (see also OBSERVATORY, BIRD).

In Europe a major obstacle to full use of ringing data has been the dispersed housing of the results, with over 30 different ringing schemes holding data and working autonomously. To meet this problem EURING, the European Union for Bird Ringing, was established in 1963 to standardize both methodology and terminology throughout the continent. The advent of computer facilities permitted the inauguration of an international data bank of European recoveries, at Arnhem in the Netherlands. This now stores recovery data for more than half the birds ringed in western Europe. Even in western Europe not all countries contribute to the Data Bank, while data from eastern Europe are as yet very unevenly represented.

In North America a single banding scheme covers the entire continent. The main direction of effort has been towards birds of economic importance and the high annual intake of recoveries necessitated early use of computers to facilitate analysis. Sophisticated capture–recapture techniques have been evolved for use in population studies, while in the field of passerine migration annual corporate studies were introduced under the code name 'Operation Recovery'.

Intensive or private techniques. The aim of most intensive marking techniques is to permit the recognition of individual birds at a distance, and there is little point in so marking birds unless the research worker is prepared to spend long hours of observation or to publicize widely a request for sightings. National and international discipline in the launching of colour marking programmes is essential to prevent inadvertent duplication of codes, but is too often lacking.

Most early studies used celluloid rings, but these rarely incorporate light-fast pigments so that the colours fade in a year or two. For a time anodized aluminium was used, but modern plastics such PVC and Darvic have proved more satisfactory. 'Traditional' colour ringing usually involves the use of several different rings on each bird: for example yellow over blue left leg, yellow over red right leg. On bigger birds this has generally been superseded by the use of large laminated plastic rings engraved with large figures and/or letters. On geese, in favourable conditions, the detailed combination of letters and numbers may be read by telescope at distances up to 300 m.

Other devices. For species which spend much time in the water, engraved leg rings may be of limited use. This has led to the development of neck collars, chiefly used on geese and swans, of nasal discs, used on ducks and of small plastic patches temporarily cemented to the plumage of head or wing. For the easier identification of birds on the wing, tags have been developed. Most are attached by a stainless steel pin, passed either through the patagium or elsewhere in the wing; some wrap round the wing, overlying the scapulars. Tags may be colour-coded or carry a combination of letters and figures.

Radiotelemetry has been used to facilitate the tracking of birds by aeroplane, but is chiefly (and increasingly) employed for very intensive local studies. The equipment permits detailed, round-the-clock monitoring of movements, but despite advances in the miniaturization of both transmitter and battery, the weight factor still renders the technique unsuitable for use on small birds. The high unit cost of the equipment, which is often lost, means that few individuals can be marked in any one programme (see RADIO TRACKING AND BIOTELEMETRY).

Radio-isotopes, bonded to conventional metal rings, have been used to obtain round-the-clock records of the incubation roles of male and female seabirds.

Web tags. In detailed studies of Anatidae it may be important to recognize the young as individuals from soon after hatching, at which stage their legs and feet are much too tiny to take a ring appropriate to a fully-grown bird. As an alternative to the wing clip already described, which is used as a permanent mark, small tags may be passed through the web of the foot, a conventional ring being substituted at a later date. Work in the United States has demonstrated that the same end can be achieved by the use of a variously placed tiny hole in the web.

Plumage dyeing has been much used on pale-coloured birds ranging in size from small waders to swans. Dye offers a short-term approach, being lost with the first moult, but because of its conspicuousness at long range it has proved invaluable in tracing the migratory paths of birds such as Bewick's Swan *Cygnus columbianus bewickii*.

Close ringing. This technique differs from the others in that the rings are not split but are true rings. Their use is confined to nestlings, which are marked while the foot is still small enough to permit the rings to be slipped on; once the foot is fully grown the ring cannot be removed. Close rings are of little value to ornithologists, but aviculturists and pigeon-fanciers use them extensively to establish individual identity and ownership; and in the law of several countries a correctly fitted close ring is taken as proof that the bird was bred in captivity (see CAGE BIRD).

In recent years the high-value, often illegal, trade in birds of prey has led to much research into a tamper-proof ring which can be 'locked' on to the leg of a bird for life. It is too soon to say whether designs evolved will successfully fulfil their function. R.S.

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MARROW: see BLOOD; SKELETON, POST-CRANIAL.

MARSH-BIRD: substantive name of 2 South American icterids of the genus *Pseudoleistes* (for family see ORIOLE (2)).

MARTIN: substantive name of some species of Hirundinidae (see SWALLOW).

MARTLET: archaic and heraldic name for a bird which may have been either the House Martin *Delichon urbica* (or other hirundine) or the Swift *Apus apus*, perhaps used for both (see HERALDIC BIRDS).

MATE: either member of a pair in relation to the other (see PAIR).

MATING: see COPULATION.

MATING SYSTEM: that part of the social organization of a species that involves the relationship between the sexes, especially copulation and the subsequent events of the breeding cycle.

In the great majority of birds—over 90% of all species—more or less long-lasting pairs are formed (see PAIR FORMATION), which usually persist through the breeding season and in some birds for life. The minority, which do not form simple pairs, show a great variety of mating systems, mostly involving some form of polygamy. Because of its prevalence in most families of birds it is generally thought that monogamy is the primitive condition in birds, and that polygamous systems are later specializations. There are two main forms of polygamy: polygyny (the mating of one male with two or more females) and polyandry (the mating of one female with two or more males). Both polygyny and polyandry may be simultaneous, when a bird has several mates at the same time, or successive (serial), when a bird has several mates in quick succession. A clear-cut classification of mating systems is difficult because they are not necessarily mutually exclusive; thus in some species polygyny is combined with successive polyandry.

Some species, especially those with LEK displays, seem to be promiscuous in their mating; but detailed study is needed in order to establish this, and it is unlikely that both sexes will be equally promiscuous. Thus in some lek species which had been thought to be promiscuous, observation of marked birds indicates that females show well-marked attachments to particular males. In general it will be expected that males will be more promiscuous than females, because of the very different parental investment in each mating by the male and female. Males invest very little in each mating, and there is no great disadvantage to them in a mating which is unsuccessful in its outcome; but females invest a great deal in each reproductive attempt, and choice of a suitable mating partner is important.

Some ecological correlates of the different mating systems are clear. Monogamy is usual when the conditions in which a species breeds are such that both parents are needed for the successful rearing of the young; polygamy and promiscuity are possible only when one parent is able to rear the young single-handed. Hence, polygamy and promiscuity are found mainly in birds with precocial young, especially if the young find their own food, and in birds with altricial young if their food is plentiful or easily found. It is probably for this reason that polygyny is found in several groups of seed-eating, fruit-eating and nectar-eating birds, and very rarely in insectivorous birds. Other factors are, however, important. For instance frugivorous birds that nest in holes tend to live strictly in pairs, probably because both parents are needed to guard the nest-hole.

Another predisposing condition for the evolution of polygyny is that a proportion of the males can occupy all the suitable nesting territories, the other males being relegated to suboptimal or unsuitable territories. If females of such species make their choice mainly on the basis of the quality of the male's territory, a small proportion of the males may acquire most of the females. This kind of system has been demonstrated in some American marsh-breeding icterids (see ORIOLE (2)) and may also apply to some weaver-birds and in less extreme form to some arctic sandpipers. A related system, apparently rare, involves the male's domination over an essential food resource. Male Orange-rumped Honeyguides *Indicator xanthonotus* defend the huge combs of the honey-bee *Apis dorsata*: the females mate only with comb-holding males, and they and their offspring have access to the combs of the males with which they have mated. In some hummingbirds a similar system probably obtains, the resource in this case being a clump of flowers held by a territorial male.

Several species of waders that breed in the far north, or in montane areas, have mating systems ('rapid multi-clutch systems'—Graul 1974) enabling them to make the fullest possible use of the short period that is suitable for nesting. The essence of such a system is that the female lays two or more clutches in quick succession; it may be combined with monogamy, the male incubating the first clutch and rearing the young and the female taking charge of the second clutch (e.g. Temminck's Stint *Calidris temminckii*, Mountain Plover *Charadrius montanus*), or with serial polyandry, the female laying clutches for two or more males (e.g., Dotterel *Eudromias morinellus*, Spotted Sandpiper *Actitis macularia*).

For details of the various forms of polygamy, and of the groups in which they occur, see POLYGYNY and POLYANDRY (see also CO-OPERATIVE BREEDING). D.W.S. (1)

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MATURATION: literally 'ripening'; in physiology, applied particularly to completion of the development of the germ-cells (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM); in ethology, the development of a behaviour pattern in a young bird without performance, i.e., without learning through practice (see BEHAVIOUR, DEVELOPMENT OF).

MATURITY: attainment of the age at which the bird is capable of reproduction (although breeding condition is a seasonal phenomenon); in practice, the criterion is usually the acquisition of full adult plumage (for immaturity see under YOUNG BIRD). In highly seasonal environments many small species first breed in their first summer, when they are just under a year old but in non-seasonal environments they may start breeding at 6–8 months of age, e.g., Zebra Finches *Poephila guttata* in Australia (see under LAYING).

The term has occasionally been restricted to mean the age at which maximum breeding capability is attained, usually one or more years after the age of first breeding.

MAVIS: popular name, in Britain, for the Song Thrush *Turdus philomelos* (see THRUSH).

MAXILLA: osteologically, a slender paired bone of the SKULL, between the jugal and the premaxilla; sometimes used more generally as a term for what is otherwise called the 'upper mandible', i.e., the upper jaw (of which the premaxillae are the chief bones) and its horny covering (see BILL); in the latter usage the term mandible is restricted to the lower part (see MANDIBLE).

MEADOWLARK: substantive name of *Sturnella* spp. (see ORIOLE (2)).

MEAN, ARITHMETIC: equivalent to 'average' in the sense in which the latter word is most exactly used—the sum of the recorded values divided by the number of observations in the sample. In a perfectly symmetrical distribution the arithmetic mean coincides with the median and modal values (see BIOSTATISTICS).

MEASUREMENT: here confined to the sense of recording the lengths of external features of birds. Measurements may be used to give a general indication of size or for a variety of taxonomic, ecological or other purposes (see also SIZE). Within a population of a species, significant differences in measurements may occur between the sexes, age classes or seasons, the latter reflecting feather growth and wear. Differences between populations may correlate with local environmental factors and over the range of a species may vary clinally or disjointedly according to subspeciation. Individual birds from the same population and age/sex group vary in size and correlated behavioural features may be found. Similar species can sometimes be separated most reliably by measurement (see also WING FORMULA).

For scientific purposes, millimetres are conventionally preferred to centimetres, but centimetres are often used in general descriptions. Care should be taken to avoid measuring feathers shortened by undue abrasion and fracture or not fully grown during moult. Innumerable features of birds can be and have been measured but the 6 described below are in most common use.

Wing. This is the most widely taken measurement, being a fair indicator of size of an individual within a species. It is easy to measure on a live bird. Wing-length is taken on the naturally folded wing from the carpal joint to the tip of the longest primary using a ruler with an end-stop. If the curvature of the wing is not corrected in any way, a 'minimum chord' is obtained. One of the two curvatures can be eliminated by pressing at the greater coverts to flatten the wing on to the ruler to give a 'flattened chord'. Most of both curvatures can be removed by flattening the wing as above and then straightening the primaries along the ruler with a firm stroking action to give a 'maximum chord' wing-length. Maximum chords can be measured most reliably and repeatedly and are to be preferred. The difference between the maximum and minimum chord can easily be 10% and thus as great as most other differences that might be being studied, so beware of published wing-lengths without the method stated. Beware too of measurements of skins which might, apart from the effect of shrinkage, be harder to flatten and straighten if this has even been attempted. In Britain, the maximum chord method is advocated by the British Trust for Ornithology for use by bird-ringers.

Tail. Tail-length is generally taken as the measurement from the point of emergence of the feathers to the tip of the longest, but may instead be of a stated pair. Measurement can be made with an unstopped ruler, dividers or vernier callipers and taken from above or below the tail. The roundedness or forkedness of a tail is taken as the distance between the tips of the central and outer feathers measured directly from an unfanned tail.

Bill. Bill-length is probably the second most widely used measurement after wing-length and is of particular interest in some seabirds, wildfowl and waders which show intraspecific variation with race and latitude. Bill-length can be measured to the cere (owls and birds of prey), to the start of the feathering, to the base of the skull or less commonly to the nares or the gape, so it is vital to note the method used in any published data. Other bill dimensions may be of ecological interest.

Tarsus. The bone is measured from the depression at the rear of its upper joint to the end of the last complete scale before the toes diverge at the front. Dividers or callipers may be used.

Total length. This is taken from bill to tail by laying the live or freshly dead bird on its back along a ruler and straightening it out. The measurement is difficult to take consistently, is of no taxonomic or ecological use and consequently is often expressed in inches in British literature. Total length is used in identification books to convey a general impression of size, though as such it is not very helpful because of the misleading influence of long bills or tails.

Wing-span. Wing-span is measured from tip to tip by straightening the wings of a live or freshly dead bird as far as they will go without undue force. Like total length, it is not easy to measure consistently and is mainly used to give an approximate idea of size especially of larger birds. Wing-span is, however, of use in flight performance models derived from aerodynamic theory (see FLIGHT).

Documentation. Measurements quoted in standard reference works are generally of museum skins which because of shrinkage will be lower than those obtained, as most now are, from live birds in the field. Many such published data are further inadequate because the method by which they were taken is not stated and the statistical necessity of giving the sample size and standard deviation is overlooked (see BIOSTATISTICS). There is thus an outstanding need for the collection and publication of standard measurements even of species which are common and frequently handled by bird-ringers. C.J.B. (2)

MEATUS: an opening, particularly of the ear (see HEARING AND BALANCE).

MECHANICAL SOUNDS: non-vocal sounds, made by the bill, wings, or tail, as contrasted with vocal utterances (see VOCALIZATION). The 3 types may be considered separately.

Bill sounds. Some of these, perhaps to be regarded as adventitious, are made by two birds together. Various clattering noises are made in the course of bill-fencing and bill-sparring in a wide range of birds, such as grebes, herons, auks, pigeons, kingfishers, woodpeckers, waxwings, thrushes, crows, and some finches. Bill-crossing and bill-tapping are common in the sexual display of albatrosses (Diomedeidae); the whetting together of the bills of a pair of Laysan Albatross *Diomedea immutabilis* has been described as producing a whistling sound.

Bill-rattling by a single bird, producing a noise like that of a nutmeg-grater, occurs among frigatebirds as an alarm note, and also as an entreaty for food on the part of the chicks. The bill-clapping of storks is well known. In the White Stork *Ciconia ciconia* it is a sign of recognition between members of a pair or group; the head is thrown down and back between the legs, to the accompaniment of raising and flapping of wings and spreading of tail. The chick, when sufficiently strong, exhibits similar behaviour towards its parents, recognizing them and soliciting food. Other species of stork also clap, but less loudly. The Shoebill *Balaeniceps rex* clatters its massive mandibles, but without posturing, as a note of alarm and an entreaty for food.

Bill-snapping as a defensive threatening sound is made by most owls and is particularly loud in such large species as the Eagle Owl *Bubo bubo* and the Snowy Owl *Nyctea scandiaca*.

In a different category are sounds made by the bill in contact with various objects. Some of these are adventitious effects of feeding or nesting actions, for example among tits, nuthatches and woodpeckers. On the other hand, specialized bill-drumming—beating a tattoo on the wood of a tree—is practised by many woodpeckers and has been most studied in the Great Spotted Woodpecker *Dendrocopos major*. In this species both sexes produce a loud, harsh vibrating sound by an extremely rapid rain of blows at a selected point, most commonly near the end of a broken or dead branch, but exceptionally on some quite different sort of sounding-board such as the lead-covered top of a wireless mast. The sound produced depends upon the resonant properties of the branch; the normal duration is about a second, and the normal frequency may exceed 20 blows per second. At the higher rates the human ear runs the sounds together to form a continuous vibration which may be audible at distances up to 1 km. The strength diminishes after the first or second blow, and the rate accelerates steadily from 15 per second to 25 per second so that the sounds tend to die away and rise in pitch. The drumming period extends in Britain from the end of February to the first week in May; the sound serves to attract mates, and both birds drum before coition. In the Lesser Spotted Woodpecker *D. minor*, the sound tends to be less powerful and higher in pitch, and may last for 2 s at a frequency of 22 blows per second; both sexes drum before performing the sexual 'butterfly dance'. The Northern Flicker *Colaptes auratus* of North America beats a rolling tattoo on dead branches in spring, and sometimes uses metal telegraph poles for the purpose.

Wing Sounds. The normal flight of some birds is inaudible except when there is a dense flock within close range. Owls are particularly silent, even at ultrasonic frequencies audible only to their prey, due to special adaptations of their feathers (these are absent in the fishing owl, *Scotopelia peli*). The flight of other birds may make a considerable noise. Ducks produce rather musical sounds with their wings when flighting; the audible intensity of the sound depends to a great extent on atmospheric conditions and wildfowlers are agreed that it reaches its maxi-

White Storks *Ciconia ciconia* bill-clappering at nest. (*Photo: E.J. Hosking*).

mum effect on still, frosty mornings. Teal *Anas crecca*, especially in planing down, make a metallic-sounding 'swoop', and among other surface-feeding species the Shoveler *Anas clypeata* stands out for the amount of sound emitted during level flight—as, in a different group, does the Shelduck *Tadorna tadorna*. On the whole, however, it is the diving ducks that make most sound, and notably the Goldeneye *Bucephala clangula*—commonly known in America as the 'Whistler' because of the penetrating sound made by its wings, especially in the case of old drakes. The Mute Swan *Cygnus olor*, alone among its kind, produces a high-pitched harp-like note from its primaries on the downbeat.

Various gallinaceous birds have noisy flight. Flying Pheasants *Phasianus colchicus* create a musical high-pitched whistle with their wings; and the 'whirr' of wings of Red Grouse *Lagopus lagopus scoticus* and Partridge *Perdix perdix* are familiar. The American Wood Stork *Mycteria americana* makes a most amazing noise as the air rushes through the wings when it dives from a height to its feeding grounds. The Rhinoceros Hornbill *Buceros rhinoceros* has been described as making a sound 'like that of a chugging steam locomotive' with its wings.

Hummingbirds are so called because of the sound made by the extremely rapid vibration of their wings; it reminded Salvin of a piece of machinery actuated by a powerful spring. The humming sound is produced by wing-beats as fast as 80 to the second (although the largest species, the Giant Hummingbird *Patagona gigas* beats its wings only 8–10 times per second). As originally noted by Darwin, different species produce a different 'hum'. In the male Broadtail *Selasphorus platycercus* the primary feathers taper at the tips and the air filtering through the openings produces a distinctive rattling whistle, whereas the female has normally shaped feathers and hovers with the usual humming or buzzing sound.

The foregoing examples relate to ordinary flight, although the sounds are in some cases not heard under all conditions. There are other instances where a characteristic sound is emitted only at special times, and usually as an element of display; these include cases where the sound is the result of wing-clapping, although that can happen also in other circumstances. This last point is particularly relevant to the pigeons; wing-clapping is common in domestic pigeons, notably tumblers, and many wild species start with a few clapping strokes when taking off—the sound varies considerably from one species to another. In the Woodpigeon *Columba palumbus* the male, near the top of its display flight, makes 1–3 vigorous claps with its wings; the sound has been attributed to forcible downstrokes analogous to the crack of a whip, but as in other cases it is more likely to be due to the wings striking each other.

Even the silent-flying owls do this. In the breeding season the Short-eared Owl *Asio flammeus* will circle on extended wings with only occasional beats, and from time to time will drop like a stone for some distance clapping its wings 4–6 times in rapid succession beneath its body; the wing-tips appear to meet only at the first clap, but contact at the carpal region is said to take place throughout the clapping. Clapping is also used when the nest is threatened. The Long-eared Owl *A. otus* performs zig-zag flights between the tree-trunks, and then rises above the tree-tops clapping its wings beneath the body at the end of each beat; both sexes do this, the female less frequently, and again the action is also used when the nest is threatened. Similar habits have been described for other owls.

In the breeding season the male Nightjar *Caprimulgus europaeus* produces a series of wing-claps; the tips do not appear to meet, but possibly the carpal joints do. The male may clap as many as 25 times in succession while gliding with tail spread and wings raised obliquely. The female also claps, and apart from the mating season has been observed to do so when accompanied in flight by her two young in early September. In America the Common Nighthawk *Chordeiles minor* indulges in 'sky-coasting', and, when the bird makes the turn, the air rushing through the primaries produces a booming sound such as one might imitate by blowing across the bung-hole of an empty barrel.

The Ruffed Grouse *Bonasa umbellus* of North America 'booms', while at rest, by striking its wings against its breast. It is a great performer in the mating season, and both sexes 'boom' before coition. The sound has been described as a deep-toned thump, like the muffled beating of a great heart, followed by a quickly accelerating drumming roll like distant thunder. Various other gallinaceous birds have similar, if less notable, performances; for instance, the crowing of the cock Pheasant *Phasianus colchicus* in spring is associated with flapping and thumping.

Both sexes of the Red-throated Diver *Gavia stellata* produce a loud rushing noise with their wings when, in May and June, they volplane down to the loch uttering wild raucous cries. The American Woodcock *Scolopax minor* has the first 3 primaries modified and attenuated as a musical instrument used during the nuptial flight; the writer observed this at twilight in March, when the birds produced a cadence of musical whistling during the rapid descent following the upward spiral. Various plovers in the breeding season make wing noises during flight; thus the male Lapwing *Vanellus vanellus* makes a 'zooming' noise.

Among the passerines, mention may be made of the birds-of-paradise; those species with specialized wings and drooping tails, such as Princess Stephanie's Bird-of-paradise *Astrapia stephaniae*, produce an attractive sound comparable with rustling silk. The Neotropical manakins (Pipridae) perform peculiar dances with both buzzing sounds and clashes that resemble loud thumb-snappings; their outer primaries are strikingly attenuated in some species, and some also have modified secondary feathers (see MANAKIN). Other examples include the wing sounds made by flappet larks *Mirafra* spp. and todies *Todus* spp.

Finally, a case of wing-sound made by two birds: in courtship flight the drake Pintail *Anas acuta* passes beneath the duck so closely that their wings clatter together with a loud noise like a football rattle.

Tail sounds. Of these the chief are the 'drummings' or 'bleatings' of snipe *Gallinago* spp. during aerial evolutions in the breeding season. The Common Snipe *G. gallinago* produces a resonant, tremulous sound lasting about a couple of seconds and sometimes frequently repeated; both sexes do it, but chiefly the male. The sound accompanies a rapid descent at an angle from a considerable height. Experiments have provided definite proof that the sound is a result of vibration of the outer pair of rectrices, which—when the tail is spread fanwise—are detached from the remaining 6 pairs; but that the wavering element is due to the action of the wings in intermittently deflecting air against the tail. The sound can be artificially reproduced by various devices, such as attaching the musical feathers in the appropriate position to a cork and whirling it at the end of a string; the latter imparts a vibratory motion and serves (as a rigid stick will not) to simulate the tremulous effect naturally derived from wing movements.

The musical feathers, the outermost rectrices (7th pair), show a specialized structure, the essential features of which are comparable with those of a harp. The outer web is narrow and formed of stiff rami that can be easily separated. The inner web is very broad and formed of long, stiff rami making an acute angle with the shaft and having radii and hamuli so arranged that the whole web is strongly locked together. The adjacent feathers (6th pair) show something approaching the same structure, whereas the 5 central pairs are soft and unmusical.

In some other species of snipe that make similar sounds the total number of rectrices is greater—16, 18, 20, or even 26–28; this last occurs in the Pintail Snipe *G. stenura* of Asia, in which 8–9 on each side are attenuated, the outermost so much so that they resemble pins. The number showing specialization varies considerably with species; in *G. nobilis* of northern South America there are 3 on each side. The quality of the sound also varies; in Latham's Snipe *G. australis* it is more voluminous—a tremendous rushing noise—and in the Auckland Island Snipe *Coenocorypha aucklandica* the bleat is high-pitched. The Great Snipe *Gallinago media* and Jack Snipe *Lymnocryptes minimus* possess no musical feathers, and the same is true of the European Woodcock *Scolopax rusticola* and the American Woodcock *S. minor*.

A sound made by the Lyre-tailed Honeyguide *Melichneutes robustus*, in the course of elaborate flying evolutions, is thought to be produced by vibration of the outer rectrices, as in the Snipe. P.M.-B. (J.D.P.)

MEDIAN COVERTS: see TOPOGRAPHY.

MEDULLA: for that of the adrenal glands see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

MEDULLA OBLONGATA: part of the hindbrain (see NERVOUS SYSTEM).

MEGAGEA: see under ARCTOGAEA; DISTRIBUTION, GEOGRAPHICAL.

MEGAPODE: substantive name of species of Megapodiidae (Galliformes, suborder Galli); in the plural, general term for the family. Alternative English names, given to species found in Australia, are 'Scrubfowl', 'Brush-turkey'—and in one instance 'Mallee Fowl' or 'Lowan'. Such general terms as 'mound-birds', 'mound-builders', and 'incubator birds'—this last a common American usage—have been applied to the group. The family is a small one. The members are characterized by their habit of not incubating their eggs. Instead they lay them in holes in the ground or in mounds of rotting vegetable matter and leave them to be incubated by natural heat.

The family comprises 6 genera, which can be divided into 3 ecological groups, viz., scrubfowl (*Megacephalon* and *Megapodius*), brush-turkeys (*Alectura*, *Aepypodius*, and *Talegalla*), and the Mallee Fowl (*Leipoa*). Of these *Megacephalon*, *Alectura*, and *Leipoa* are monotypic, the species being *M. maleo*, *A. lathami*, and *L. ocellata*. The genus *Aepypodius* includes 2 species, *A. arfakianus* and *A. bruijnii*; and *Talegalla* includes 3, *T. cuvieri*, *T. fuscirostris*, and *T. jobiensis*. Peters recognized 9 species, including 28 subspecies, of *Megapodius*, but E. Mayr reviewed the genus and reduced these to 3 species—*M. freycinet*, *M. laperouse*, and *M. pritchardii*. Some later authors have increased the number of species but not convincingly.

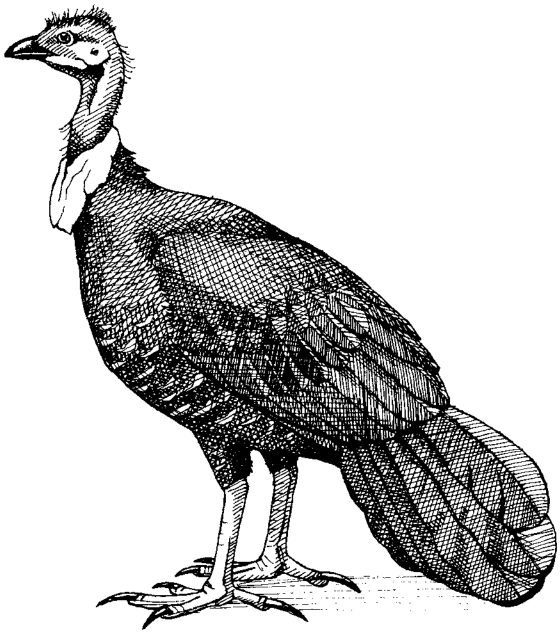
Characteristics. With the exception of *Megacephalon maleo* which is more colourful, scrubfowl are dull brownish birds with sombre plumage and small crests. *M. maleo* is distinguished by having a black tail, black wings, and pink underparts, and its head bears a prominent casque. All are about 50 cm in total length.

The brush-turkeys are black, with vertically folded tails, and are longer than scrubfowl, being 66–71 cm in total length. Their heads and necks are bare, except for numerous coarse hairs. Similar in size to the brush-turkeys, the Mallee Fowl is coloured brown in keeping with the red-brown soils of its habitat, and each feather of the wing coverts bears a prominent white spot edged with black.

Megapodes are ground-living birds. Scrubfowl and brush-turkeys are very active, although secretive, and seldom fly unless hard pressed. They are quite vocal, particularly in the evenings. According to K.H. Bennett, the Mallee Fowl's 'actions are suggestive of melancholy, for it has none of the liveliness that characterizes almost all other birds, but it stalks along in a solemn manner as if the dreary nature of its surroundings and its solitary life weighed heavily on its spirits'.

Habitat. The brush-turkeys are generally restricted to tropical rain-forest, both lowland and highland, but in a few places in Australia *Alectura* extends into drier, more inland scrubs. The scrubfowl are also mostly found in rain-forest but also are common in monsoon forest and gallery forest in riverine locations.

The Mallee Fowl is unique in inhabiting a semi-arid environment. It is confined to the dry scrubs of inland Australia; it is characteristic of, but by no means confined to, mallee scrub, which consists of several species of dwarf eucalyptus. The only extension of its range from the inland area occurs in Western Australia, where it is found in a narrow strip of heathland on the south-western coastline.



Brush Turkey *Alectura lathami*. (*N.W.C.*).

Distribution. Of the brush-turkeys, *Aepypodius* spp. and *Talegalla* spp. are confined to New Guinea, and *Alectura lathami* to the eastern coast of the Australian mainland.

Megapodius freycinet, with many subspecies, extends from the Nicobar Islands in the west to central Polynesia in the east, and from the Philippines in the north to the tropical northern coasts of Australia. Included in this range are coral islands with little vegetation, heavily vegetated continental islands, and mainland jungles. The birds are found in all these habitats but rarely extend far inland. *M. pritchardii* and *M. laperouse* have a similar habitat, but more restricted ranges, in central Polynesia and the Mariana Islands respectively. The Maleo *Megacephalon maleo* is found in Sulawesi.

Populations. Eggs of megapodes are used as food by indigenous peoples and, in places, traded for other goods in the markets. In New Britain and some other places the harvesting of eggs of *M. freycinet* is the prerogative of certain clans and age-groups and some ceremony is attached to it. Prayers are said to ensure that the birds return in good numbers to the breeding ground each season. In some cases, because of access to firearms and to a cash economy involving the eggs, the traditional methods are now upset and predation could be a serious population problem, but in the past the rituals were, in effect, a primitive but effective programme of harvest regulation and management.

The present position is that due to habitat destruction, perhaps accelerated utilization of the birds and their eggs and also perhaps because of declining volcanic heat in some regions, some megapodes have declined in this century. Concern has been expressed especially for *Megacephalon maleo* and *Megapodius pritchardii* but detailed data are lacking. The 3 species in Australia, *Leipoa ocellata*, *Megapodius freycinet* and *Alectura lathami*, are still in a strong position despite clearing of habitat in the interests of agriculture and, in *Leipoa*, the competition for food imposed by grazing stock and rabbits.

Movements. Australian populations of *Megapodius freycinet*, *Alectura lathami* and *Leipoa ocellata* are sedentary. There are no precise data on other species but, although some populations make roosting flights to off-shore islands, there seems to be no doubt that all are essentially sedentary.

Food. There are no precise data on the food of any megapode, but general observations suggest all are omnivorous. The food mostly consists of insects, small animals, seeds and fruits. The food of the Mallee Fowl is better known than that of other members of the family and consists largely of the seeds of the *Acacia*, *Cassia* and *Beyeria*, and the flowers of several ephemeral herbs as well as ground-living insects and small lizards. The Mallee Fowl is apparently independent of free water, but will drink if water is available.

Behaviour. The brush-turkeys and the Mallee Fowl are solitary to the extent that, except when eggs are to be laid, the male drives the female from the mound. The other species, where there have been observations, live in pairs and, with mound-building species, two or more pairs can use the one mound but visit it at different times so that confrontation is avoided.

Voice. There is no detailed description of the repertoire of sounds of any megapode. The male Mallee Fowl possesses a very loud, booming call and the female a high-pitched crow. The brush-turkeys have gobbles and loud grunts and the scrubfowl loud cries that are likened to gurgles and shouts.

Breeding. The simplest type of incubation is found in *Megacephalon*, and some populations of *Megapodius freycinet*. The birds simply lay each egg in a pit dug on a beach or in sandy soil exposed to the sun. The hole is filled in and the eggs are hatched by heat conducted from the soil surface. The site is not visited again, and so no temperature control is exercised. A suitable incubation temperature is apparently achieved by careful selection of the location of each egg-pit. On some islands in the Pacific, the Solomons and in New Britain, the egg-pits of *Megapodius* species are dug into soil heated by volcanic action, the eggs being incubated by that agency. On Dunk Island, off the Queensland coast, some *M. freycinet* lay their eggs in fissures in rocks exposed to the sun, the heat-retaining capacity of the rock ensuring a relatively constant temperature by day and night.

In other places, particularly in denser jungles, *Megapodius freycinet* constructs large mounds of earth up to 11 m in diameter and 5 m high, including a variable amount of vegetable material which, by fermentation, supplements the heat of the sun. The eggs are laid in tunnels up to 1 m long dug into the mound. The amount of vegetable material in the mound varies according to its location. Some mounds are built of almost pure soil and others of almost pure vegetable material, and all intermediate stages exist. Several pairs of birds participate in the construction of these mounds. Apparently the exact composition is determined by the local air temperature and amount of insolation; heavily shaded mounds require a greater supplement of heat of fermentation than those exposed to direct sunlight.

Studies of *M. freycinet* in north Queensland have shown that in a large leafy mound the temperature fluctuated from 30–38°C but the egg was always laid in the warmer parts of the mound. There was evidence that the birds were conscious of the temperatures in the mound but it cannot be said if they exercised any control over it.

There is no such variation in the nesting mounds of the brush-turkeys, all of which construct mounds composed mainly of plant material; these are commonly about 4 m in diameter and 1 m high. In the warm, moist jungles the mound ferments rapidly and generates much heat. The males regularly test the temperature of the mound by probing with their bills; the temperature-perceiving organ is not known but is possibly the tongue. In the first burst of fermentation the temperature of mounds rises to a high level, and the male exercises some control over it by digging into the top and turning over and mixing the material. Not until the temperature is declining does he permit the female to approach and lay eggs.

Throughout the incubation period the male remains in charge of the mound. In captive birds it has been shown that the temperature does fluctuate but the egg is always placed in the warmer parts of the mound. It is suspected, but not proved, that the male exercises some control over mound temperature. It has also been suggested that digging in the mound is important in controlling the oxygen supply available to the embryo.

In its arid inland habitat the Mallee Fowl must adopt more complicated methods to secure a suitable incubation temperature. The air temperature fluctuates widely during the day and the year; accordingly, the soil does not keep a suitable constant temperature. Leaf mould does not form on the ground, litter is sparse, and fallen leaves dry and wither and do not ferment.

To provide the proper constant temperature, the birds dig a hole in the ground up to 5 m in diameter and 1–1.5 m deep. During the winter they fill the hole with vegetable material swept up from the ground over a radius of some 45 m, and when it is moistened by a shower of rain the whole is covered by a layer of sandy soil 50 cm or more thick. Sealed from the dry air, the vegetable material ferments and generates heat, which later in the season is supplemented by solar heat.

It has been shown that in the spring fermentation heat is the more important and the birds need to open the mound frequently to allow heat to escape, so as to maintain the incubation temperature of 34°C. In midsummer the thickness of the soil cover is increased so as to slow the penetration of the sun's heat into the mound; by then the sun is the most important source of heat and is greater than is needed. In autumn the sun's heat is less and the fermentation heat has been exhausted. Then the birds open and flatten the mound daily to allow the sun's rays to penetrate it and warm the eggs. The result of all of this is a very uniform temperature in the mound for several months.

Details of egg laying have been recorded for only one megapode, the Mallee Fowl. The number of eggs laid varies from 5 to 35. Variation in clutch size is very great, both between different females in one year and in the same female in different years. The eggs are laid at intervals of several days, the length of the interval being apparently determined by the nutritional state of the female. As many as 35 eggs have been laid by a female *Alectura lathami* in captivity. Up to 20 eggs have been taken from pits of *M. freycinet* in New Britain, but in north Queensland one female, watched quite regularly, laid 12 or 13 in the one season.

Each egg begins to incubate as soon as it is laid and, as the eggs are laid throughout a period of several months, the first eggs are hatched and the chicks have left the mound long before the last eggs are laid. The chicks, on hatching, dig their way unaided to the surface of the mound and run into the scrub. They are capable of running very swiftly within a few hours of hatching and can fly within 24 hours. They never see their parents and live completely independent and solitary lives. H.J.F.

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Frith, H.J. 1956. Breeding of the Mallee Fowl *Leipoa ocellata* Gould. CSIRO Wild. Res. 4: 31–60.

Frith, H.J. 1962. The Mallee-Fowl: the Bird that Builds an Incubator. Sydney.

MEGAPODIIDAE: see GALLIFORMES; MEGAPODE.

MEGASUBSPECIES: a subspecies or group of subspecies which is considered almost to deserve the status of an ALLOSPECIES. The status of such a geographically representative form may be represented typographically. For instance, if the Red Grouse of Scotland, *scoticus*, is considered to be merely a distinct subspecies of the continental Willow Grouse *Lagopus lagopus*, it is represented by a simple trinomial, *L. lagopus scoticus*. As a megasubspecies it may be shown as *L. (lagopus) scoticus*. As an allospecies it may either be represented simply as a species *L. scoticus*; or its relationship to *L. lagopus* may be indicated by the use of square brackets, *L. [lagopus] scoticus*.

Amadon, D. & Short, L.L. 1976. Treatment of subspecies approaching species status. Syst. Zool. 25: 161–167.

MEIOSIS: division of a germ-cell involving reduction in the number of chromosomes (see CELL; GENETICS).

MELAMPITTA: substantive name of the 2 species of *Melampitta* of New Guinea (for family see RAIL-BABBLER).

MELANIN: see COLOUR.

MELANISM: see PLUMAGE, ABNORMAL.

MELEAGRIDINAE: see under GALLIFORMES; and TURKEY.

MELIPHAGIDAE: a family of the Passeriformes, suborder Oscines; HONEYEATER; SUGAR-BIRD (1).

MELIPOTES: substantive name of the 3 species of *Melipotes* of New Guinea (for family see HONEYEATER).

MEMBRANE BONE: one that, in the course of development, ossifies directly without going through a cartilaginous stage (see SKELETON, POST-CRANIAL).

MEMBRANES, FOETAL: see DEVELOPMENT, EMBRYONIC.

MEMBRANES, SHELL: see EGG.

MENDELIAN INHERITANCE: see GENETICS.

MENTUM: chin (see TOPOGRAPHY).

MENURAE; MENURIDAE: see PASSERIFORMES, suborder Oscines; LYREBIRD.

MERGANSER: substantive name of *Mergus* spp. (see DUCK).

MERGINI: see DUCK.

MERISTIC: a statistical term for data values that vary in whole units, such as the number of eggs in a clutch. In contrast, 'linear' values vary continuously, as in the measurement of wing length, where precision is limited only by the precision of measurement (see also BIOSTATISTICS).

MERLIN: *Falco columbarius* (see FALCON).

MEROBLASTIC: the type of embryonic development found in birds (see DEVELOPMENT, EMBRYONIC).

MEROPES; MEROPIDAE: see CORACIIFORMES; BEE-EATER.

MERRYTHOUGHT: the FURCULA; and see SKELETON, POST-CRANIAL.

MESENTERY: a fold of peritoneum in the abdominal cavity, enclosing part of the intestine together with blood vessels and nerves supplying it (see ALIMENTARY SYSTEM).

MESETHMOID: bony interorbial septum (see SKULL).

MESIA: substantive name of the Silver-eared Mesia *Leiothrix argentauris* (see BABBLER).

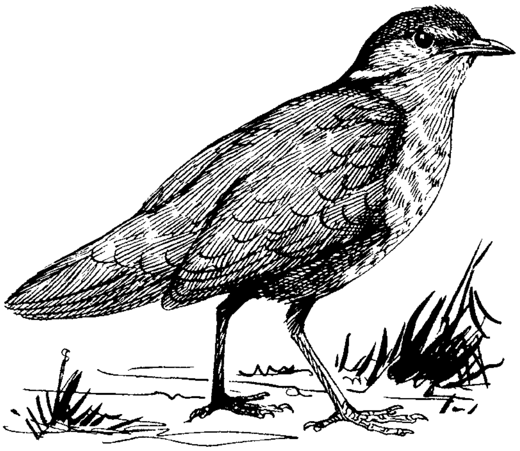
MESITE: name used for 2 of the 3 species (*Monias* being the other) of the family Mesitornithidae, sole member of the order Mesitornithiformes.

The family is endemic to Madagascar. Although placed here in its own order, its systematic position is by no means certain. At one time or another it has been considered as galliform, gruiform, ralline or even passerine, specimens reminding at least one student of ground-babblers of the genus *Eupetes* (family Timaliidae, subfamily Orthonychinae).

Characteristics. The 3 species are *c.* 30 cm long, with long and broad tails, short wings and moderate-sized feet. The bill is short and straight in *Mesitornis*, longer and curved in *Monias*. There are 5 pairs of powder-down patches. The Brown Mesite *Mesitornis unicolor* is rufous brown above, with a single white stripe along the sides of the neck, somewhat paler, more greyish below. The sexes are alike. The White-breasted Mesite *M. variegata* is longer billed, but with a shorter tarsus. It also differs in having the sides of the head streaked with whitish, rufous and blackish, the throat and chest whitish spotted with black. The Monias (alternatively Bensch's Rail) *Monias benschi*, unlike the 2 *Mesitornis* spp., shows well-marked colour dimorphism. Both sexes are greyish above, with a white superciliary streak. The male, however, is whitish on the throat and chest, the latter spotted with black, whereas the female has this whole area heavily marked rufous chestnut.

Habitat. All 3 species are strongly terrestrial. *Mesitornis unicolor* inhabits evergreen forest; *M. variegata* thick woodland relatively clear of underbrush; and *Monias benschi* subdesert scrub with a shady substrate covered thickly with leaf litter.

Distribution. *Mesitornis unicolor* is known from widely scattered localities in the humid east, but *M. variegata* is only known from Ankarafantsika, some 100 km south-east of Majunga, and from near Tsarakibany, in the extreme north. *Monias benschi* is confined to the coastal south-west, from north of Tulear to the Mangoky River.



Brown Mesite *Mesitornis unicolor*. (*C.E.T.K.*).

Populations. Due to habitat destruction, the status of all 3 species is a matter for deep concern; particularly of *Mesitornis variegata*, so localized.

Movements. All may be assumed to be extremely sedentary.

Food. Nothing is known about the diet of the *Mesitornis* spp., but *Monias benschi* feeds on fleshy fruits and insects.

Behaviour. *Monias benschi* runs with quick, pigeon-like steps, bobbing the head and depressing the tail at each step. It is capable of flying short distances, but does so only rarely. It tends to be gregarious, and has even been recorded in groups of up to 20. There is no information regarding *Mesitornis unicolor* or *variegata*, except that the latter has been recorded in pairs. Probably in all respects they resemble *Monias benschi*.

Voice. A variety of calls, including a 'choral song', have been described for *Monias benschi*, but the most typical one is *nak-nak-nak-* - -; hence the local name 'naka'. *Mesitornis variegata* is said to emit a brief *tsik*, but nothing at all is on record for *unicolor*.

Breeding. The nest of all 3 species is placed in a shrub or small tree within 2 m of the ground, in such a situation that it could be reached without flying (in the case of *Monias benschi* a kind of inclined 'ramp' has been noted). It is a flat, thin platform of twigs with some lining of grass, leaves and other soft material, scantily constructed. The eggs are nearly oval, whitish, somewhat glossy, spotted with brown, tending to form a wreath at one end. The chicks are covered with down at the time of hatching. In *Monias benschi* the down is rufous brown on the upperparts, white on the underparts, but in the *Mesitornis* spp. it is said to be entirely black. All 3 species have been claimed to be nudifugous, although for *Monias benschi* the age at which the young leave the nest is positively stated to be unknown.

Two nests of *Mesitornis unicolor* each contained a single egg being incubated by a female, which allowed herself to be caught on the nest. For *M. variegata*, however, the clutch-size is said to be 2 or 3, and possibly more than one female is involved. At all events, one nest of *Monias benschi* contained 2 eggs, apparently laid by different females, associated with a single male. Incubation was by the male and at least one female. In the case of another nest, the family consisted of one male, one female and 2 young, which were fed by both parents. (A.L.R.) C.W.B.

Appert, O. 1968. Beobachtungen an *Monias benschi* in südwest-Madagaskar. J. Orn. 109: 402–417.

King, W.B. 1978. Red Data Book. Morges.

Lavauden, L. 1937. Histoire de Madagascar. 12, Oiseaux. Suppl. Paris.

Rand, A.L. 1951. The nest and eggs of *Mesoenas unicolor* of Madagascar. Auk 68: 23–26.

Sibley, C.G. & Ahlquist, J.E. 1972. A comparative study of the egg white proteins of non-passerine birds. Bull. 39. Peabody Mus. Nat. Hist.

MESITORNITHIDAE: see MESITORNITHIFORMES; MESITE.

MESITORNITHIFORMES: an order, comprising the sole family Mesitornithidae (see MESITE). In Wetmore's system treated as a suborder Mesitornithes of the order Gruiformes.

MESOBLAST: the middle layer of the embryo, developing between the epiblast and endoblast that are formed at a very early stage (gastrulation)—see DEVELOPMENT, EMBRYONIC.

MESOENATIDES: alternatively 'Mesoenades' and 'Mesitornithes' (see MESITORNITHIFORMES).

MESOGYROUS: see ALIMENTARY SYSTEM.

MESOMYODI: see PASSERIFORMES.

MESOPTILE: term applied to the second of two nestling down plumages, in cases where there is such a sequence, the first then being called 'protoptile' (see PLUMAGE).

METABOLISM: the processes of biochemical breakdown and synthesis of nutrients that take place within the cells of all body tissues. Catabolic processes provide the energy necessary for the maintenance of body temperature and for muscular work, as well as supplying precursor compounds for the anabolic processes of growth and body maintenance. The central metabolic reactions (often called intermediary metabolism) are those involving carbohydrates, fats and proteins (Fig. 1) but we may also speak of the metabolic reactions of individual elements, especially of minerals, e.g. calcium metabolism (see EGG). Metabolic reactions are all catalyzed by specific enzymes under hormonal control (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

The biochemical breakdown of carbohydrate and fat (and in some circumstances protein) liberates energy partly as heat, which contributes to thermoregulation (see ENERGETICS; HEAT REGULATION), and partly as chemical energy by the formation of a high-energy compound, adenosine triphosphate (ATP), which fuels many other metabolic reactions and is itself utilized directly by muscle cells to perform work.

Carbohydrate metabolism. The breakdown of carbohydrates ultimately involves their complete oxidation to carbon dioxide and water but the initial stages of this process (glycolysis) can occur anaerobically (in the absence of oxygen) to yield small but useful amounts of energy as ATP. Under anaerobic conditions the end point of glycolysis is lactic acid. Cells cannot tolerate excessive amounts of lactic acid, however, so that heavily working muscle can obtain sufficient energy from ATP produced in this

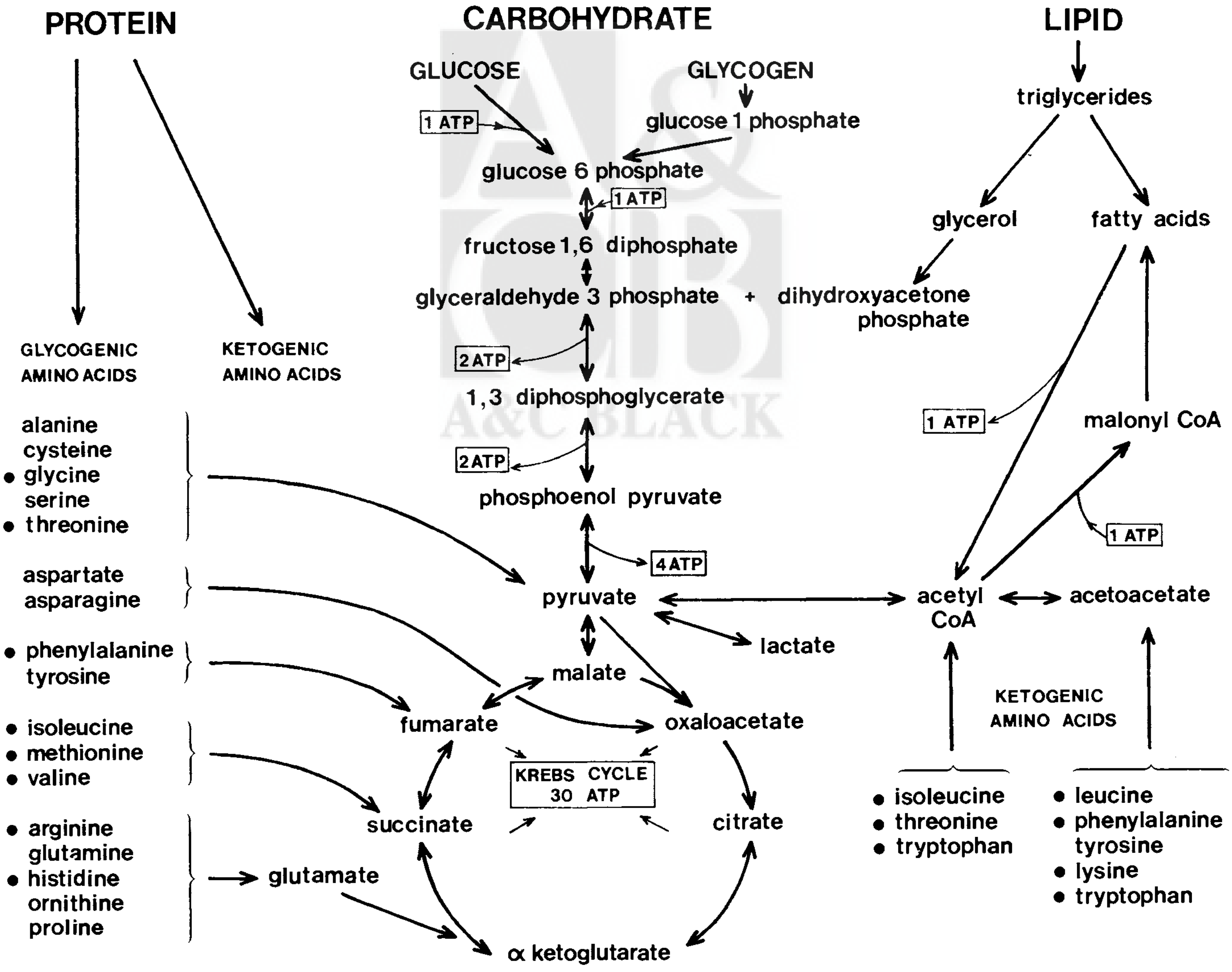


Fig. 1. Biochemical pathways of intermediary metabolism. Essential amino acids are marked •.

pathway for only a limited period before fatigue due to lactic acid build-up develops. The lactic acid accumulation constitutes an 'oxygen debt' since it must eventually be removed by oxidation. Anaerobic glycolysis with lactic acid as an end-point releases only 7% of the energy of a glucose molecule. However, in the presence of oxygen, lactic acid is not formed and complete oxidation can occur, trapping some 37% of the total energy of one glucose molecule as ATP. The remainder is liberated as heat.

Glucose or other intermediate stages of glycolysis essential for energy production must sometimes be provided from non-carbohydrate sources. The enzymes for this occur primarily in the liver and are particularly important in the embryo because yolk contains very little carbohydrate. These enzymes decrease markedly after hatching in granivorous birds with a high carbohydrate diet, but carnivorous species retain them.

Carbohydrate metabolism is controlled by the pancreatic hormones insulin, glucagon and avian pancreatic polypeptide. Insulin lowers blood glucose, promoting the synthesis of glycogen in the liver, while glucagon stimulates the breakdown of liver glycogen.

Fat metabolism. Birds store lipid as an energy reserve for overnight metabolism and in large amounts for long-distance MIGRATION. Lipid has almost twice the energy value as the same dry weight of carbohydrate and, unlike carbohydrate, can be stored without large amounts of additional water. The weight saving is obviously advantageous for flight.

Some fat is taken in the diet but birds also convert large amounts of dietary carbohydrate to lipid before use, which is consistent with the low Respiratory Quotients (RQ values of 0.75–0.80) measured in birds (see ENERGETICS). In birds the liver is the main site of lipid synthesis and is 20 times more active than other sites in the body, whereas in mammals adipose tissue itself is important in lipid synthesis. A product of glycolysis, pyruvate, is the normal starting point for lipid synthesis, being converted first to fatty acids and then to triglycerides. Since the liver has only limited storage capacity, the triglycerides are liberated into the bloodstream to be transported either to target tissues and metabolized, or to fat depots and stored. Mobilization of stored fat involves hydrolysis to free fatty acids and glycerol. Fatty acids are readily oxidized inside muscle cells, the later stages of oxidation occurring along the same pathways as the breakdown of carbohydrate. The complete breakdown of fatty acids enables 41% of the total energy stored as lipid to be trapped by ATP and then used by the muscle cell, a figure agreeing well with that obtained by the complete combustion of carbohydrate.

The structure of bird flight muscle reflects which metabolic pathway normally provides energy. 'White' muscle has few mitochondria (cell structures where oxidation occurs), few lipid inclusions, and is poorly oxygenated. It is, however, rich in carbohydrate (glycogen) which can be rapidly metabolized anaerobically. Such muscle is adapted to short-duration bursts of hard work, for example during take-off. In contrast, 'red' muscle has little glycogen but is rich in fat, myoglobin (the oxygen-carrying pigment responsible for the red colour), mitochondria and the enzymes for fatty acid oxidation, all of which enable the muscle to sustain energy output for steady prolonged flight.

Protein metabolism. Proteins enter the metabolic pathways as amino acids. Two processes, transamination and deamination, are central to protein metabolism. Transamination involves the transfer of an amino group, $-NH_2$, to another carbon skeleton, so that all amino acids, other than a few 'essential' amino acids (see NUTRITION), can be interconverted. The deaminated carbon chains of some amino acids may be metabolized by pathways leading to intermediates in carbohydrate metabolism and so take part in carbohydrate synthesis or oxidation (the glycogenic amino acids); others may take part in fatty acid synthesis (ketogenic amino acids). Glutamate plays a central role in regulating nitrogen metabolism; it can be deaminated or synthesized without involving a receptor or donor amino acid and it can give up an amino group as waste ammonia, NH_3. In mammals this waste ammonia is detoxified by conversion to urea. However, this requires the enzyme carbamylphosphate synthetase, which birds lack. Instead birds form uric acid (see EXCRETORY SYSTEM), a nearly insoluble compound whose particular advantage is that, as the waste product of embryonic metabolism, it can be stored harmlessly within the egg.

Protein metabolism is under hormonal control; indeed, hormones are often classified as anabolic or catabolic with respect to protein. Adrenal corticosteroids increase protein mobilization and insulin and glucagon also directly affect amino acid transport and metabolism. P.J.J.

Sturkie, P.D. (ed.). 1976. Avian Physiology. New York.

METACARPUS (adj. metacarpal): name of certain bones of the 'hand' (see SKELETON, POST-CRANIAL).

METAL-TAIL: substantive name of HUMMINGBIRDS of the genus *Metallura*.

METAPATAGIUM: a membranous fold of skin between the body and the posterior margin of the upper wing (see MUSCULATURE; WING).

METATARSUS (adj. metatarsal): name of bones of the foot, 3 of them fused together in birds, and at their upper ends with the distal row of tarsals, to form the TARSOMETATARSUS (see also LEG; SKELETON, POST-CRANIAL).

METEOROLOGY: see BIRDS AND WEATHER.

MEW: archaic or poetic name, also 'sea-mew', for a gull (Laridae sp.), cf. German 'Möwe'; also, in American usage, adjectival name of *Larus canus* (see GULL).

MEWS: term used in FALCONRY.

MICROECA: substantive name of most species of *Microeca*, a genus of Australasian flycatchers (see FLYCATCHER (1)).

MICROPODIFORMES: name formerly used for the order APODIFORMES; SWIFT.

MICROPSITTINAE: see PARROT.

MICROSMATIC: with poorly developed olfactory sense (see SMELL).

MIGRATION: term used hitherto in ornithology for only those movements of bird populations occurring at predictable times of each year, between breeding and one or more non-breeding areas, and therefore involving flights in predictable directions. Movements which do not include an obligatory return journey or preferred directions of flight have been classed as 'DISPERSAL', 'nomadism', 'emigrations' and 'IRRUPTIONS' rather than 'true' migrations. But the functions of all these types of movement may be similar: to allow exploitation of different geographical areas at different stages of the annual cycle and in response to seasonal changes in population density and in the environment (see below). They may also follow from vegetational changes in an area, resulting from plant succession.

This long-established classification has resulted from emphasis on populations rather than individuals. Thus DISPERSAL has been distinguished from migration because only the latter need involve a change in the geographical centre of distribution of the population. Each individual, however, that takes part in the outward dispersive movement, from e.g., a seabird colony, might in fact fly in a preferred direction rather than at random; but different individuals would have to move in different preferred directions if the centre of distribution were not to change. Since dispersals usually occur at predictable times of year, and since, especially in seabirds, the individuals of the species concerned may reassemble at the breeding locality in the following year, the difference from 'true' migration lies only in the degree of unanimity amongst individuals concerning the preferred direction of departure.

In the more specific terminology of Berndt and Sternberg (1968), dispersals are movements that lead to observed dispersions (locations in space) of individuals of a population. Their terminology was developed for comparisons of the locations of individuals in successive breeding seasons, later termed 'natal dispersal' and 'breeding dispersal' by Greenwood (1980). Such studies consider only the resultant distances and directions involved, and not the routes by which the changes in breeding locations occur, which may or may not involve long-distance return migrations between breeding seasons.

Even in 'true' migrations, the routes, and therefore directions, by which individuals of a species return to their breeding areas are not necessarily the reverse of those followed on the outward journey. For example, the Pied Flycatcher *Ficedula hypoleuca* returns from Africa to its northern breeding range by a more easterly route. Fidelity to a previously used breeding site occurs commonly in long-distance migrants, and fidelity to a wintering site is found regularly in some wildfowl, especially geese, and estuarine waders. Some marked individual passerines have returned to the same 'wintering' area in Africa (Moreau 1972), but fidelity to a non-breeding locality may be the exception rather than the rule amongst passerines. This is especially true for species whose foods outside the breeding season occur unpredictably either in space (e.g., fruit and berry crops) or time (e.g., mass emergence of insects). Indeed, although some northern European thrushes, such as the Redwing *Turdus iliacus*, are generally considered to be 'true' migrants, the movements of individuals within the wintering range are best described as itinerancy (*sensu* Moreau 1972). It is but a short step further to include within the class of 'true' migrants species that may shift their breeding localities, within a year, e.g., Quail *Coturnix coturnix*, or between years, e.g., Crossbill *Loxia curvirostra*, and which also move about within their 'wintering' range. The difference from nomadism, which refers to movements of species that do not normally revisit either breeding sites or non-breeding areas, is thus one of degree and not kind.

Migration has also been defined in terms of a change of habitat, but in birds this does not always occur, e.g., Oystercatchers *Haematopus ostralegus* may move several hundred km between coastal breeding sites on sandy beaches in northern Britain and similar wintering habitats in southern Britain. On the other hand, the definition adopted by Baker (1978) in an attempt to find one which applies to individuals of all animal species—namely 'the act of moving from one spatial unit to another'—is too general, although it avoids the need to define habitat boundaries. It would be better to exclude unintentional movements (birds blown outside their normal range) and those used in everyday foraging and roosting behaviour by restricting the term migration to movements leading to a change of home range.

In bird species whose migrations involve long non-stop flights, physiological as well as behavioural changes usually occur before departure. The most marked behavioural changes occur in nocturnal migrants, particularly small passerines, which develop an additional activity rhythm during the hours of darkness, when they normally roost.

Methods of observation. Information on the daily and seasonal timing of migration of species, populations and individuals, on directions, routes and distances of flight, and on flight performance has been collected by the following methods.

(1) Direct observation usually of visible migration but sometimes of audible movements also (especially at night). Under favourable weather conditions for migration, many birds pass too high to be seen with the naked eye, but flights at moderate altitudes can be detected with the aid of binoculars, a method pioneered in the Netherlands to study diurnal migration of Chaffinches *Fringilla coelebs*. The directions of flights at lower altitudes are often influenced heavily by topography and thus may change frequently; hence it is difficult to establish preferred directions with accuracy from direct observations.

(2) Seasonal timings of migration may be established by noting dates of arrival at, and departure from, the breeding and non-breeding areas. This method gives reliable information on first arrivals and last departures, but continued passage through possible breeding or wintering areas may not be detected. However, at intermediate stopovers on migration routes it has been used successfully for determining the duration of passage, particularly of night migrants.

(3) Radar observations using long-range surveillance equipment, have proved complementary to those visual observations which record only low-altitude flights. They have been particularly useful for measurements of flight directions over long distances and uninfluenced by topography. Data on seasonal patterns of movement have been established chiefly for groups of species with similar flight characteristics. Recognition of individual species has not often been possible. The most detailed studies of the influence of weather on migratory departures and flight behaviour have been made with the aid of RADAR.

(4) Direction of flight can be determined by watching the silhouettes of migrants crossing the face of the full (or nearly-full) moon. The method demands prolonged observation of the moon's disc through a telescope or binoculars. Identification of migrants to the specific level is rarely possible. As the method can be used effectively for at most 7 days each month, it cannot provide much information on seasonal patterns of movement and has been largely superseded by the use of radar. It has been used most successfully in the USA (Lowery and Newman 1966). In northern Europe, cloud associated with the flow of maritime air from the Atlantic often renders observation at full-moon periods impossible.

(5) Marking of birds, with numbered metal rings, combinations of coloured rings, or plumage dyes, all of which can be used on a large scale, has provided a considerably quantity of data on migration routes, destinations and (less precisely) timing of movements. Bias in the regularity and reliability of reports from different parts of the world, however, requires results to be interpreted with caution. Nonetheless, the results can be assigned unambiguously to particular species.

(6) Radiotelemetry has given detailed information on the flight tracks and movements of individual birds. By the early 1980s, the weight of transmitter and power pack had been reduced sufficiently to permit attachment to birds of the size of Starlings *Sturnus vulgaris* for migration studies, and further miniaturization of transmitters and batteries is to be expected. Because of the restricted range of frequencies that may be used and the high cost of radio-tags, most studies to date concern only 20–30 individual birds. Limited detection range also restricts the value of the technique for migration studies, but radio-tags promise to give useful data on the behaviour of migrants immediately before departure, even if the birds cannot be followed thereafter (see RADIO TRACKING AND BIOTELEMETRY).

(7) Automated recordings of daily activity patterns of captive migrants can show when nocturnal migratory behaviour develops and for how long it continues. When the directional components of total activity have been separated, information has been obtained on preferred directions of departure of different species, and on cues for obtaining compass information (see NAVIGATION).

Patterns of migration

1. Time of day. Most long-distance passerine migrants, travelling from temperate or arctic breeding areas to tropical non-breeding areas, depart an hour or two after sunset, as recorded by radar in several parts of the Northern Temperate Zone. Although they fly chiefly at night and usually land at dawn, some make non-stop flights of several days' duration over inhospitable habitats, e.g., Blackpoll Warbler *Dendroica striata* from North to South America over the Western Atlantic Ocean. Many primarily nocturnal migrant passerines are insectivorous during the breeding season, but they may also feed on fruits before and, in daytime pauses, during autumn migration.

Most short-distance passerine migrants travelling chiefly within the Northern Temperate Zone, fly by day, often departing slightly before sunrise. But, in contrast to nocturnal migrants, they move for only a few hours in a morning before stopping to feed, unless they are aerial feeders such as Swallows *Hirundo rustica*, which may continue to migrate all day, feeding as they travel. Many diurnal migrants are primarily seed- or fruit-eating species, especially outside the breeding season in northern latitudes. A few of these species also migrate by night, e.g., Brambling *Fringilla montifringilla*. Soaring birds, including the White Stork *Ciconia ciconia*, and birds of prey such as the Black Kite *Milvus migrans*, move chiefly during the middle of the day when thermals which assist their flight are most active. Shorebirds (Charadrii) may depart at any time of day or night, since their activity patterns are also governed by the tidal cycle. Their departures often coincide with those times when they would normally fly to high-water roosts.

Exceptionally, nocturnal migrants may not leave until the middle of the night. Wave-like migratory departures from roosts several hours after dusk have been recorded by radar; they refer to Starlings leaving Britain in spring to return to breeding areas in continental Europe.

Several advantages have been suggested for migration at night: the availability of more than one astronomical cue to assist navigation so that migrants may obtain directional information from fixed patterns of stars, rather than from the changing position of the sun in the sky; reduced likelihood of predation, particularly important at the end of a flight when the migrant's speed may have fallen; and improved atmospheric conditions for detection of sound signals, which may give information about terrain below the bird, or about the positions of conspecifics; also the daylight hours become available for feeding.

2. Patterns of migration in species, populations or individuals moving each year.

2a. Distances and directions. The most prominent and extensive movements of land birds occur in a north–south direction. Most passerines breeding at high latitudes in the western Palearctic move towards equatorial regions of Africa during the Northern Hemisphere autumn, whereas those breeding in eastern Siberia move chiefly towards south-east Asia and Australasia (Moreau 1972). In the New World, extensive southward movements occur in autumn towards central and South America, though many species do not travel further than the southern states of the USA. The same pattern is broadly true of waterfowl movements in the New World, whereas in the Palearctic most species move further west than south to spend the (northern) winter in countries bordering the North Sea and the Mediterranean, and in West Africa. Autumn movements of several arctic-breeding wader species in the New World involve long south-eastward flights overland to the east coast near the Canadian/USA border, followed by southward flights to South America; others migrate southwards along the west coast of North America or make long overwater flights to 'wintering' areas on the Pacific Islands, the most spectacular flight being that of the Lesser Golden Plover *Pluvialis dominica fulva* from Alaska to Hawaii, a distance of about 4,000 km. Waders from Greenland fly south-east to Europe and then southwards to West and South Africa; many from Siberia, even from longitudes far to the east, move westwards in autumn to the western European seaboard. Some then continue southwards to north-west Africa. Others may fly overland from Siberia via the Caspian Sea to South Africa, whereas yet other species from eastern Asia move southwards to Australasia. Many of these long-distance routes approximate to great circles—the shortest distance between two points on the earth's surface.

Seabird movements are more complex still. Within the Atlantic region, many species move primarily on a roughly north/south axis, which may also involve crossing from the western side of the North Atlantic off Canada to the western side of Africa (Arctic Tern *Sterna paradisaea*), or from the eastern side of the North Atlantic off the British Isles to the eastern coast of South America (Manx Shearwater *Puffinus puffinus*). The tern continues its movements beyond southern Africa into the Antarctic Ocean, thereby flying some 25,000 km on the round-trip from and to its breeding grounds. Conversely some seabirds breeding in the southern Atlantic spend the non-breeding season in Northern Hemisphere waters, e.g., the Great Shearwater *Puffinus gravis*, which breeds on the Tristan da Cunha group of islands and congregates during the northern summer to moult off the Newfoundland coast. Similar extensive movements occur within the Pacific, e.g., those of the Mutton Bird or Short-tailed Shearwater *Puffinus tenuirostris* from breeding sites in southern Australia to moulting areas in the Bering Straits. This migration follows an almost circular route, at first north and westwards to Japan and later south and eastwards along the western coast of the USA before crossing back to Australasia.

Migrant land birds breeding at mid-latitudes in the Northern Hemisphere often do not move as far south in autumn as those from higher latitudes. In western Europe, the directions of most movements of passerines lie between south and west, to wintering areas in the British Isles, the Iberian Peninsula and the Mediterranean coasts and islands. In the Southern Hemisphere, which lacks extensive ice-free land masses further south than those at mid-latitudes in South America and southern Africa, most migrant species move northwards after breeding but rather few cross the Equator and none enter the Northern Temperate Zone. Some of the most extensive movements are made by aerial feeders, such as the Brown-cheeked Martin *Phaeoprogne tapera* from Argentina to Venezuela and central America.

Within the tropics, generalizations about directions of migration are hardly possible, since many movements are associated with the alternation between wet and dry seasons. These result from the seasonal movements of air masses and accompanying belts of rains, often in different directions in different parts of the tropics. Associated with each of these weather systems, which affect flowering and fruiting of plants, may be a separate migration system, as has been documented by Ward (1971) for *Quelea quelea* in different parts of Africa.

Short-distance movements between different altitudes also tend to occur in a variety of directions, dependent on the alignment of mountain ridges such as the Andes and the Alps. For example, the Grey-flanked Cinclodes *Cinclodes oustaleti* nests in the Chilean Andes above an altitude of 3,500 m and spends the non-breeding season along the sea coasts nearby.

2b. Time of year. Amongst species that migrate every year, major differences in seasonal timing occur, according to the feeding requirements of each species on the breeding grounds, the climatic zones crossed during their migrations and the timing of other events, such as moult and reproduction, in their ecophysiological cycles. Generalizations are difficult to make. Land-birds nesting in the high Arctic, north of the tree-line, usually depend upon the emergence of insects for successful reproduction; they must arrive in the Arctic late in the spring (May or June) and so pass through the lower latitudes well after many, including their own, species have begun nesting there. The lower-latitude breeding species usually do not move such long distances after the breeding season, and may still be present on their breeding grounds when the higher-latitude species return in late summer and early autumn. The lower-latitude species often have protracted migration periods.

Of more general relevance are situations leading to variations in timing of movements within a species. An observer may notice the occurrence of several periods of passage of the same species during a single season through a refuelling area on the migration route. These can arise in autumn in several different ways: (1) Different breeding populations may reach the same place at different dates, e.g., Dunlin *Calidris alpina* from Iceland and Greenland pass through the British Isles in August and September, en route for north-west Africa, whereas those from northern Russia reach the end of their migration route in the British Isles, arriving from mid-September onwards. (2) Young birds, particularly of species deserted by their parents soon after hatching, may leave arctic breeding areas many weeks after the adults. Adult Grey Plovers *Pluvialis squatarola* move from their breeding areas in Siberia to moulting grounds in western Europe 4–5 weeks before their juveniles reach the same areas. (3) Males and females may migrate at different times. This occurs in many shorebirds, in some of which males (and in others females) leave the breeding grounds first; also amongst certain wildfowl in which males take no part in care of their young and desert their mates once they have begun incubation, e.g., Eiders *Somateria mollissima*, in which males move to moulting grounds well before females. (4) Young of later broods may migrate later than those from first broods, e.g., House Martins *Delichon urbica*, whose second broods may not fledge until September. Indeed a higher proportion of young from later broods may be migratory, as in Great Tits *Parus major* in northern parts of continental Europe. (5) In single-brooded species with long periods devoted to incubation and care of the young, failed breeders may migrate earlier than successful breeders, e.g., European Shelduck *Tadorna tadorna* moving to their moulting grounds in north-west Germany.

In addition to these situations which lead to several waves of passage, the duration of a single migratory wave may be prolonged in species with a wide spread in dates of laying, particularly those in which birds breeding for the first time do so later than experienced breeders.

Some of these temporal patterns of movements are noticeable also in spring. Different breeding populations often occur at a locality on passage on different dates. Indeed, departures of different populations from a common wintering ground may take place in different months, as in the case of the races of Yellow Wagtails *Motacilla flava* wintering in Zaire. Males of species that defend territories during the breeding season usually return to the breeding grounds before females. Birds attempting to breed for the first time may migrate later than older birds. Indeed in some waders, e.g., Bar-tailed Godwit *Limosa lapponica*, immature birds may migrate towards the breeding grounds not only later than potential breeding birds, but also without completing the journey. Migrations of species within the tropics may be less predictable on a calendar basis, since the timing of the wet and dry seasons is also less predictable than that of the seasons at higher latitudes.

Amongst the smaller insectivorous passerines, several species contain partially migratory populations, particularly at higher latitudes. These comprise some individuals that leave their breeding grounds each autumn and return each spring and others that are resident. In mild winters, the residents survive better than the migrants, which suffer mortality not only on the more southerly wintering grounds but also during migration; in cold winters on the breeding grounds the residents survive worse (e.g., Goldcrests *Regulus regulus* in Finland). Partial migrants tend to move south later in autumn but return earlier in spring than long-distance migrants breeding in the same areas (e.g. Willow Warbler *Phylloscopus trochilus*).

3. Patterns of migration in species, populations, or individuals moving only in some years. Amongst the types of migrants falling into this category, the most prominent are those taking part in IRRUPTIONS. Others include those populations in which certain individuals are partial migrants, moving in some years but not in others, or different distances in different years, albeit along the same preferred direction. The British race of Redpolls *Carduelis flammea cabaret*, which utilizes the seeds of birch *Betula* in winter, comes into this category.

Large seabirds, such as albatrosses, that attempt to breed only every other year but move away from the breeding colony between attempts, may also be considered as irregular migrants.

Finally, some species, particularly those that feed by probing in damp earth or picking prey from the surface in short grasslands (see PLOVER) may move in response to the onset of freezing conditions. These 'hard-weather migrants', like the Lapwing *Vanellus vanellus* and Skylark *Alauda arvensis*, move in directions most likely to lead them to unfrozen feeding areas, i.e., between west and south. In mild winters, no such movements take place; in other years, their timing is dictated by the occurrence of the severe weather.

Functions of migration. Successful migration enhances the lifetime reproductive output of an individual, either by increasing its chances of survival or by allowing it to breed where it can rear more young than if it remained resident in another site, or for both reasons. In some species migration allows colonization of areas in which individuals could not survive throughout the year.

In relation to increased reproductive performance, migration to higher latitudes provides longer hours of daylight, between the spring and autumn equinoxes, in which young can feed or be fed. This is particularly important to species such as the passerines that forage visually and not by touch, and thus are dependent upon daylight feeding. Disturbance and predation pressures from mammals may also be less at higher latitudes, since few predatory mammals can survive there through the winter. This may permit greater nesting success for ground-nesting species, e.g., shorebirds.

The chances of survival of migrant individuals during the breeding season are greater in temperate and arctic areas than they would have been in the (often tropical) non-breeding areas, for reasons considered above and later. Against this must be balanced the costs of the journey. A similar equation can be drawn up for seasonal movements within tropical regions according to the timing of wet and dry seasons. In many cases, food is more abundant or more predictable in the breeding area, particularly once nesting has begun, than it would have been in the non-breeding area at the same time of year.

'Moult migrations' are also concerned with enhancing the chances of survival of the individual—in this case, normally a waterfowl. Aggregations of certain species, or sex- or age-groups, of ducks and geese occur in areas of plentiful food and/or improved protection from mammalian predators when they are at their most vulnerable, having shed all their flight feathers in rapid succession.

For many species breeding in the North Temperate or Arctic regions and migrating southwards in autumn, the clemency of weather they face in the non-breeding area increases, the further it lies from the breeding area. Taken to its extreme in trans-equatorial migration, movement can eliminate the hazards of severe weather, except on the flight itself, by taking birds from the northern summer to the southern summer and back again in a single year. In species whose average life expectancy is more than a few years, individuals would be expected to produce most offspring during their lifetimes by devoting resources chiefly to survival in the early years of life and to reproductive efforts later. The longer-distance migrations of young, of species such as Black-headed Gulls *Larus ridibundus* from central and northern Europe, to less severe winter conditions than encountered by adults agree with such a prediction. Theoretical considerations of reproductive investments by males and females may explain why the non-breeding areas of the two sexes sometimes differ. For example, in waterfowl, females often move to safer places; in some terrestrial species, males may attempt to stay on or close to breeding territories whilst females migrate to more favourable climates.

Dingle (1980) has suggested that most migrants may be 'fugitive' species, which cannot compete successfully with residents, and are displaced into marginal habitats, whose resources are less predictable in space and time than are those occupied by the residents. As in insects, successful utilization of marginal habitats can be achieved only by mobility (a biological response to adversity), so fugitive species of birds have been pre-adapted to take advantage of seasonally available resources in mid- and high-latitudes. The habitats occupied by passerine migrants in the non-breeding season tend to have transient resources—hence the itinerancy reported by Moreau (1972) in Africa.

Evolution. Long-distance migration must have evolved many times in many species. Most of the migration patterns seen today, in all their variety and complexity, must have altered considerably in the last 10,000 years, since the last glaciations. (Intra-tropical movements may, however, have existed relatively unaltered for a much longer period.) The glaciations were not responsible for the origin of migrations, only for modifying distances moved. Many existing routes bear no relation to the geographical patterns of advance and retreat of the glaciers. However, the movement patterns of several species appear conservative. For example, although the Wheatear *Oenanthe oenanthe* has spread as a breeding species from the Palearctic eastwards into Alaska and westwards into Greenland, the non-breeding area has remained within Africa and birds from the outlying breeding areas rejoin those from the Palearctic on their way south in autumn.

Although easier achievement of energy balance, by migrating from severe climates, may be an important advantage for some present-day migrants from high-latitude breeding areas, other species have evolved adaptations which permit survival through the worst weather in those same areas, e.g., the resident Scandinavian Yellowhammers *Emberiza citrinella* have thicker plumage than the migratory Ortolan Buntings *E. hortulana*. Hence, migration need not have evolved solely for energetic reasons.

In Africa, central America and other areas used by non-breeding passerine migrants, resident and migrant species are often segregated by habitat or microhabitat. This has been taken as evidence for competition and shortage of food in the non-breeding areas, but such a deduction ignores the differences in the types of habitat used by the two groups of species. Migrants are usually found in habitats where they can utilize superabundant but erratically distributed food resources, both in time and in space. These habitats are probably unsuitable for breeding attempts for most species, unless food concentrations remain for long enough to enable completion of a breeding cycle at least once every few years.

Migration may thus have evolved in the non-breeding areas by colonization of, or displacement of species into, habitats that provided adequate food for survival of nomadic individuals but were insufficiently predictable for successful reproduction; followed by further movements to temperate and higher latitudes where productivity at certain seasons was sufficiently great and predictable.

These generalizations may apply only to passerines. Myers (1981) points out that both migrant and resident shorebirds present during the southern summer in coastal areas of Argentina use dependable food resources, albeit erratically distributed in space. He suggests that the migrant sandpipers that evolved in the Northern Hemisphere have failed to establish themselves as breeding species in Argentina chiefly because their densities there are so high that behavioural and competitive interactions do not allow sufficient time and resources for successful breeding. The few local breeding species of shorebirds are taxonomically and ecologically distinct from the migrants.

Preparation for migration. In longer-distance migrants, two distinct phases of preparation can be identified. The first, termed *Zugdisposition*, is concerned with physiological preparation for the energy demands of migratory flight. The second, *Zugstimmung*, leads to the behavioural changes needed to initiate and maintain prolonged flight. It may involve a change in the daily rhythm and orientation of activity, under hormonal control. In caged birds, *Zugstimmung* is expressed as *Zugunruhe* (migratory restlessness), a phenomenon which has been exploited in studies of orientational preferences. Field studies of the behaviour of migrants at a refuelling area (Rappole and Warner 1976) have highlighted differences in behaviour between birds in *Zugdisposition* ('feeders') and those in *Zugstimmung* ('flyers') within the same species. Feeders attempted to acquire territories and did not gain weight unless they did so; flyers foraged in groups and gained little weight. Flyers flocked to assist in synchronizing their departures.

Physiological preparation. Fat is the main fuel used for extended flights by birds. Weight for weight, it provides more than twice as much energy when oxidized as does glycogen, the carbohydrate fuel used by many (but not all) species of migrant insects. Before migration, fat is stored chiefly in subcutaneous and visceral deposits, sometimes known as fat pads. Increase in the mass of a pad results from accumulation of fat within existing adipocytes (fat storage cells), rather than from proliferation in the number of such cells. In general terms, the mass of fat stored before a migratory flight is related to the distance to be flown, especially in terrestrial birds making obligatory sea- or desert-crossings. In species, such as the Ruby-throated Hummingbird *Archilochus colubris*, that migrate across the Gulf of Mexico, fat may form about 50% of the total mass of a bird before its departure. A similar load is carried by some Sedge Warblers *Acrocephalus schoenobaenus* migrating from the British Isles towards West Africa in autumn and by some waders leaving Britain for the high Arctic in spring. The extent, if any, of the safety margin of fat carried by different species, above that required for flight to the destination in calm air, is not known. Possibly some species rely on flight with following winds to make a successful journey.

Not all species begin migration with the maximum fat load they are known to carry. In spring in the North Temperate areas, many songbird migrants that move up to a few thousand km in a series of relatively short flights may set out from their 'wintering grounds' with rather small deposits of fat. This may be an adaptation to link the rate of their movement northwards with the timing of improvement in weather conditions. In autumn, long-distance migrants begin to move southwards from their breeding grounds with small fat stores, but build up reserves en route towards geographical barriers. For songbirds that change diet to include ripe berries in late summer, it becomes progressively easier for them to increase their rate of food intake, as they move south, if they start soon enough, since most fruits ripen earlier at lower latitudes.

Glycogen is not an important source of energy for long flights. The chief storage organ is the liver, and the maximum quantity that has been recorded represents less than 1% of the total mass of a bird. However, although this and other components of the lean mass of a migrant—skeleton, water and protein (chiefly muscle and gut)—do not change measurably during fat deposition in some migrant species, there are definite increases in flight muscle mass before migration in a few passerines and shorebirds, e.g., Dunlin, and of decreases in flight muscle mass, to below 'normal' levels, in several shorebirds after flights from Europe to Mauritania, W. Africa (Dick and Pienkowski 1979). Such changes in muscle mass would be expected if migrants attempted to fly at optimum speeds (see below), which should be high when they first depart and are heaviest, but decrease as they use up their fuel during flight (Pennycuick 1978). A reduction in flight speed without a change in wing-flapping rate could be achieved by reducing power output, i.e., by reducing muscle mass.

Control of fat deposition. In birds, fat is synthesized in the liver and transported to the storage sites in the blood as low-density lipoproteins. The source of the increase in the rate of fat synthesis before migration is chiefly an increase in daily food intake. If food is restricted, fat deposition can be prevented in captive birds. Metabolic changes which would allow greater availability of materials for fat storage without an increase in food intake—namely, a reduction in maintenance energy, more efficient assimilation of the normal diet, or change to an 'energy-rich' diet—are not of general importance, though they have been claimed as important additional factors for a few species. Most laboratory studies have revealed that an increase in food intake precedes, or is independent of, the timing of onset of nocturnal activity in captive migrants, so that an independent means of control of food intake must be sought. Prolactin has been implicated as the hormone most heavily involved both in stimulating appetite and in increasing the rate of fat synthesis in the liver. Its effects are dependent on the time of day at which it is administered to captive birds, and circadian rhythms of prolactin release are known to occur in free-living birds.

Once fattening has begun, it may produce gains of body weight of as much as 5% per day in small warblers *Acrocephalus* (Gladwin 1963). However, rates of use of fat during flight are much faster. Hence, unless migration is accomplished in a single non-stop flight, pauses for 'refuelling' must separate periods of flight by several days at least.

Control of the timing of migration.

1. Ultimate factors. Migration must be timed to bring individuals to potential breeding areas at the most appropriate times (see BREEDING SEASON). Movement away from the breeding area may be timed by the need to moult at a particular site, or to reach a certain refuelling site as soon as possible before its food resources have been depleted, or to establish a feeding site in the non-breeding area.

Thus the timings of movements are ultimately controlled by the influence of seasonal fluctuations in the availability of food on reproductive success and survival.

2. Proximate factors. Since long-distance movements cannot be undertaken without adequate preparation, both physiological and behavioural, certain timing factors must operate to initiate these processes in advance of the dates when migration 'should' take place.

For transequatorial migrants, the timing of start of fat deposition and migratory restlessness at the end of the non-breeding season and after breeding is controlled chiefly by an internal circannual rhythm, synchronized perhaps by changes in daylength on the breeding grounds (see RHYTHMS AND TIME MEASUREMENT). For migrants wintering in the Northern Temperate Zone, preparation for spring migration is initiated chiefly by the increase in daylength beyond a certain threshold. Preparation for autumn migration in these species may be timed as a 'carry-over' effect from the spring, since many species lose their sensitivity to photostimulation in late summer after breeding. Alternatively, they may rely on a circannual rhythm for timing of fat deposition and changes in behaviour in autumn, as presumably must the juveniles of such species. Once initiated, the rate of development of migratory condition can be modified by secondary timers such as temperature, particularly in spring.

In intra-tropical migrants, whose movements are related to the alternation between wet and dry seasons, rainfall, or its indirect effects on food abundance, is most likely to act as the proximate timer.

Once adequate levels of fat deposition have been achieved, weather conditions provide the 'fine tuning' to the timing of a migratory flight. There exists an interplay between the degree of physiological preparedness and the favourability of the weather in determining whether or not a migrant will depart. The effects of weather on migration have been reviewed by Richardson (in Alerstam *et al* 1978). Particularly in spring, the rate of advance of passerine migrants is closely correlated with the northward movements of certain isotherms, which suggests that temperature, as well as the presence of following winds, may exert an important influence on departures. Once migration is underway, if migrants then land with low fat reserves, their migratory behaviour may be suppressed temporarily whilst they regain weight. However, such physiological inhibition of migration in individuals may be over-ridden by social factors in species that fly in flocks by day or that feed upon the wing.

Flight performance. Pennycuick (1969, 1975) has predicted from models of the mechanics of bird flight that each individual should migrate at a speed which maximizes the range it can achieve for each gram of fat oxidized. For migrants carrying large loads of fat on departure, the maximum-range speed should decrease as fuel is used up. This awaits confirmation by radar observations. So also do a series of predictions concerning rates of climb and altitudes of flight, published by Pennycuick (1978).

Body temperatures of flying birds normally lie above those of resting birds, so that cooling of the bird during migration can be considered a major problem. This is achieved by two routes—direct loss of heat by convection from the surfaces of the flight muscles and underwings, and evaporative cooling via the respiratory system. It has been claimed that water requirements rather than the size of energy reserves may limit the flight range of many migrants, but conclusive evidence is lacking. Migrants may alter the relative importance of the two routes of heat loss by adjusting the altitude at which they fly: direct convective loss increases at the lower temperatures found at higher altitudes. However, many other features are involved in choice of flight altitude.

Most passerines fly at altitudes of less than 1,500 m, but at the end of a long flight over the western Atlantic birds have been recorded as high as 6,800 m above the sea. It is not known whether they had adopted a 'cruise-climb' strategy on the flight from the north-eastern USA. Migrant shorebirds have been recorded at greater altitudes. Canada Geese *Branta canadensis* have been seen by radar to fly over the Canadian Rockies on migration. The altitudes chosen by passerines may be affected by the favourability of the wind direction if this varies with height above ground (see also FLIGHT; FLIGHT, SPEEDS OF).

Most migration of songbirds takes place on a broad front, especially by night. By day, concentrations of migrants may form along 'leading lines'—topographical features marking the boundaries between habitats. Particularly effective are coastlines, if the preferred migration directions would lead landbirds over the sea. Such 'leading lines' are followed primarily when migration occurs into a headwind, for birds fly low under these conditions. Other concentrations may occur along escarpments, which may provide shelter for small passerines, or mountain ridges which provide updrafts to assist soaring birds on migration. Other groups of species may follow narrow migration routes because their areas of origin are restricted. For example, shorebirds congregate on estuaries as refuelling areas during migration. These are often well separated geographically. They then depart on narrow routes for the next section of their long-distance journeys.

Flocking of migrants occurs chiefly by day—possibly as an anti-predator adaptation. Although large numbers of birds migrate by night, evidence for tightly-bunched flocks is scarce, though individuals of many species call in flight, which may serve to keep loose groupings together, perhaps to assist in maintenance of the preferred direction.

Even if migrants prepare adequately for flight, choose appropriate weather conditions for departure, and fly at suitable altitudes, long-distance migration will be successful for an individual only if it chooses an appropriate direction of flight. The mechanisms of orientation and navigation are dealt with elsewhere (see NAVIGATION). Two points are relevant here: (1) weather conditions at the time of departure restrict the orientational cues available for use—for example, the stars are obscured by total cloud cover; and (2) weather conditions during flight determine whether or not a migrant can maintain its preferred flight track. Strong side or headwinds may force a small slow-flying songbird to abandon its track and allow itself to be blown off course (see DRIFT).

See photo RADAR. P.R.E.

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MIGRATORY RESTLESSNESS: the unsettled behaviour of birds immediately before they are due to depart on migration, also called 'pre-migratory restlessness' or (using a German term) 'Zugunruhe' (see MIGRATION).

MILK, CROP: see CROP MILK.

MILK, PIGEON: see CROP MILK.

MILLERBIRD: *Acrocephalus familiaris* of the Hawaiian Islands (for subfamily see WARBLER (1)).

MILVINAE: see HAWK.

MIMESIS: same as MIMICRY (adjective 'mimetic').

MIMICRY: the resemblance, by evolutionary convergence, of one species to another for mutual or one-sided benefit. This phenomenon is widespread among insects but rare in birds where, however, it has not been searched for in a systematic manner.

Mimicry in birds commonly involves plumage and shape, sometimes also posture, movements or voice. Cases of alleged mimicry must be carefully evaluated before drawing conclusions regarding their functional and evolutionary basis. Interspecific resemblance may be simply the expression of close relationship, or of parallel adaptations to a common environment and shared specializations.

Defensive mimicry. A docile and palatable animal may evolve a resemblance to a pugnacious or unpalatable one in order to achieve protection from enemies (Batesian Mimicry). From encounters with the unpleasant species, predators learn to avoid it and, in the process, will avoid similar species, whether unpleasant or not; avoidance may also be innate. The two African forest flycatchers *Stizorhina* resemble almost to perfection the two ant-thrushes *Neocossyphus*, presumably shunned by predators because of the smell of formic acid transferred to them from their food. The 'snake mimicry' of cornered Wrynecks *Jynx* includes 'scaly' plumage pattern, undulating movements of the extended neck, and hissing. Brooding titmice *Parus* may move their necks, feign attacks and hiss like snakes toward an intruder from the darkness of their nest cavity (hence no plumage mimicry is required).

In other cases, association with a pugnacious model may be a prime selective force. Examples are 5 Moluccan–New Guinea orioles *Oriolus* which are more dull-coloured than their continental congeners but which resemble, species for species, 5 pugnacious honeyeaters *Philemon* with which they share feeding sites; and 2 African black flycatchers *Melaenornis*, which resemble 2 pugnacious drongos *Dicrurus* with which they frequently associate.

The benefit obtained by a mimic will increase as the model becomes relatively more common. Should a model become rare, the advantage gained by the mimic will decrease, as will selection pressure in favour of resemblance. However, a highly deterrent model need not present itself very often to maintain its beneficial influence on the mimic. Several cuckoos of the genus *Cuculus* have evolved a striking resemblance to specific birds of prey which as a rule do not markedly outnumber the cuckoos. The main purpose of this resemblance is thought to be protection from other raptors. Whether it confers any net advantage to the cuckoos in their parasitic activities remains uncertain.

Another form of defensive mimicry (called Müllerian) implies that several 'unpleasant' species converge in appearance in order mutually to reinforce their deterrent effect on a predator—a situation well known from butterflies but so far not demonstrated in birds. The concept of 'social mimicry' advocated by some authors may, however, include aspects of this kind.

Aggressive mimicry. The model in this case may or may not be a victim of the mimic. Eggs of parasitic cuckoos usually mimic those of locally preferred foster-parents. Nestling whydahs *Vidua* have gape patterns of the same shape and colour as their foster-siblings, species by species, which will elicit feeding by fosterers and prevent the parasite from being ejected. Similarly, nestlings of some parasitic cuckoos (the Drongo Cuckoo *Surniculus lugubris*, the koels *Eudynamis*, the Channel-billed Cuckoo *Scythrops novaehollandiae* and various *Clamator* species) have a plumage resembling their most frequent foster-siblings, usually drongos or crows; and young Parasitic Weavers *Anomalospiza imberbis* are said to mimic the plumage of young *Cisticola* warblers, a frequent host genus.

There may also be cases where a raptor resembles an abundant innocuous species, enabling it to approach its prey unnoticed. The white morph of the Indo–Australian Goshawk *Accipiter novaehollandiae* probably evolved in response to the presence in great numbers of white cockatoos *Cacatua galerita*. On islands where goshawks occur but not cockatoos, the white morph is absent. In this instance, the model presumably is not affected by its role in the interaction between predator and prey, since the latter does not include cockatoos. The occasional adoption by hunting Merlins *Falco columbarius* of a 'passerine' flight mode has also been interpreted as aggressive mimicry. The dangers of interpretation are highlighted by the case of the Zone-tailed Hawk *Buteo albonotatus*, whose resemblance in silhouette, flight, and plumage to the innocuous Turkey Vulture *Cathartes aura* may have originated as an aggressive disguise but may now serve mainly as a means of avoiding being mobbed by passerines (see also BROOD-PARASITISM; COLORATION, ADAPTIVE; MIMICRY, VOCAL). C.E.

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MIMICRY, VOCAL: imitation by birds of sounds other than their specifically characteristic vocalizations. The place that the ability to imitate sounds plays in the development of the vocalizations of a species is dealt with to a certain extent elsewhere (see LEARNING; VOCALIZATION). However, the vocal performances of those birds that can not merely imitate sounds characteristic of their own species or of other species of birds but can even imitate the human voice and other sounds of non-avian origin, pose problems of quite a different order for students of animal behaviour and of phonetics.

Consonant and vowel sounds. Roughly speaking, there are two types of consonant sound in human speech, the plosives (of which p, b, t, and d are examples) and the fricatives (which include f, v, and varieties of s, z, and ch sounds, all on the whole of relatively high frequency). The first group, the plosives, really involve different ways of stopping and starting sounds more or less suddenly, with more or less explosive force, and with greater or less infusion of high frequencies. Since birds in the course of producing their normal vocalizations are obviously capable of stopping and starting their sounds with extreme suddenness, we should expect them to be able to produce something like our consonants; but since their tongue, larynx, and mouth cavity are so different from ours, and since the overall size of the vocal organs of most birds is so much smaller than ours, we should not expect sound-spectrograms of birds' voices to show more than a slight and very general resemblance between the stopped sounds of birds and those which we ourselves produce. Thus we find that the sound-spectrograms of normal bird voices do not give us any very clear evidence of distinguishing between, say, p and b, or t and d. When we come to the fricatives we find that the resemblances are a good deal closer, and we can distinguish in bird vocalizations sounds that are closely similar to a number of our own fricative consonants; it is for this reason that, when we attempt to represent the sounds of small birds in words, we find ourselves making such lavish use of the letters f, v, s, x, and z. Thus, the closest similarities between human consonants and the sounds made by birds as part of their normal repertoire are found amongst those that depend on the range and relative intensity of the higher frequencies present.

When we come to the vowels, the problems posed by bird vocalizations are of peculiar interest to the phonetician. Twenty-three different vowels or vowel-like sounds are recognized in human speech. These are the incidental results of the fact that we have more than one resonator. Vowels occur whenever our throats and mouth cavities are stirred into resonance simultaneously, whether this is due to vocal cords (as in speech and song, when the sound is said to be 'voiced') or whether it is merely due to the airstream passing through both cavities, as in whispering. Four types of modulation occur in speech: (i) start-stop, (ii) vocal cord, (iii) frictional, and (iv) cavity modulation. Of these, (i) and (iii) affect the flow of air from our lungs, (ii) and (iii) convert it into audible sound waves, while (iv), broadly speaking, varies the quality of the sound. The different types of consonants discussed above are produced by differing combinations of these types of modulation but always contain (i) or (iii) or both. When pure vowels or vowel-like sounds are produced in ordinary speech, only (ii) and (iv) occur. The vocal resonances that give the vowel sounds their characteristic qualities are determined by the shapes and sizes of the resonators and are under very precise control by the movements of the lips, jaw, tongue, and soft palate; but it stands to reason that this cavity modulation will affect the sounds produced by the vocal cords very much more than those produced by frictional modulation, since the sounds produced by the vocal cords arise behind the cavities concerned whereas those produced frictionally arise in front.

Talking birds. At first sight the vocal equipment of birds does not appear to have the cavities necessary to enable them to produce anything at all similar to our vowels, and examination of sound-spectrograms of bird vocalizations often shows that when we think we hear a particular vowel we may be deceiving ourselves. In some cases all that the bird seems to be doing is to change the overall pitch of the sound in the same general manner as we may change pitch during vowel production, but without producing the characteristic human resonance patterns. However, there is no doubt that some species of birds, particularly those such as parrots Psittacidae and mynahs *Acridotheres* spp., which can be taught to produce plausible imitations of human speech, do in fact do something more than this and can, in a manner not yet by any means understood, produce a surprisingly accurate copy of the vocal resonances hitherto regarded as peculiar to human speech. A great deal more anatomical and physiological research will be necessary before it will be possible to account fully for the talking abilities of birds, and until this further knowledge is available speculation is apt to be profitless.

Quite apart from the physiological problems arising in connection with bird imitation of human speech, there are other questions concerning the evolution and biological function of this mimetic ability. Talking birds are so familiar to us that the significance of the performance has often been overlooked. No satisfactory evidence is available that either parrots or mynahs ever use their remarkable powers of imitation in the wild; these seem to lie completely latent. Within the primates we find a great variety of vocal mechanism which, it would seem, should enable some of these apes to produce excellent imitations of human speech, yet not even the chimpanzee can be taught to do this. That the birds with their entirely different and apparently much inferior vocal equipment can on occasion overcome almost perfectly the problems of phonation posed by human speech is indeed mysterious.

Why these birds should learn to imitate human speech when kept in captivity is perhaps a little more understandable. Many birds such as Budgerigars *Melopsittacus undulatus* and mynahs learn to talk best when they are kept in close contact with human beings but away from their own kind. This is probably because, as they develop a social attachment to their human keepers, they learn that vocalizations on their part tend to retain and increase the attention that they get, and as a result vocal production, and particularly good vocal imitation, is quickly rewarded by social contact. This seems an obvious explanation of the fact that a parrot when learning will tend to talk more when its owner is out of the room or just after he has gone out—as if he is attempting, by his talking, to bring him back. If this theory about the psychology of talking birds is correct, it makes their process of learning appear very similar to that of the human infant in its first attempts to talk. Mowrer (1950), in advancing this hypothesis, has suggested that birds and babies make their first efforts at reproducing words and other sounds because these sounds seem good to them—they are, in fact, self-stimulatory. Mothers often talk or croon to babies when attending to them, and so the sound of the mother's voice has become associated with comfort-giving measures. So it is to be expected that, when the child, alone and uncomfortable, hears its own voice, this will likewise have a consoling, comforting effect. In this way Mowrer supposes that the human infant will be rewarded for his own first babbling and jabbering without any necessary reference to the effects that these sounds produce upon others. Before long, however, he will learn that if he succeeds in making the kind of sound his mother makes he will get more interest, affection, and attention in return; and so the stage is set for the first steps in the learning of human language. In spite of all the differences, it seems hard not to believe that something of the same sort is happening in the learning of human speech by pet birds.

Mimicry in wild birds. While many birds learn their songs, or at least some phrases of them, by imitation from others of their own species, it is well known that some species incorporate into their songs sounds copied from completely alien species or even sounds of non-avian origin. This tendency to mimic a wide variety of sounds can probably be regarded as a special development of the ability to learn songs from the parents or other conspecifics. It has been shown that some species that show no traces of imitation of alien sounds in their songs nevertheless include quite a number of such sounds in their sub-songs. When these sub-songs are transformed at the beginning of the breeding season into the true songs, all the sounds of alien origin are omitted. This fact will perhaps give a clue to the development of this faculty of general mimicry, for it is significant that sub-songs seem to have little or no communicatory function, whereas the songs themselves, at least in territorial species and probably in many others too, are important in transmitting information to other members of the species about the circumstances of the singer, e.g., whether mated or not, whether established in a territory, and sometimes also constituting an individual recognition mark.

There is no doubt that a very large number of species occasionally imitate alien sounds, but only very few species are good general mimics. Even in those which are renowned for their mimicry, such as the Starling *Sturnus vulgaris*, the Marsh Warbler *Acrocephalus palustris*, and the Mockingbird *Mimus polyglottos*, it is far from easy to make any estimate of how much of the vocal repertoire has been picked up in this way. It is estimated that an average male Marsh Warbler mimics 76 species (range 63–84). Of particular note is the observation that about half the mimicked species are from the Marsh Warbler's breeding area in Europe, while the other half are from its wintering grounds in Africa. As regards the percentage of total song that consists of mimicry, for Mockingbirds estimates are from 5%–18%, for Starlings about 10% and for White-eyed Vireos *Vireo griseus* about 53%.

The robin chats *Cossypha* spp. are said to include some of the best mimics among African birds. *Cossypha dichroa* seems to interact vocally with the models: it tends to match vocalizations of species it mimics in direct response to their songs. In Australia, the bowerbirds Ptilonorhynchidae, the lyrebirds Menuridae, and the scrub-birds Atrichornithidae are all renowned as mimics; and Chisholm (1937) has pointed out that it is the ground-living members of these and a number of other families in Australia that are most skilled and persistent in their mimicry.

Marshall (1950) points out that most vocal mimics in Australia are strongly territorial (although not necessarily using their vocalizations in territorial defence), and that most of them carry out much of their mimicry near the ground in wooded country where visibility is limited. He suggests that the lack of visibility places a premium on communication by sound. A number of hypotheses have been put forward to account for the biological significance of mimicry, all of which may be correct, since mimicry probably serves a variety of functions in different species. (a) *Mimicry is a method of acquiring a large repertoire.* There is some evidence that variety in bird song is attractive to females (an 'acoustic peacock's tail') and mimicry may simply be a way of increasing repertoire size. In one study of Mockingbirds there was some evidence that individuals with larger repertoires paired earlier. (b) *Mimicry is important in interspecific territoriality*. Some species mimic many of their competitors (e.g. *Cossypha dichroa*) and may use their mimicked song in interspecific territoriality. (c) *Mimicry as a form of deception*. The Thick-billed Euphonia *Euphonia laniirostris* is reported to mimic the mobbing calls of other species nesting near its breeding site, thus inducing them to mob predators while the Euphonia retreats to a safe distance. It is possible that there are other examples of mimicry used to deceive competitors, rivals or predators, but as yet there is no convincing evidence for this. (d) *Mimicry in reproductive isolation*. The parasitic Paradise Whydah *Vidua paradisea* learns part of its song by mimicking that of the host species *Pytilia*. Song in *Vidua* plays a role in mate attraction, and it appears that a female prefers to approach *Vidua* males singing the song of the foster-species by which she was reared. Thus song learning ensures that the brood parasites selectively mate with individuals reared by the same hosts, thereby maintaining host-specific reproductively isolated parasite species. W.H.T. (J.R.K.)

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MIMICS: sometimes used as a general term for the Mimidae.

MIMIDAE: a family of the Passeriformes, suborder Oscines; MOCKING-THRUSH.

MINER: substantive name of *Manorina* spp. (see HONEYEATER).

MINER (alternatively **MINERA**): substantive name of *Geositta* spp. (see OVENBIRD (1)).

MINERAL REQUIREMENTS: see NUTRITION.

MINIVET: substantive name of *Pericrocotus* spp. (see CUCKOO-SHRIKE).

MINLA: substantive name of the 2 species of *Minla* of south-east Asia (see BABBLER).

MIOMBO: an environment, consisting of sparse leguminous woodland (*Brachystegia*), characteristic of large parts of south-central Africa.

MIRROR: a white spot on the otherwise black wing tip of certain species of gulls (Laridae).

MISTLETOEBIRD: *Dicaeum hirundinaceum* (see FLOWERPECKER).

MIST NET: see TRAPPING.

MITES: see ECTOPARASITE.

MITOSIS: ordinary cell-division, without reduction in the number of chromosomes (see CELL).

MOA: substantive name of the species, all extinct, of the family Dinornithidae, order Struthioniformes, suborder Apteryges.

The moas were wingless, cursorial birds, of moderate to very large size, endemic to New Zealand; a moa bone found in Australia is now believed to have been taken there from a New Zealand site by man (Scarlett 1969); fossil remains are extremely rare, virtually all the abundant material so far discovered being of Post-Glacial age; the living birds were hunted by the prehistoric Maoris, and extinction became complete only within the last few centuries. Examples of the largest species, *Dinornis maximus*, estimated to have stood more than 3 m high, were the tallest, though not the heaviest, birds ever known, being exceeded in mass by the largest Dromornithids and some Aepyornithids.

Discovery. In the early years of European exploration in New Zealand there is no unequivocal evidence that the Maoris had any memory of the former existence of giant birds, or that they had a name for them, although the archaeological record proves that their ancestors were hunting moas only a few hundred years previously. The name 'moa' did feature, but only very rarely, in a few Maori traditions, but there was no clear indication of what it meant, beyond that it implied some kind of monster, man or bird. After Europeans had found bones of giant, extinct birds, the name 'moa' (the widespread Polynesian word for 'chicken') was applied to these birds.

Specimens of moa bones were first exhibited and described by Richard Owen, who was shown, in 1839, the shaft of a femur brought to England by Dr John Rule. Owen's verdict was that the femur indicated the existence in New Zealand of a large struthious bird, probably as large as the Ostrich *Struthio camelus*. With more material received in the next few years, he was soon able to elaborate his descriptions and referred to his genus, *Dinornis*, 6 distinct species. These descriptions were further elaborated over a period of nearly 40 years (Owen 1879). Notable subsequent reviews are those of Hutton (1892), Archey (1941) and Oliver (1949) who listed 27 species in 7 genera. Cracraft (1976) suggested a considerable reduction to 13 in 6 genera. Acceptance of this proposal depends largely on whether marked variations in skeletal size reflect real specific differences or simply sexual dimorphism. More recently Millener (1981, 1982) has merged 2 of the species admitted by Cracraft, thus indicating that only 12 species should be considered valid.

All classifications have agreed in regarding moas as 'ratite' birds (see EARLY EVOLUTION OF BIRDS), and this assumption has not been challenged except by theoretical inference. Despite earlier suggestions of a polyphyletic origin for the group, there is now overwhelming evidence for monophyly (reviewed in Sibley and Frelin 1972). Within the ratites the moas appear to be most closely related to the kiwis (Apterygidae) and perhaps more distantly to the Aepyornithidae (see ELEPHANT-BIRD). Their closest non-ratite relatives are possibly the Galliformes (Cracraft 1973).

Evolution. The ancestry as well as virtually the entire evolutionary history of the moas is largely speculative, as their fossil record is sparse. The most abundant remains are Holocene in age, some are undoubtedly Pleistocene, but none are, other than tentatively, of Pliocene age or older. It can be reasonably assumed, however, that the moas developed from volant ancestors of southern continental (Gondwanaland) distribution and that flightless ancestors of the moas were present (see FLIGHTLESSNESS) on the New Zealand landmass at the time of its late Cretaceous (*c.* 80 million years BP) separation from Gondwanaland.

Adaptive radiation in the moa lineage presumably began in the earliest Tertiary but, as noted by Cracraft (1976), the remarkably diverse Holocene assemblages most probably resulted from a later, Pleistocene, radiation. The changes in landform, climate and vegetation during the Pleistocene, more marked and more rapid than any in the Tertiary, while stimulating adaptive radiation, must almost certainly have effected extinctions amongst the Tertiary forms. The radiation of the moas, obviously strongly favoured by the absence of mammalian predators, is paralleled by the faunas of a number of other oceanic islands and indeed within New Zealand by a number of other avian families, notably the Rallidae.

Deposits. The oldest known moa remains are a very few, isolated bones found in marine deposits of ?Pliocene and Pleistocene ages. The oldest radiometrically dated remains in terrestrial deposits are of late Pleistocene age (McCulloch and Trotter 1979). All recognized species, however, occur in Holocene deposits.

The largest deposits of moa bones are found in situations that indicate death from natural causes, accumulation having continued over a long period. The richest deposits have been found in swamps where huge mixtures of bones prevented much identification of individual skeletons, and attempts to assemble them resulted in many mistakes in the early descriptions of supposed species. An important swamp deposit found in 1937 at Pyramid Valley, Canterbury, has provided numerous individual moa skeletons associated with a considerable variety of other avian remains. Sand dune deposits, especially in the far north of the North Island, have yielded abundant moa and associated faunal remains of Holocene age. Caves have frequently provided well-preserved individual skeletons while those in drier regions have also produced dried integument and feathers (Buller 1888).

Significant finds, especially of moa footprints, have been made in river deposits and in the early days of European settlement, when large areas of forest and scrub were being cleared, skeletons were found on the surface of the ground.

The wealth of material from these predominantly Holocene deposits is such that it is likely that all those species of moa which survived the Pleistocene are now known. We still, however, know nothing of the earlier Tertiary forms.

Moa bones are common in early archaeological sites from one end of the country to the other. They are, however, rarely intact, having been broken up by the Maoris to make bone fishhooks and other artefacts. The largest, and greatest number, of these 'moa-hunting' sites are along the coast, especially at river mouths, but sites also occur inland, even in the high country of the South Island. At least two early prehistoric rock drawings in Canterbury show birds that can be identified as moas with reasonable certainty.

Reconstruction. Interpretation of plentiful bones, quantities of eggshell, a few unbroken eggs, a few feathers and pieces of skin, some gizzard contents, occasional footprints and, of course, associated faunal and floral remains provide substantial clues to the habits and habitats of moas.

The general robustness of the bones of moas and especially the relative lengths of their hind limb elements indicate that most were sturdy and slow-moving. Even the most lightly-built would appear to have been far more ponderous than any of the extant savanna-dwelling ratites. Superficially the birds probably had the looped neck stance of emus *Dromaius* and cassowaries (Casuariidae) rather than the erect carriage of the Ostrich and rheas (Rheidae). Surviving feathers, at least of *Megalapteryx*, are less 'degenerate' than the norm for struthious birds. They have aftershafts but no barbules and some show vane pigmentation (purplish black centres with golden buff edges). Eggshell, which is usually white and occasionally pale green, is not abnormally thick for the size of the eggs. Moa nests, presumed to be those of *Anomalopteryx*, were discovered by Hartree in two North Island districts. All contained single eggs or chicks in scoop nests on sheltered ledges or cavities. Buller, however, produced evidence of a brood of 4 in *Dinornis robustus*.

Ecology. Whenever moa remains have been found, the associated fauna and flora are indicative of a forest habitat, as is only to be expected in the light of New Zealand's vegetational history (see Fleming 1979). Only in alpine and recently active volcanic zones and, during the Pleistocene, in isolated periglacial regions, can there have existed extensive grassland.

Moas appear to have been entirely herbivorous, berries, seeds and shoots of a wide variety of forest trees having been found as gizzard contents (Burrows 1980), suggesting a close analogy to the browsing, forest-dwelling cassowaries of New Guinea and north-eastern Australia. Collections of gizzard stones of various, most frequently quartzose, lithologies have been found.

Distribution. Five of the 6 moa genera, but only 4 of the 20 or so species were common to both North and South islands. This dichotomy, into what are in many cases North Island–South Island 'species-pairs', is doubtless the result of the two islands having been effectively isolated from each other since the Post-Glacial inundation of Cook Strait some 10,000 years ago. On neither island, however, does any one species appear to have been restricted to a particular altitudinal or geographic zone, although both *Megalapteryx* and *Anomalopteryx* have not commonly been found in coastal sites, and some of the larger species are rare in steeper country. Generally, however, moa bone deposits, wherever they occur, yield a considerable variety of species.

The finding of moa remains predominantly in lowland or coastal sites (both natural and archaeological) has led to the assumption that moas were most abundant in these regions. It is more probable that this distribution simply reflects the distribution of sites in which moa remains were most readily preserved. Indeed there were probably few areas in New Zealand, except perhaps the most mountainous, that were not at some time inhabited by moas.

The occurrence of the remains of many different species of moas in a single site has, on the assumption that all were deposited at essentially the same time, been taken to indicate that these many species shared the same habitat. However, the time it may have taken for such deposits to accumulate has been a factor all too often overlooked. As a result, excessive estimates of population density and extravagant theories of catastrophism have often been invoked to explain accumulations which more probably have resulted from prolonged and intermittent deposition.

Extinction and the impact of man. All the moa genera known have been found in archaeological sites, so that moas clearly were widespread when New Zealand was first colonized by prehistoric Man from East Polynesia about 1,000 years ago. All the moas were extinct or extremely rare by the time of European settlement which occurred in the years following Cook's first visit of 1769.

The exact date of moa extinction will always be hard to define, but the latest radiocarbon dates for archaeological sites containing any number of moa skeletons suggest that the 15th century AD was the last time that moas were at all numerous; and that by 1800 AD they were extinct or virtually so.

Because all the known moa genera became extinct in the short period of prehistoric settlement, it is likely that the arrival of man was an important factor in their demise. It is clear from archaeological evidence, particularly in the South Island, that moas were hunted extensively.

Moas must also have been seriously affected by the widespread burning of forest which accompanied the spread of the prehistoric population. However, large areas in the remoter parts were never seriously disturbed by prehistoric hunting or burning, so that the disappearance of the moa cannot everywhere be ascribed to the direct effect of man. It is possible that natural environmental changes were also detrimental, although the fluctuations of the Holocene were never as drastic as those of the Pleistocene, which the moas had previously survived. The prehistoric introduction of the Polynesian rat *Rattus exulans* and the domestic dog may also have affected the moas.

Possible survival into the 19th century. The discovery, in an excellent state of preservation, of bones of an individual *Megalapteryx* in an open fireplace in a rock shelter near Lake Te Anau led to the suggestion that this bird was hunted by Maoris in the period after European settlement. In the absence of radiocarbon dating this conclusion is highly speculative, as the state of preservation of bones cannot be taken as a reliable guide to age.

It is quite clear that none of the largest species were ever seen by Europeans, but there is a possibility that at least one of the smaller ones, *Megalapteryx didinus*, still survived in the southern province of Otago into the early part of the 19th century. Sealers from Foveaux Strait were in the habit of spending many months in the south-western fiords and living off the land. Most of the birds they described to F. Strange in 1852 are recognizable, except a larger one which they called 'the fireman', because of a call reminiscent of the wooden rattles carried by firemen on duty. Maori informants about the same time frequently referred to kiwis and to a larger bird which they called the Roa. European lexicographers have since attached this name to one of the larger kiwis, *Apteryx haasti*, but this species does not and apparently did not occur in the south-western area, and there is a possibility that the Roa was in fact a small moa.

Among reported direct observations by Europeans, one of the most arresting is that given in her later years by a Mrs Alice McKenzie of South Westland. As a child of 7, about the year 1880, she claimed to have seen a large bird of dark bluish plumage standing close to her. It was about 1 m in height, and her clearest recollection was of its large protruding eyes, broad beak, and powerful scaly legs.

Classification. The following classification, adapted from Archey (1941), Oliver (1949), and Scarlett (1972), represents the more traditional diagnosis of the group.

Order DINORNITHIFORMES
Family Dinornithidae
- Genus *Dinornis* Owen—6 species, 3 in each island.

Family Emeidae
- Subfamily Anomalopteryginae
  - Genus *Anomalopteryx* Reichenbach—2 species, the larger in both islands, the smaller only in the North Island.

Genus *Megalapteryx* Haast—2 species, the larger in both islands but very rare in the North Island. The smaller, rare and confined to the South Island.

Genus *Pachyornis* Lydekker—4 species, the largest in both islands although very rare in the North Island; 2 confined to the North Island and the fourth known only from the unique South Island holotype.

Subfamily Emeinae

Genus *Emeus* Reichenbach—1 species, probably confined to the South Island.

Genus *Euryapteryx* Haast—4 species, the largest in both main islands and from cultural deposits only on Stewart Island, the others confined to the North Island.

In the classification proposed by Cracraft (1973, 1976), a single order, Palaeognathiformes, encompasses the tinamous and ratites, with the moas occupying 6 genera within a single family (Dinornithidae). Cracraft admits only 4 species in *Dinornis*, 2 each in *Anomalopteryx*, *Megalapteryx*, *Pachyornis* and *Euryapteryx*, and one in *Emeus*. Millener (1981, 1982) has shown that only the one species *A. didiformis* is admissable in the genus *Anomalopteryx*. (R.A.F.) R.J.S.C. and P.R.M.

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MOBBING: term used for collective and noisy demonstration (see DISTRACTION BEHAVIOUR) against a predator by birds of one or several species. This behaviour is typically shown when small passerines surround a perched owl in daytime and when a party of hirundines pursue a hawk. Only rarely is the predator actually struck by the mobbing birds.

Herring Gull *Larus argentatus* mobbing White Storks *Ciconia ciconia*. (*Photo: E.J. Hosking*).

MOCKINGBIRD: see MOCKING-THRUSH.

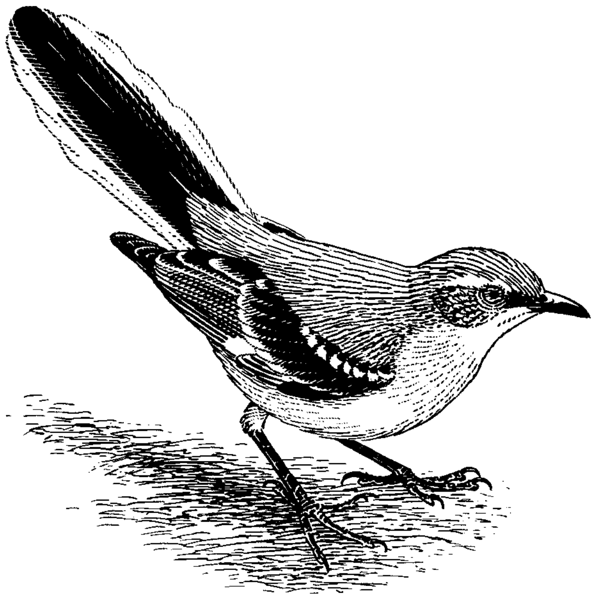
MOCKING-THRUSH: general term for the 33 species comprising the Mimidae (Passeriformes, suborder Oscines), consisting of the mockingbirds and their allies, though not used as the substantive name of any of the species. (*Donacobius atricapillus*, formerly known as the Black-capped Mocking-thrush, is now considered to be an aberrant wren (see WREN (1)). The name 'mockingbird' is used for the 13 members of the genus *Mimus* (including *Nesomimus*), the 2 blue mockingbirds of the genus *Melanotis* and the monotypic genus *Mimodes*. The name 'thrasher' is used for the 10 members of the genus *Toxostoma* as well as the 2 members of the genus *Margarops*, and the monotypic genera *Rhamphocinclus*, and *Oreoscoptes*. The members of the monotypic genera *Dumetella* and *Melanoptila* are known as 'catbirds'. The monotypic *Cinclocerthia* is known as the 'trembler', owing to its habit of vigorously quivering its wings during most intra- and interspecific social interactions.

Characteristics. This New World group is related to the thrushes (Turdinae), and nearly all are suggestive of them in appearance, especially the 2 *Margarops* thrashers and the 2 catbirds. They range from 20–33 cm in length. They have rounded, short wings characteristic of birds that do not fly extensively. The relatively long-winged arboreal *Margarops* thrashers are exceptions. Most have long tails. The bill is strong, medium to long, and in many species, especially the thrashers of the genus *Toxostoma*, is slightly to strongly decurved. Most species are shades of white, grey and/or brown, the exceptions being the blue mockingbirds and the iridescent Black Catbird *Melanoptila glabrirostris*. Many have white areas in the wings and on the tips of the tail feathers. Dark spots are found on the ventral surfaces of various thrashers and several of the mockingbirds. The crissum (under tail coverts) of several species exhibits contrasting coloration, ranging from the chestnut of the Grey Catbird *Dumetella carolinensis* and the Crissal Thrasher *Toxostoma crissale* to various shades of reddish-brown in other thrashers and mockingbirds.

The mocking-thrushes are very varied in ecological adaptation for such a small number of species. Several, notably the 2 catbirds, are structurally quite like many other unspecialized brush-dwelling insectivorous–frugivorous thrushes. However, the group also includes the Trembler *Cinclocerthia ruficauda*, which with its elongated cranial structures, short legs, reduced sternum, narrow interorbital structures, and eyes oriented for close binocular vision, is adapted to probing arboreal epiphytes. The *Margarops* thrashers have developed powerful pectoral systems adapting them for much flying in their arboreal habitat. A particularly interesting group of specializations is found in the 10 *Toxostoma* thrashers. Evolutionary stages leading to powerful pelvic systems, reduction of the pectoral system, including the length of the wings, and modification of skull structural relationships, including lengthening and increased curvature of the bill, have been demonstrated. The species exhibiting the least degree of modification are the Brown, Long-billed and Cozumel Thrashers (*T. rufum*, *T. longirostre*, and *T. guttatum*). The most extreme modifications are found in the Le Conte's, Crissal and California Thrashers *T. lecontei*, *T. crissale*, and *T. redivivum*), species which are weak flyers, and are specialized to search for invertebrates by hoeing soft desert soils and litter with their long decurved bills.

Habitat. Typical members of the group are either largely terrestrial or dwellers of thickets, brush or low trees.

Distribution. The mocking-thrushes can be divided into 2 major groups. The larger includes the mockingbirds of the genus *Mimus*, which range from southern Canada through northern Central America, the West Indies, through non-rain-forest areas of South America to Tierra del Fuego, and the Galapagos Archipelago where the 4-member endemic superspecies *Mimus* (formerly *Nesomimus*) *trifasciatus* is found. This first group also includes 2 monotypic genera, *Oreoscoptes montanus* of western North America and *Mimodes graysoni*, found only on Socorro Island in the Revillagigedo Archipelago off the west coast of Mexico. Evidence suggests that both these species are closely related to *Mimus* and the English name of the latter has been changed to Socorro Mockingbird. Also included in this section of the family are the 10 thrashers of the genus *Toxostoma* which are confined to the United States and Mexico, the



Northern Mockingbird *Mimus polyglottos*. (*R.G.*).

Grey Catbird of North America, and the Black Catbird which is found only in coastal Central America from Yucatan to Honduras.

The second group includes the Blue Mockingbird *Melanotis caerulescens* of Mexico, the Blue and White Mockingbird *M. hypoleucus* of southern Mexico and Central America, and 3 West Indian endemic species, the Pearly-eyed Thrasher *Margarops fuscatus*, the Scaly-breasted Thrasher *M. fuscus* and the Trembler *Cinclocerthia ruficauda*. The endangered West Indian endemic species, *Ramphocinclus brachyurus*, although clearly a mocking-thrush, cannot unequivocally be associated with either of the two major groupings.

Movements. Migration is well developed in some species that breed in temperate zones.

Food. Invertebrates and various fruits are the principal foods.

Behaviour. During the non-breeding season, some species (*Mimus parvulus* and *Ramphocinclus brachyurus*) move about in small groups, possibly families. Group territories are sometimes defended. Individual Northern Mockingbirds *Mimus polyglottos* will often defend a favourite food source during winter months. Mockingbirds are often extremely aggressive in defending the area about the nest, vigorously attacking and striking predators in their efforts to drive them away.

Voice. The mocking-thrushes are renowned for vigorous and versatile song. Nearly all are continuous singers. In most, the songs consist of a wide variety of syllables which are assembled into species-characteristic phrases, the detailed patterns of which are often highly varied. Some members of the group, especially the mockingbirds and notably the Northern Mockingbird, are excellent mimics. The degree of mimicry varies widely among individuals, ranging from slight in many birds to extensive in a few. Mockingbirds typically incorporate mimicked sounds, syllables, and songs into their own species-characteristic song patterns. The Northern Mockingbird, for example, usually repeats the model 2–4 times as it does its own sounds. Night singing is prominent during the breeding season and, in members of the genus *Mimus*, song may continue as the bird flies up and flutters above its song perch. The Sage Thrasher *Oreoscoptes montanus* sings on the wing as it circles over its treelees sagebrush plain habitat.

Breeding. Nests are typically placed in bushes or dense trees and are open cup-like structures, sturdily built of twigs, often incorporating leaves, and lined with rootlets and hair. The Pearly-eyed Thrasher prefers holes in forest trees. Eggs number 2–5, rarely more, the greater numbers occurring in some individuals of species living in high latitudes, the smaller numbers occurring in tropical species. The ground colour of the eggs ranges from pale whitish-blue to intense blue-green. The mockingbirds (*Mimus* and *Mimodes*), the Sage Thrasher, and the *Toxostoma* thrashers generally have spotted eggs. The eggs of all others are unmarked. In most species, incubation lasts about 13 days and is performed by the female. In some, the male assists. Both parents feed the young, which fledge in about 13 days. In some species, nest helpers have been observed. Social organization during the breeding season is monogamous and territorial. (A.H.M.) J.L.G.

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MODE: see BIOSTATISTICS.

MOHO: alternative name of the Oriole Babbler *Hypergerus atriceps* (for subfamily see BABBLER).

MOHOUINAE: see WARBLER, AUSTRALIAN.

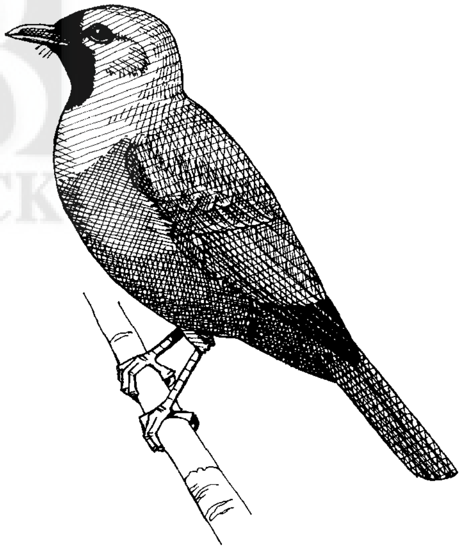
MOLLYMAUK: sailors' name, with several variants, for the smaller species of Diomedeidae (see PETREL); also applied to some other sea birds.

MOLT: American spelling of MOULT.

MOMOTIDAE: see CORACIIFORMES; MOTMOT.

MONAL: substantive name of *Lophophorus* spp. (see PHEASANT).

MONARCH: substantive name of several species of monarchine flycatchers (see MONARCH FLYCATCHER).



Black-faced Monarch *Monarcha melanopsis*. (*N.W.C.*).

MONARCH FLYCATCHER and allies: substantive name of family Monarchidae (Passeriformes, suborder Oscines). This group, though in the main distinctive, remains to be clearly circumscribed and defined, particularly in anatomical terms. Boles (1981) regarded it as a subfamily, Myiagrinae, of the Pachycephalidae, together with the Australo-Papuan robin-flycatchers (*Petroica* spp.) and whistlers, Pachycephalinae.

The nucleus of the group consists of the Indo-Pacific and Australian genera *Monarcha*, *Arses*, *Pomarea*, *Neolalage*, *Clytorhynchus*, *Chasiempis*, *Metabolus*, *Mayrornis*, *Myiagra*, *Hypothymis* and *Philentoma*, the African '*Trochocercus*' (probably an artificial genus) and the Afro-Indian *Terpsiphone*, some 87 species. To these have been added the African fantail-like *Elminia* and *Erythrocercus* (Traylor 1970); the fantails themselves, Rhipiduridae, are here given family status but see Beecher (1953), Boles (1979). Other genera that have been referred to this group include the somewhat drongo-like *Peltops* of New Guinea, the Indo–Malaysian *Hemipus* (currently in the Campephagidae), the mudnest-building *Pomareopsis* and *Grallina* (Grallinidae), and the egregious Fijian Silktail *Lamprolia*. The association with the monarchs of the Australo–Papuan boat-billed flycatchers *Machaerirhynchus* has been questioned by Storr (1958). Certain other African genera included in the Monarchidae have been removed by Traylor (1970), *Platysteira*, *Batis* and relatives to the Platysteirinae, and *Hyliota* and *Stenostira* to the Sylviidae (see also Pocock 1966, and Beecher 1953).

Characteristics. The body is of general passerine proportions (overall length 12.5–20 cm, but see *Terpsiphone*, below), though with a tendency for relatively short tarsi and a relatively long tail. The wings are moderately long and pointed, the tail squared or rounded (strongly graduated in *Machaerirhynchus*, forked in *Peltops*); the tarsal envelope laminiplantar; the bill with a tendency in some species for dorsoventral flattening (pronounced in *Machaerirhynchus* and *Myiagra ruficollis*), with slight terminal hook and subterminal notch usually present on upper mandible, and gape usually armed with rictal bristles. The nostril is rounded, usually exposed, and open (slightly lidded in *Peltops*). Other modifications to external morphology include crests or incipient crests (e.g. *Terpsiphone*, '*Trochocercus*', *Hypothymis*), nuchal frills (*Arses*), long streamer-like median rectrices (*Terpsiphone*) and blue eye-wattles (*Arses*, *Terpsiphone*, *Hypothymis*). The plumage is most often in combinations of grey, blue, black (often glossed), white, rufous and brown, though sometimes largely or wholly one of these; less frequent combinations include black and yellow (*Monarcha chrysomela*), black, white, olive-green and yellow (*Machaerirhynchus*) and black, white and red (*Peltops*). Many species are strongly sexually dimorphic; the young are wholly or largely unspotted. Legs and bills are grey-blue to blackish and blackish-brown, irides usually dark brown (orange or red in *Peltops*).

Distribution, habitat and movements. The typical monarchs inhabit the Oriental, Australasian and Afrotropical regions; they are notably well-represented in the Pacific, where several endemic genera occur. Habitats range from primary rain-forest and second-growth through open woodland to shrub savanna. Tropical and subtropical populations may be sedentary or, in the case of higher-altitude breeders, descend to the lowlands after breeding; some populations of high latitudes migrate to lower latitudes after breeding, e.g., southern Australian populations of the Leaden Flycatcher *Myiagra rubecula* and Black-faced Monarch *Monarcha melanopsis*, and northern Indian populations of the Paradise Flycatcher *Terpsiphone paradisi*.

Food. Chiefly insects: dragonflies, termites, grasshoppers, bugs (including cicadas and lerps), beetles, flies, butterflies and moths (including caterpillars), bees and ichneumon wasps, also spiders. In addition the Shining Flycatcher *Myiagra (Piezorhynchus) alecto* of waterside thickets takes isopod crustaceans, tiny shellfish and crabs, the Restless Flycatcher *M. (Seisura) inquieta* worms and centipedes, and the Spectacled Monarch *Monarcha trivirgata* small snails.

Behaviour. Monarch flycatchers are usually solitary or in pairs, sometimes family groups; some species also noted in mixed feeding parties. Most species hunt by moving briskly through the foliage of trees, shrubs or herbage, flicking wings and fanning tail in the manner of FANTAILS, presumably to dislodge their prey; many also catch flying insects in aerial sallies (a habit not pronounced in *Monarcha*, however). Variations of these methods occur. The 2 species of frilled monarchs (*Arses*), for instance, habitually climb up and down the trunks of trees flushing insects from bark-crevices; the Shining Flycatcher has been observed creeping along near the ground among mangrove roots or swamp-litter; and the Restless Flycatcher hunts mainly by flying slowly over open ground and hovering above its prey before pouncing. As in the fantails, prey too large to be swallowed whole may be held under the foot and eaten piecemeal.

Displays are not well-documented. Species with crests, incipient crests, nape-tufts or nuchal frills will raise these when excited. Courtship display observed in male Paradise Flycatcher consists of a slow rising and dropping flight with long tail-streamers undulating. Group-displays involving repeated chasing or following within a restricted area have been observed in *Arses* and *Machaerirhynchus*.

Voice. Calls are short and simple, the quality variously described as dry, grating, harsh, rasping, buzzing or scolding, the notes often with a rising inflexion. Some species are not recorded as possessing a song (e.g., Azure Monarch *Hypothymis azurea*); songs of others are described as a series of simple whistles (*Myiagra*), slow rattled ringing trills (*Arses*), a musical jumble of loud mellow notes and fluting whistles (*Monarcha*) and a low pleasant rising and falling warble (*Terpsiphone*).

Breeding. Nests are cup-shaped, mainly of vegetable matter, often bound with spiderweb and adorned with cocoons, lichen and bark; usually supported from beneath, on a horizontal branch (e.g., *Myiagra*) or in a vertical fork (e.g., *Monarcha*, *Mayrornis*) at heights from 1–20 m, exceptionally partly or wholly suspended by rim (*Arses*, *Erythrocercus*, and apparently, *Machaerirhynchus* and *Peltops*). The 2–4 eggs are whitish or very pale pastel shades, spotted and blotched with reds, greys and browns, in two chief types of distribution: (a) marked more or less uniformly over the shell, e.g., *Monarcha*, (b) markings concentrated in wreath, e.g., *Myiagra*, *Elminia*. Whether this variation is of taxonomic significance remains to be determined. Incubation lasts 14–17 days; the young fledge after 12–18 days according to species. Where information is available, both sexes build the nest, incubate, and feed the young; in some the female does most of the nest-building and incubating, but the male has been recorded as doing most of the building in *Machaerirhynchus flaviventer*. S.A.P.

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MONARCHIDAE: family of PASSERIFORMES, suborder Oscines; MONARCH FLYCATCHER.

MONIAS: *Monias benschi*, sometimes misnamed 'Bensch's Rail' (see MESITE).

MONJITA: substantive name of most species of *Xolmis*, a genus of tyrant-flycatchers inhabiting open country in South America (see FLYCATCHER (2)).

MONKLET: substantive name of the small PUFFBIRD *Micromonacha lanceolata* of tropical America.

MONOCULAR VISION: see VISION.

MONOPHYLETIC: of a single evolutionary ancestry (contrasted with POLYPHYLETIC).

MONOSPECIFIC: in reference to a genus containing only one species.

MONOTYPIC: term applied to a taxon that has only one unit in the immediately subordinate category, e.g., a genus comprising only one species, or a species not divisible into subspecies—contrasted with POLYTYPIC.

MONOTYPY: see under TYPE SPECIES.

MONTANE: appertaining to mountains; term applied particularly to the avifaunas of elevated areas in which the bird-life is strikingly different from that of adjacent areas of less altitude. The contrast tends to be especially pronounced at high levels in low latitudes; and it has been one of the puzzles of ornithology that particular sedentary species, sometimes not even showing subspecific differentiation, are found on isolated tropical mountain ranges separated by wide areas of unsuitable country in which such birds are never encountered (see AFROTROPICAL REGION).

MOOD: 'the preliminary state of "charge" or "readiness for action" necessary to the performance of a given course of instinctive behaviour' (W.H. Thorpe).

MOON-WATCHING: see MIGRATION.

MOOR FOWL: antique term (in British game laws) for the Red Grouse *Lagopus lagopus scoticus*; cf. HEATH FOWL.

MOORHEN: substantive name of *Gallinula* spp.; applied without qualification, in Britain, to *G. chloropus* (see RAIL).

MOORUK: native name in New Guinea, sometimes used as English, for Bennett's Cassowary *Casuarius bennetti* (see CASSOWARY).

MOPOKE: popular name, also written 'more-pork', used in Australia for *Podargus strigoides* (see FROGMOUTH), and both there and in New Zealand for subspecies (or related forms) of *Ninox novaeseelandiae* (see OWL). The name purports to represent the call.

MORILLON: British fowler's name (probably obsolescent) for immature Goldeneye *Bucephala clangula*, once thought to be a different species (see DUCK).

MORPH: term introduced (J.S. Huxley 1955) to replace the less precise 'phase', denoting any one of the different forms of a species population subject to polymorphism (including dimorphism, where there are only two morphs)—see POLYMORPHISM.

MORPHOLOGY: literally, the science of form or shape; nowadays commonly extended to cover all external characters, including coloration, or even used synonymously with 'anatomy' (literally, internal structure as revealed by dissection); and it may be applied not only to the study but to its subject matter, as a collective term for the 'morphological' characters of a taxon.

MORTALITY: see AGE.

MOSAIC EVOLUTION: see under ARCHAEOPTERYX.

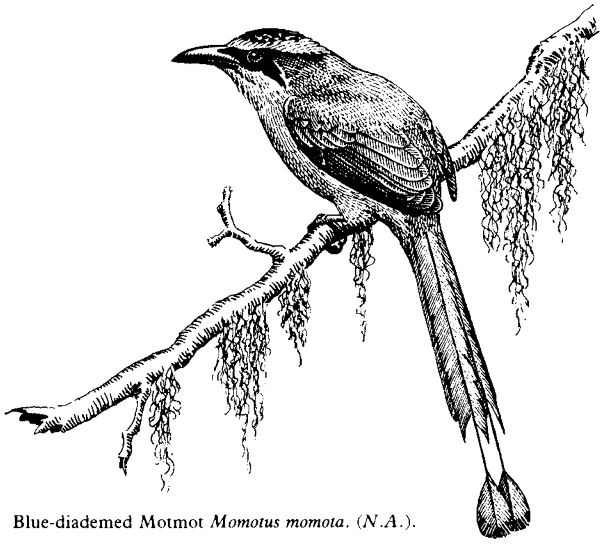
MOSSIE: or Cape Sparrow, *Passer melanurus* (see SPARROW (1)).

MOTACILLIDAE: a family of the PASSERIFORMES, suborder Oscines; WAGTAIL.

MOTHER CAREY'S CHICKEN: sailors' name (from 'Mater cara') for storm-petrels of various species (Hydrobatidae)—see PETREL.

MOTIVATION: see AMBIVALENCE; BEHAVIOUR, HISTORY OF.

MOTMOT: substantive name of species of Momotidae (Coraciiformes, suborder Alcedines); in the plural, general term for the family. The motmots are allied to the kingfishers (Alcedinidae) and even more closely to the todies (Todidae). The 6 genera and 9 species of motmots (*Momotus*, *Electron*, and *Baryphthengus* have 2 each) are confined to continental tropical America, chiefly at low altitudes; but the family was once far more widely distributed, as the fossil bird *Protornis glarniensis* from the lower Oligocene of Switzerland is now ascribed to it.



Blue-diademed Motmot *Momotus momota*. (*N.A.*).

Characteristics, distribution and habitat. At the present time, the Momotidae are best represented in northern Central America and southern Mexico, where in certain regions of lighter vegetation these birds are abundant and conspicuous. Among the noteworthy structural peculiarities of the motmots are the serrated edges of their broad bills, which are about as long as their heads and downcurved at the end, and their feet, of which the outer toe is united to the middle one for most of its length and only one toe is directed backward, as in kingfishers.

These beautiful birds (16–50 cm in total length) are clad in softly blended shades of green, olive-green, and rufous rather than in brilliant spectral colours; although the head is often adorned with bright blue, and a black patch is usually present on the chest or throat. The most arresting feature of motmots is the tail, which is long and strongly graduated. In typical motmots, the central rectrices far exceed the others in length, and, when they first expand, the vanes may be narrower in the subterminal region than elsewhere. In this subterminal portion the barbs are loosely attached and fall away as the bird preens, and probably also in consequence of rubbing against the vegetation through which it moves, leaving a length of naked shaft which supports a spatulate or raquetlike tip where the vanes remain intact. The length of denuded shaft varies considerably from genus to genus, and in some genera it is lacking. While perching, motmots often swing their tails, pendulum-wise, from side to side, and sometimes hold them tilted sideways. When they about-face on a perch, they lift the tail over it with a graceful flourish.

One of the most beautiful members of the family is the Turquoise-browed Motmot *Eumomota superciliosa*, which is found from southern Mexico to northern Costa Rica in semi-arid country and in clearings in rain forest. Well over half of its 35 cm is accounted for by its long tail. As in other motmots, the sexes are alike in coloration. The upper plumage is largely bright olive-green, with a patch of cinnamon-rufous in the centre of the back. Above each eye is a broad band of pale turquoise, the bird's brightest colour. The lores and ear tufts are black; and on the throat is an elongated, wedge-shaped patch of black, bordered on each side with turquoise. The remaining under plumage is greenish olive and cinnamon-rufous. The middle feathers of the greenish-blue tail have a much greater length of denuded shaft than in other motmots, so that the spatulate, blue and black ends hardly appear to be connected with the rest of the bird. This makes the Turquoise-browed Motmot more airily graceful than its relatives.

The largest member of the family is the Rufous Motmot *Baryphthengus martii*, which inhabits heavy forests from Nicaragua to Amazonia and western Ecuador. This 46-cm bird has the head, neck, and most of the underparts tawny, the back and rump and undertail coverts green. There is a black patch on each side of the head and one in the centre of the chest. Each of the central tail feathers has a short length of naked shaft. At the other extreme of size is the Tody Motmot *Hylomanes momotula*, an elusive, little-known inhabitant of forests from southern Mexico to northwestern Colombia. About 17 cm long, clad in dull green and rufous, with black ear-tufts, this small motmot has a short tail without racquet tips.

An aberrant member of the family is the Blue-throated Motmot *Aspatha gularis*, which in northern Central America and extreme southern Mexico inhabits forests of oaks, pines, and cypress from about 1,200 to 3,000 m above sea level. Here it resides throughout the year, despite the severe frosts of the winter months. About 28 cm long, this motmot is almost wholly clad in green, with a blue throat, black ear-tufts, and a black patch on the foreneck. The feathers of the long tail are strongly graduated, but the central ones have continuous webs rather than racquet tips.

Habits and food. When foraging, motmots perch motionless until their keen eyes detect a beetle, caterpillar, spider, butterfly, cicada, small frog, lizard, or snake, on foliage, on the ground, or in the air. Then they dart swiftly, seize the victim, and carry it to a perch, against which, if large, they beat it before gulping it down. Small fruits, including those of palms, plucked while the bird hovers, enter conspicuously into the diets of some of the bigger motmots. These large species often forage with the mixed flocks that follow the army ants *Eciton*, catching small fugitive insects and other creatures rather than the ants themselves.

Voice. Although the utterances of motmots are all structurally simple, they vary immensely in tone from species to species. The Turquoise-browed Motmot voices a dull, wooden *cawaak cawaak*. The call of the widespread Blue-diademed Motmot *Motmotus momota* is a full, froglike, not unmelodious *coot coot*. At dawn, the rain-forest of southern Caribbean Central America is filled with the hollow hooting of the Rufous Motmot, a mysterious sound often difficult to trace to its source, for these motmots stay high in trees. The most melodious of the motmots is the Blue-throated, whose delightfully clear and mellow notes are heard chiefly at dawn, when the members of a pair often sing in unison just after they emerge from the burrow where they slept.

Behaviour. In courtship, two or more motmots call back and forth, often continuing for surprisingly long intervals. Sometimes, while so engaged, they hold pieces of green leaf or other fragments of vegetation in their bills—a puzzling habit, since such material is not carried into the nest burrow. The Blue-diademed, or Blue-crowned Motmot dust-bathes, sometimes on roadways in the evening twilight.

Breeding. Motmots nest chiefly in burrows, which are dug by both sexes of the species for which information is available. They loosen the earth with their bills and remove it by kicking backward with their feet each time they enter to resume digging. The female Turquoise-browed Motmot seems to do the greater share of the work, but her mate sometimes gives her an insect. Often the burrow is in the vertical bank of a watercourse or road; but the Blue-diademed Motmot may dig its tunnel in the side of a mammal's burrow or a narrow pit in level ground, which makes its nests very difficult to find. In this species, as in the Blue-throated Motmot, the burrow may be crooked, with one or several sharp turns; but that of the Turquoise-browed Motmot is often only slightly curved. Motmots' tunnels up to 4.3 m long have been recorded, but most are much shorter. Along the bottom of an occupied tunnel are two distinct parallel grooves, made by the birds' short legs as they shuffle in and out. In limestone regions, motmots sometimes nest in caverns or in niches in the sides of wells.

Two to 4, rarely more, broad, roundish, pure white eggs are laid on the bare floor of the enlarged chamber at the end of the burrow. They are incubated by both parents. One member of a pair of Blue-diademed or Broad-billed Motmots enters the burrow early in the morning and sits for 6–8 hours, rarely longer. At midday or later, the other replaces it and remains in the burrow until the following dawn. While incubating, motmots regurgitate many chitinous fragments from their insect food and an occasional seed, all of which are trampled into the floor of their chamber. The incubation period of the Blue-throated Motmot is 21–22 days; that of the Turquoise-browed Motmot, 15–19 days.

Nestling motmots, hatched blind and with no trace of down on their pink skins, are brooded and fed by both parents, who do not try to keep the nest clean. Young Blue-throated and Turquoise-browed Motmots leave the burrow at 28–31 days of age, and young Blue-diademed Motmots at 29–38 days, but those of the small Broad-billed Motmot fly when only 24–25 days old. They remain in the nest until they are well feathered, much in the pattern of the adults, and fly well. Their stubby tails, of course, still lack the racquet tips. Blue-diademed Motmots and Turquoise-browed Motmots are single-brooded.

Turqoise-browed Motmots start to dig their burrows as the spring or early summer breeding season approaches. Blue-diademed Motmots often begin in the autumn to dig burrows in which they will breed 4 or 5 months later. Blue-throated Motmots dig their burrows even earlier, in June or July, soon after their young are fledged. These tunnels are soon finished, and are then used as dormitories by the constantly mated pair throughout the winter months, when nights are cold and frosty. Even after eggs are laid in these old burrows in the following spring, both parents continue to sleep in them, as they do with the nestlings. After the latter emerge, they do not return to sleep in the burrow; but the parents sometimes continue to lodge in it until a new burrow is completed nearby. The motmots of the lowlands, however, appear not to use their burrows as dormitories, and only one parent sleeps with the eggs and young, until the latter are about 5 days old. A.F.S.

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Skutch, A.F. 1945. Life history of the Blue-throated Green Motmot. Auk 62: 489–517.

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King Penguins *Aptenodytes patagonicus* (left) after and (right) during moult. (*Photo: N. Rankin*).

MOULT: or 'molt' in American usage, the periodic shedding and replacement of plumage, and, in some species, of certain accessory structures of epidermal origin, e.g., tarsal scales and horny sheaths of the bill (see FEATHER; PLUMAGE; BILL); the term is also applied to the period during which moulting occurs. The extent of moult and its timings during the year are adaptively integrated with the other main events of the ecophysiological cycle, namely reproduction and migration (if this occurs)—see BREEDING SEASON; MIGRATION.

Function. Periodic replacement of feathers is needed to maintain a high level of flight performance; to assist in regulation of body temperature by modifying the rate of heat loss from the skin; to maintain the waterproof nature of the plumage of some species; and to allow seasonal changes in appearance, often associated with reproduction (though such changes may occur through abrasion of feather edgings; see later).

Mechanism. Feathers grow from follicles in the skin. During the whole life of a bird, a series of feathers are produced from each follicle. At certain times, the dermal papilla at the base of the follicle is stimulated and in turn activates growth of the epidermis to produce a new feather. This pushes the old feather out of the follicle (Watson 1963). Stimulation of the papilla is usually under internal physiological control, but may occur in response to loss of a feather by plucking or by 'fright moult', the simultaneous shedding of large numbers of feathers from certain parts of the body, a phenomenon that sometimes occurs when birds are frightened by a potential predator.

Pattern. Within each pteryla or tract of feathers (see PTERYLOSIS), feather loss and replacement proceeds in a regular sequence. In general, within tracts of contour feathers, waves of moult pass outwards from the mid-line and downwards towards the tail. Moult of flight feathers begins from certain foci in each tract, often proceeding in both directions with sequential loss of adjacent feathers, but sometimes in only one direction, as in moult of the primary feathers of most passerine birds, in which the short innermost primary is shed first and moult proceeds steadily towards the longer outermost feathers.

Members of several other orders of birds, e.g. Procellariiformes, Accipitriformes, normally follow the pattern of 'descendent' moult of the primaries found in the passerines. However, in the Falconiformes, moult commences with loss of primary 4 (and in the parrots with primary 5) and then progresses sequentially both inwards and outwards from this focus. In the budgerigar *Melopsittacus undulatus*, for example, before the tenth primary has completed growth, primary 5 may have been shed again, at the start of the next moult, so that two 'waves' of moult are present briefly in the same bird. The presence of more than one cycle of moult within the same set of primaries has been termed 'Staffelmauser' (= stepwise moult) by E. Stresemann and occurs in some terrestrial non-passerines and in many seabirds, particularly the larger species in which the onset of breeding is delayed for several years. The pattern is established gradually during the first few years of life. One of the most complicated patterns of moult of the primaries discovered so far occurs in cuckoos, e.g. *Cuculus canorus* in which primaries 1–4 moult descendently but the remaining set of feathers moults ascendently and alternately, i.e. 9–7–5–10–8–6; the relative timing of the moult of these two sets of primaries is not fixed. The pattern of moult of secondary feathers of large terrestrial and large seabird species is also highly irregular.

The pattern of moult in all feather tracts should be considered as adaptive. Since the distribution of pterylae and apteria (areas of skin that are bare or covered only by semiplumes or downs; see FEATHER) is important in the control of body temperature (Clench 1970), growth of new body feathers starting from the centre of each tract ensures minimum loss of skin cover during moult. Similarly, replacement of primaries from the innermost outwards allows most passerines to fly during wing moult, even though several adjacent feathers may be growing at any one moment. By means of this sequence, the inner-growing primaries are also protected by the old outermost feathers. A similar protective function of old feathers is shown in the sequence of tail moult of woodpeckers, in which the long inner pair of feathers—used for support in climbing—are retained until the other pairs have been replaced. In most other families, tail feathers are shed sequentially from the innermost outwards, or vice versa.

Control. Many experiments have been undertaken on captive birds to establish the hormonal control mechanisms leading to the activation of feather follicles. Most of these have involved hormone injections, but changes in photoperiodic regime or nutrition, known or thought to affect hormone levels, have also been used. The results and relevance of these experiments need to be viewed against the known patterns of moult of different feather tracts. Few experimental treatments have led to sequential moult of feathers in a tract at rates corresponding to what happens in the wild.

It is clear from wild birds that the focus or foci at which moult begins in each tract are the same in successive (complete) moults. Miller (1941) suggested that the first feathers to be shed may be those with increased blood supply, but this has yet to be confirmed. Alternatively, or additionally, the follicles at the foci may have lower thresholds of response to hormonal or other stimuli than other feathers in each tract. Once moult has begun, the sequential shedding of feathers could arise by stimulation of growth in one follicle by the growth of an adjacent feather, perhaps by improvements in blood supply. Alternatively, follicles in a sequence could require progressively higher levels of hormones to elicit their growth responses; or each follicle could be time-programmed to begin growth slightly out-of-phase with its neighbour (Ashmole 1968). There is some support from experiments of the concept of local (spatial) variations in sensitivity of follicles to hormonal stimuli, but long-term time-programming of responsiveness of follicles may also be involved, since different levels and combinations of hormones can elicit moult in the domestic fowl according to the number of months since the previous (natural) moult.

In general, hormonal treatments of wild birds with androgens and oestrogens inhibit moult, but the species investigated so far include chiefly those whose schedules of breeding and moult do not overlap in the annual cycle. Although breeding, moult and migration are often mutually exclusive, many species are known in which overlap of these events occurs (see later). Levels of gonad-stimulating hormones show no seasonal variations that can be correlated exclusively with moult, rather than breeding, and any inhibitory actions of the hormones FSH and LH on moult that have been demonstrated are probably attributable to the results of increased production of androgens and oestrogens. Similarly, there are no clear-cut relationships between seasonal prolactin levels and the initiation of moult. The results of direct treatments with prolactin are equally diverse, any positive effects probably occurring indirectly through alteration of androgen and oestrogen levels. Almost all the experiments involving the hormones mentioned so far were carried out before any real appreciation existed of the circadian rhythms of release of hormones from the pituitary, of circadian rhythms of sensitivity of target sites, and of seasonal variations in these rhythms.

The involvement of the thyroid in the control of moult has been the subject of extensive research, much of it summarized by Voitkevich (1966). This work, and more recent studies, have been reviewed critically by Payne (1972) who concludes that it is uncertain whether thyroid activity is directly involved in the control of the start and patterns of moult in wild birds.

Of external stimuli that might alter hormone balances and so initiate moult, changes in photoperiod have been studied most extensively. Most experiments have involved species that breed in northern temperate latitudes. In these, exposure to artificially long photoperiods, after exposure to natural short winter daylengths, usually leads to development of reproductive condition, and, in those species that moult into a special plumage for the breeding season, to feather replacements. However, the timing of this moult, relative to the timing of fat deposition for migration (if any) and of gonadal enlargement, may not parallel exactly the situation in wild populations. Other experiments have sought to prolong reproductive condition by maintaining birds on artificially lengthened photoperiods after the end of the normal breeding season. Eventually gonadal regression occurs, and the normal complete moult after breeding is usually postponed in these experimental birds until this time. Taken together, all the photoperiodic experiments indicate an effect of gonadal hormones (usually inhibitory) on the time of the start of moult.

Day-length may not be important in controlling the timing of events in the annual cycle in equatorial regions, and its importance at higher latitudes may also have been overstressed. Many species show circannual rhythms of breeding, moult and preparation for migration if held in conditions of constant photoperiod, temperature and humidity for several years. In most species these rhythms persist for more than one year, and so are not simply an autonomous sequence of events triggered each spring by an external stimulus. The circannual period length (between successive events of the same type) may differ for moult and reproduction, indicating that there is no obligatory connection between the start of a moult and the stage of breeding (see, for example, Gwinner and Dorka 1976).

Energy and nutrient requirements. The additional energy required for feather production during moult by Chaffinches *Fringilla coelebs* has been measured as 140 kCal. spread over 70 days (Dolnik and Gavrilov 1979). This was required to produce 1.4 g of feathers, whose energy content (if burnt in oxygen) would be only about 7.7 kCal. Unlike this experiment, which was carried out at 26°C, within the thermoneutral zone, most measurements of additional energy requirements during moult have been carried out at lower temperatures and so include not only the energetic costs of feather production but also an element for the increased costs of maintenance of body temperature during the period of greater rates of heat loss, from surfaces with growing feathers. Measurements of the costs of feather production in House Sparrows *Passer domesticus* have been made for two geographical populations and are slightly higher than the 100 kCal/g estimated for Chaffinches—namely 185 kCal for 1.7 g and 218 kCal for 2.0 g of plumage in the USA and USSR respectively.

Measurements of increased energy requirements during moult in captive birds held at natural temperatures indicate an increase in metabolic rate of around 30% in many passerines. However, the duration of moult in captives has often been longer than in wild birds of the same species, so the increase in metabolic rate may have been over-estimated. It is also not known to what extent wild birds compensate for the added energy costs of moult by reducing their energy expenditure on activities such as flight and foraging. Quite possibly their daily food requirements during moult are not much higher than before moult begins.

Feather KERATIN contains higher proportions of sulphur amino-acids, particularly cystine, than those present in most animal and (particularly) plant proteins. It has often been suggested that the cystine content of birds' food during moult might be limiting, rather than the energy content. Dolnik and Gavrilov (1979) have concluded that during the first part of the complete moult of Chaffinches, the increase in food consumption by captive birds chiefly provides the required amounts of the sulphur amino-acids, and that heat production from the daily food intake exceeds that required for thermoregulation at this period.

Most species maintain feather growth by both day and night even though they feed only by day. This may result in the transfer of amino-acids from muscles to growing feathers either in the short-term (overnight, as in some passerines) or the longer term (several weeks, as in the Canada Goose *Branta canadensis*, in which the wing, but not the leg, muscles atrophy during the flightless period).

Moulting during breeding. Since moulting does require extra energy, and therefore extra food intake unless activity can be reduced, the separation of moulting and breeding could be adaptive on energetic grounds, particularly in species that feed their young in the nest and therefore cannot 'afford' to reduce energy expenditure on foraging. One might expect most overlap of breeding with moult in species in which feather replacement spans a long period of the year, so that the extra energetic demands are small at any one moment, and in those living in tropical areas where thermoregulatory energy requirements should not be increased by moult.

The first of these generalizations is broadly correct, but the second is not. Many tropical species show seasonal breeding, and moult is often delayed until the end of the reproductive period. In those species that utilize foods whose abundance does not vary seasonally, moult may be protracted and overlap with breeding. Other species may vary the timing of breeding from year to year, but show consistency in the timing of onset of moult. This leads in some years to separation but in others to overlap between breeding and moult, and occurs especially in arid-zone birds which breed whenever droughts are broken by irregular rainfalls. The multitude of different schedules and degrees of overlap of breeding and moult in different species are reviewed thoroughly by Payne (1972).

Duration of moult of flight feathers. Amongst European passerines, few species renew their primary feathers in less than 5 weeks. In closely related species, e.g., the finches, migratory species take less time to complete primary moult than do sedentary ones. This is true even within a species, e.g., the wagtail *Motacilla alba*, in which Finnish populations of the migratory *M. a. alba* complete moult in 45–50 days, whereas the sedentary British *M. a. yarrellii* take 76 days, on average, to grow new primaries. Wing-moult of the sedentary species often commences later in the year than that of related migratory species.

Suspended moult. Under certain circumstances, birds that have begun feather growth may interrupt their moult, growing feathers being completed but feathers next in sequence to be moulted being retained until a later date. This occurs in some species that breed irregularly; moult is interrupted during breeding. (Others, with protracted moults, may continue to moult during breeding, as detailed earlier.) Moult of flight feathers may commence before migration in some species, particularly those breeding in the arctic, but may be interrupted during migration itself. A few species may undertake short migrations with incompletely grown outer primaries.

Flightlessness. Some birds lose the power of flight during moult. This occurs for part of the moult period in certain arctic passerines that migrate south soon after breeding and compress moult of the flight feathers into a 5–6-week period. More than 5 adjacent primaries may be growing at any one time and all pairs of tail feathers may be shed simultaneously (Haukioja 1971). Individuals of the same species, e.g., Willow Warbler *Phylloscopus trochilus*, breeding at more temperate latitudes, spread their wing moult over a slightly longer period and do not lose completely the ability to fly. Nevertheless, most passerine species become less active and less conspicuous during moult, in part to avoid avian predators (Newton 1966) but presumably also to reduce daily existence energy requirements.

In 11 families of birds, many comprising fairly large-sized species, for example the ducks, geese and swans, divers and grebes, all flight feathers are shed simultaneously, and individuals are unable to fly for a period of a month or more. Because they are vulnerable to mammalian as well as avian predators at this period, some species spend the moult on large lakes, offshore islands or the open sea. This may require a 'moult-migration' from the breeding area to a relatively safe moulting site. Most northern European Shelduck *Tadorna tadorna* gather to moult in July and August on the sandbanks in the Heligoland Bight; many species of arctic-nesting geese undertake such migrations, those involving non-breeding individuals often leading them to still higher latitudes (Salomonsen 1968).

Eclipse plumage. In some groups the full adult plumage, in which the birds breed, is replaced at the end of the reproductive season by a dull 'eclipse' plumage that is worn for only a very few months before a fresh adult plumage is acquired; this is found among the ducks, cuckoo-shrikes, sunbirds, and weavers. It is particularly striking in the males of typical duck species, which lose their very distinctive plumage early in the breeding season and become more like the cryptically coloured females.

In these birds, the body plumage is lost before the wing feathers are replaced, and the second moult of the body plumage, into the colourful breeding plumage once again, may commence before the wing feathers are fully grown. Therefore, although the drakes are protectively coloured during most of their flightless period, it would appear that the advantage of reacquiring the colourful breeding plumage early, in terms of enhancing their chances of successful matings, outweighs the value of prolonging the period in which they are protectively coloured, even though this may increase each individual's chances of survival.

Frequency. All birds moult at least part of their plumage once a year, many species twice, and a few thrice. If breeding and moult do not overlap, the main function of the 'postnuptial' moult is the renewal of worn and faded plumage; it is therefore general and almost always complete. In some groups, such as birds-of-prey and swallows, the moult of the remiges and rectrices may be delayed until mid-winter. This adaptation seems to be correlated with migration, during which birds of the two named groups are often in close association.

The 'prenuptial' moult, when present, is usually partial. It intensifies the secondary sexual characters by brighter colours or by adding plumes or other adornments (e.g., the facial warty excrescences in the Ruff *Philomachus pugnax*). This moult tends to be more evident in males than in females; exceptions include the phalaropes. Part of the colour change apparent at this season is in some species due to abrasion of the edges of feathers. Miller (1961) found that the Andean Sparrow *Zonotrichia capensis* has two complete moults annually, each of two months' duration.

In the Ptarmigan *Lagopus mutus* there is a partial moult during the late summer and autumn, when an admixture of the grey breeding dress and the brownish autumn plumage is observable before the birds pass into the white plumage of winter. Assumption of this winter plumage has been shown to depend on a fall in temperature; this, by responsively increasing metabolism and acting through the endocrine system, suppresses melanin production (Salomonsen). The prenuptial moult in spring, later in males than in females, brings the birds into breeding dress (see also COLORATION, ADAPTIVE).

The moult can be a purely local and normal condition, as in the case of defeathering of the incubation patch area which is initiated by the hormone prolactin, prior to the increased vascularity, epithelial hypertrophy, and oedema in preparation for incubation (Bayley 1952).

Terminology. From the beginning of the 20th century, the terminology used to describe moults and plumages was based on temperate-zone passerine birds, in which breeding and moult are usually separated in time. This led to use of terms such as 'pre-' and 'post-nuptial' moult, which are difficult to apply to many tropical birds and to others in which there is total overlap or no constant relationship between the timings of moult and reproduction. Humphrey and Parkes (1959) reviewed the then-existing descriptive systems and proposed one of their own which is now widely used. They recognized that new 'aspects' (plumages) arise from new feather generations in at least some of the feather tracts, and that since new feathers push out old (except in fright moult or defeathering of the incubation patch), moults should therefore be named with reference to the incoming generation. These generations are named in a way that avoids seasonal, reproductive or age criteria. The first covering of true feathers is named the juvenal feather generation, and this plumage never recurs after later moults.

At some later stage, the incoming feather generation in a particular tract is identical in appearance with one that has developed at an earlier time in that same tract. The interval between these moults is known as a cycle, and is normally of 12-months' duration. If only one feather generation is produced within a cycle, it is termed basic; if two, the second is termed alternate; in those rare cases in which three generations are produced in a single feather tract during one cycle, the third is termed supplemental. The moults are described as pre-basic, pre-alternate, etc. The appearance of a bird can be deduced from knowledge of the feather generations (basic, alternate, juvenal, etc.) present in each feather tract at the time in question.

Moult of accessory structures. These cases can be divided into three classes. First, there are those that come under the heading of secondary sexual characters accompanying and supplementing the prenuptial moult, being developed expressly for the breeding season and being discarded at its end. Typical examples are found in the auks, the Puffin *Fratercula arctica* providing a familiar instance; in this species the highly coloured parts of the bill, the two small supraorbicular excrescences, and the puffy 'rosettes' at the angles of the gape are shed. Also, the Hornbill Auk *Cerorhinca* ('*Ceratirhina*') *monocerata* moults the internaral protuberance. A further example is the 'bill-horn' of the males of the American White Pelican *Pelecanus erythrorhynchus*, the horn falling off at the end of the breeding season.

Secondly to be mentioned is the moulting of the claws in ptarmigan *Lagopus* spp. It is very probable that the tarsal scutellae are also moulted regularly; evidence in support of this is provided by the case of a Song Thrush *Turdus philomelos* with abnormal cutaneous horns on its head and on one leg, these being cast each time the bird moulted. Probably this applies to all pathological structures arising from tissues of epidermal origin, including those of the uropygeal OIL GLAND (which in certain circumstances can produce a 'horn' that is moulted regularly).

The third category consists of structures that serve a temporary function only. In the Hoatzin *Opisthocomus hoazin* the young have functional claws on the 1st and 2nd digits of the manus for the first week of life only; these are shed and during after life the claws are represented by minute callosities. A further instance of structure of this nature is afforded by the 'heel' pads of woodpeckers and wrynecks, toucans, and scansorial barbets, this structure falling off when the birds leave the nest.

(J.M.H.) P.R.E.

Most papers quoted in the text are included in one of the following three reviews:
In Farner, D.S. & King, J.R. (eds.). 1972. Avian Biology. Vol. 2. New York.
Palmer, R.S. Patterns of molting. Chapter 2.
Payne, R.B. Mechanisms and control of molt. Chapter 3.
Stettenheim, P. The integument of birds. Chapter 1.

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Haukioja, E. 1971. Flightlessness in some moulting passerines in Northern Europe. Ornis Fennica 48: 101–116.
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MOULT MIGRATION: a regular movement by certain birds to and from an area where they moult (see MIGRATION; MOULT).

MOUND-BIRDS; MOUND-BUILDER: see MEGAPODE.

MOUNTAINEER: *Oreonympha nobilis* (for family see HUMMINGBIRD).

MOUNTAIN-GEM: substantive name of *Lampornis* spp. (for family see HUMMINGBIRD).

MOUPINIA: substantive name of the 2 species of *Moupinia* of south-east Asia (for family see BABBLER).

MOURNER: substantive name of species of *Laniocera* and *Rhytipterna* (for family see FLYCATCHER (2)).

MOUSE-BABBLER: substantive name of the 3 species of *Crateroscelis* of New Guinea (for family see RAIL-BABBLER).

MOUSEBIRD: substantive name, alternatively 'coly', of the species of Coliidae (sole family of the Coliiformes); in the plural ('mousebirds,' 'colies'), general term for the family.

The family contains 6 species, all very similar to each other and so specialized in character that the family is generally placed in an order of its own—the only order endemic to Africa.

Characteristics. All are small-bodied, weighing 38–68 g, two-thirds of the length of 30–36 cm contributed by the characteristically long graduated tail. The plumage is drab grey or brown relieved in most species by a patch of red, blue or white on the head, neck or rump or by barring or speckling. The body feathers are soft and hair-like with remarkably long aftershafts, and are poorly waterproof. The wings are short and rounded, with 10 primaries and 10 secondaries. All species have a pronounced crest which is normally carried erect. The sexes are alike. The bill is short, slightly downcurved, and strong. The 4 toes are normally all directed forward, but the outer toe on each side can also point backwards. The usual perching attitude is with the feet and shoulders at about the same level, the belly hanging down exposed between the legs, but mousebirds occasionally perch normally too. On the ground they can hop, run or walk surprisingly fast. The flight normally consists of alternate bursts of flapping and gliding but can be fast and direct; often a flock will fly straight into the centre of a bush. They are highly gregarious, and probably as similar to each other in behaviour and ecology as in structure.


Blue-naped Mousebird *Colius macrourus*. (*N.A.*).

Habitat. Most of the wooded and bushy environments of Africa south of the Sahara, avoiding open plains and forest interiors.

Distribution. Throughout the Afrotropical region. The 4 species of the *Colius striatus* group include the widely distributed *C. striatus*, the allopatric *C. castanotus*, the partly sympatric *C. colius* and the almost completely sympatric *C. leucocephalus*; none of these species extends west of the River Niger. The members of the *C. macrourus* superspecies replace each other geographically, *C. macrourus* in the north and north-west to the Atlantic coast and in the east, *C. indicus* south of about 8°S; some authors put these 2 species in the genus *Urocolius* (e.g. Schifter 1972).

Populations. Mousebirds are often extremely numerous, especially around small-scale cultivations; although several species are widely sympatric, normally one is noticeably commoner than the others in any particular locality.

Movements. Mousebirds are highly sedentary; movements are probably confined to feeding and roosting flights.

Food. Mousebirds are almost exclusively vegetarian; nearly half the diet in some populations is leaves, the rest fruit, seeds and nectar with little if any animal matter. In gardens and on small fruit and vegetable farms they may be serious pests locally, but they do not adapt well to large-scale monocultures and so are of little importance agriculturally except to small-scale farming. Their diet is notable for the high proportion of plant species containing toxins or irritants. Mousebirds drink pigeon-fashion, sucking water up with the head lowered.

Behaviour. Mousebirds are gregarious at all times of year, moving in parties of normally up to 30 birds, roosting in tight huddles, sunbathing and dustbathing together, and often nesting in close proximity. Allopreening is common. Roosting birds cluster tightly together in trees and bushes, sleeping with the head upright but withdrawn into the shoulders; suggestions that they are incompletely homoiothermic are unfounded, but heavy rain can impair their insulation to the extent that they die of cold. Courtship behaviour is poorly known, but *C. indicus* and *C. macrourus* have a perch-jumping display in which one or both birds bounce up and down, sometimes with one wing held up.

Voice. They are highly vocal birds, whistling and chattering almost incessantly. Flight and alarm calls are hard or buzzing; *C. macrourus* has a clear whistle on the wing.

Breeding. Nests may be solitary or loosely clumped, shallow cups or open platforms in bushes; some are built on top of old nests of the same or other species, and most are ornamented with fresh green leaves. Eggs are dull creamy white, immaculate in some species, speckled and blotched in others. Clutch size is normally 3 but ranges from 1 to 8, the larger clutches often caused by more than one female laying in the same nest. Eggs weigh 2.7–2.9 g. Both sexes incubate, for 11–14 days. Chicks are fed by regurgitation, by both sexes, and fledge after 15–20 days. Adults incubate and brood very tightly.

Moult. Birds may begin moulting as early as 2 months after fledging. Moult is protracted; it is normally serially descendent but ascendent and stepwise moults have also been recorded. A.W.D.

Rowan, M.K. 1967. A study of the colies of southern Africa. Ostrich 38: 63–115.
Schifter, H. 1972. Die Mausvögel (Coliidae). Die Neue Brehm-Bücherei No. 459. Wittenberg Lutherstadt.

MOUSTACHIAL: applied to a streak, in some plumage patterns, running back from the base of the bill.

MOUTH: see BILL; TONGUE; also ALIMENTARY SYSTEM; RESPIRATORY SYSTEM.

MUD-HEN: popular name for the American Coot *Fulica americana* (see RAIL).

MUDLARK: see MAGPIE-LARK.

MUDNEST-BUILDERS: see MAGPIE-LARK.

MULE: aviculturist's term for a hybrid between a Canary and another species of finch.

MULGA: name for a type of bush country in Australia, characterized by *Acacia aneura*.

MÜLLERIAN MIMICRY: see MIMICRY.

MULTI-BROODED: see CLUTCH-SIZE.

MUNIA: substantive name in Asia of various species of Estrildidae; in the plural, sometimes used as a general term for the group (see ESTRILDID FINCH).

MURRE: alternative substantive name (preferred in American usage) of guillemots of the genus *Uria* (Alcidae)—see AUK.

MURRELET: substantive name of species of *Brachyramphus* and *Synthliboramphus* (see AUK).

MUSCICAPIDAE: a family of PASSERIFORMES, suborder Oscines, forming part of a group of 12 families of Primitive Insect Eaters, the main body of which consists of the so-called Muscicapid assemblage. This embraces an exceptionally large number and wide variety of largely insectivorous, mainly Old World, ten-primaried song-birds in which bright coloration and conspicuous patterns and structures are scarce. Hence, the group is treated in Peters *Check-list of Birds of the World* on reasonable grounds as one family, Muscicapidae, comprising the subfamilies Turdinae, Timaliinae, Cinclosomatinae, Paradoxornithinae, Polioptilinae, Sylviinae, Malurinae, Muscicapinae, and Pachycephalinae. Most of these had been treated as families by most authors. Though the differences seem trivial in some cases, particularly in many species of the Old World tropics, the lumping of these groups obscures such differences as do exist and results in a family which (at least in bird systematics) is very large and unwieldy. In the classificatory system used here the Muscicapid assemblage includes the families Turdidae (THRUSH), Sylviidae (WARBLER (1)), Muscicapidae (FLYCATCHER (1), Rhipiduridae (FANTAIL), Monarchidae (MONARCH FLYCATCHER), Pachycephalidae (THICKHEAD), Timaliidae (BABBLER), and Aegithalidae (TIT, LONG-TAILED). The general opinion is that the members of these families are closely related and probably more so to each other than to the remaining families of the group of Primitive Insect Eaters with the exception of the Mimidae (MOCKING-THRUSH) which on recent evidence may be very close to the Turdidae.

MUSCLE: see MUSCULATURE.

MUSCULAR CONTRACTION: see ENERGETICS.

MUSCULATURE: the system of muscles, which are the specialized organs for effecting movement. Collectively these form the 'flesh', which in an average bird constitutes almost half the total body weight.

Characters of muscular tissue. The essential feature of muscular tissue is its specialization for contraction, in the course of which force is developed. Muscle tissue in birds and other vertebrates occurs in three principal forms. Unstriated ('smooth' or 'involuntary') muscle consists of quite short fusiform cells in which longitudinal filaments may be discerned with appropriate techniques, but little else. Striated or voluntary muscle consists of very much longer multinucleate fibres, which show a characteristic pattern of crossbanding. Cardiac muscle, found only in the heart (see HEART), consists of a network of fibres showing some distantly spaced crossbars. Unstriated muscles occur mainly in such situations as the gut, viscera, glandular ducts or feather bases; they are innervated by autonomic nerves (see NERVOUS SYSTEM) and are not normally under the control of the will. Striated muscles occur principally in association with the skeleton (see SKULL; SKELETON, POST-CRANIAL), hence their alternative name of skeletal muscles. They are innervated by cranial and spinal nerves and are under the control of the will. It is with these that the remainder of this article is concerned. For a fuller review of the structure and properties of avian skeletal muscles, the reader is referred to Bock (1974).

Contraction. A muscle exerts force only when contracting, and has no intrinsic means of lengthening; stretching of a muscle can only be brought about by an external force, usually that of another muscle. Muscle contraction can take place without shortening if the force it develops is equalled by an opposing external force; 'isotonic contraction' refers to contraction involving change in length, and 'isometric contraction' to the situation when the muscle produces force without changing in length. Many muscles function primarily through isometric contraction, providing holding or stabilizing forces, e.g., in the maintenance of body posture. However, all muscles play some part in this, exhibiting a low level of contraction ('muscle tone') even when apparently at rest.

Fibre types. Striated muscle fibres show important variations in structure and histochemical properties which are correlated with physiological differences, though the details of the relationship are very imperfectly understood at present. Two main sets of types of fibre are recognized in avian muscles: red and white muscle fibres, distinguished by myoglobin content, and twitch and tonus fibres, distinguished by innervation and structural details.

Red and white fibres may eventually prove to be simply the extremes of a continuum, but the dichotomy is a familiar one, since muscles consisting largely of white fibres (e.g., the breast muscles of a chicken) are very obviously different from those composed mainly of red (e.g., the same muscles in a pigeon). No bird possesses muscles composed entirely of white fibres, though the pectoral muscles of hummingbirds appear to consist entirely of red. Apparently red fibres fatigue more slowly, but white fibres can produce a higher rate of work over a short period.

Twitch and tonus fibres also show some differences in rate of fatigue, but should not be equated with white and red; there appears to be no simple correlation between the two types. Twitch fibres respond to a stimulus with a rapid contraction which ends almost immediately the stimulus ceases. Tonus fibres respond to stimuli with a contraction which builds up more gradually, and falls off very slowly after stimulation stops. Most bird muscles that have been studied consist of a mixture of the two types, but in varying proportions. Probably a high proportion of tonus fibres indicates a postural function, while a high proportion of twitch fibres suggests a more active role.

Muscle architecture. In describing the gross structure of a muscle it is usual to refer to the attachments of its two ends as 'origin' and 'insertion'. The origin is strictly the end attached to a stationary bone, while the insertion is the attachment on a bone which is moved by the muscle's contraction. In practice, very often both bones are moved by the muscle, but the terms are still employed, if arbitrarily, for convenience.

The arrangement of fibres within the muscle—its architecture—is of great importance in understanding its action and adaptations.

Two basic arrangements are generally recognized. In parallel-fibred muscles, the fibres are oriented along the line of action of the muscle, and run from origin to insertion; hyoid muscles such as M. stylohyoideus or M. cleidohyoideus furnish good examples. Pinnate muscles are those in which fibres are attached, at least at one end, to a tendon—a structure composed largely of collagen, which functions to transmit the force of the fibres to a bone. The simplest type of pinnate arrangement (unipinnate) is with fibres attached at one end to one surface of a tendon or aponeurosis (tendinous sheet), and at the other to a bone. Bipinnate muscles have fibres attached to either surface of an aponeurosis, and multipinnate muscles have several internal aponeuroses ('raphes'), usually arising alternately from origin and insertion, and interdigitating.

The functional properties of parallel-fibred and pinnate muscles differ in important ways, stemming basically from the length and number of fibres in the muscle. Fibre length affects only the speed and range of shortening of a muscle, while the force that it can develop depends fundamentally on fibre number. In general, parallel-fibred muscles can have much longer fibres, but the number that can be accommodated is much less than that possible with pinnate architecture. Pinnate muscles are generally to be found in situations requiring the development of large forces, but relatively little shortening ('excursion'). Extremes of pinnate development, with several raphes and large angles of pinnation commonly occur in muscles sited very close to an articulation, such as the jaw muscle M. adductor mandibulae externus caudalis, or other situations involving little or no excursion, such as with the Mm. intertransversarii linking adjacent cervical vertebrae.

One- and two-joint muscles. An important distinction should be made in regard to the siting of muscles. One-joint muscles are those which arise on one bone and insert on the next in succession, spanning a single articulation. Two-joint muscles arise on one bone, miss the next and attach on the third in the series, thus spanning two articulations. (Three or more joint muscles also exist but, with the exceptions of some neck muscles, their forces are usually redirected via tendons traversing pulley or sling devices—a feature of avian limb systems which enables the weight of major muscle masses to be concentrated closer to the bird's centre of gravity.) Two-joint muscles minimize energy expenditure for many actions and, due to their length, can shorten faster than one-joint muscles. Disadvantages are that they cannot individually control the forces about each articulation, and lack the stability for holding the system under static conditions. Thus, in most major systems such as limbs or jaws, two-joint muscles provide a large part of the force, with just sufficient one-joint muscles for precise control of movement at each joint, and for stability.

Nomenclature. Muscles may be named after site, shape or action, or on the basis of presumed homologies (see HOMOLOGY). Complications have been caused by attempts to homologize bird muscles with those of mammals, producing conflicting terminologies. The Nomina Anatomica Avium (Baumel *et al* 1979) should resolve this confusion, and its nomenclature is followed here. For a detailed survey of bird muscles see George and Berger (1966).

Subcutaneous muscles. These are thin sheets or bands of muscle lying under the skin, and often adhering to it. The presence or absence of M. biceps brachii, pars propatagialis, is of significance in the diagnoses of several major groups. Subcutaneous muscles are striated, with the exception of M. expansor secundariorum, the only non-striated muscle specifically mentioned in this account (see Muscles of the wing).

Cranial muscles

1. Ocular muscles. These are the small muscles concerned with moving the eyeball, and differ little from those in other vertebrates. Included here also is the levator muscle of the upper eyelid and the muscles (M. pyramidalis and M. quadratus) responsible for the movements of the nictitating membrane (see VISION).

2. Jaw muscles. Although only 8 in number, these muscles have attracted the attention of many investigators, since they show extensive variation among birds, correlated at least in part with differences in food and feeding techniques. Present terminology is based on the detailed study by Lakjer (1926).

The action of these muscles includes not only opening (depression) and closing (adduction) of the lower jaw as in mammals, but also extensive movements of the upper jaw. Muscles which raise the lower jaw fall into two groups. Those which originate on the skull (M. adductor mandibulae externus and M. pseudotemporalis superficialis) are two-joint muscles, frequently of multipinnate architecture; those which arise on the quadrate (M. pseudotemporalis profundus and M. adductor mandibulae caudalis) are one-joint muscles, which, with M. pterygoideus arising on the pterygoid, bring about retraction as well as adduction. M. pseudotemporalis profundus is absent in parrots, many kingfishers, and various other birds. M. pterygoideus is a muscle of considerable complexity. In many birds, especially passerines, it has a slip (M. retractor palatini) attached to the skull base, thus acting solely to retract the palate. M. pterygoideus has also given rise in parrots to a unique muscle, M. ethmomandibularis, which originates on the interorbital septum, and acts purely as an adductor of the lower jaw.

Protraction of the upper jaw is effected by M. protractor quadrati et pterygoidei, and depression of the lower by M. depressor mandibulae. Striking enlargement of one or both of these muscles is seen in birds whose feeding habits involve opening the bill against resistance, e.g., M. protractor in *Gallinago* or M. depressor in *Heteralocha* (Burton 1974a and b).

Muscles of the tongue and hyoid apparatus. Like the jaw muscles, these show much variation related to feeding adaptations, and are often also of taxonomic interest. Extremes of complexity are encountered in groups with highly modified tongues, notably parrots and woodpeckers. The tongue and hyoid muscles may be grouped into two categories: *Extrinsic* muscles have an attachment at one end to the lower jaw, and are responsible for large-scale movements of the entire tongue and hyoid apparatus. They include M. branchiomandibularis, with its insertion wrapped around the hyoid 'horn', which pulls the whole apparatus forward, and M. stylohyoideus which retracts it. *Intrinsic* tongue muscles have both origin and insertion within the hyoid apparatus, and permit finer control and more delicate movements; for example, M. ceratoglossus flexes the tongue downwards relative to the basihyal, while M. hypoglossus obliquus returns it to the resting position.

Muscles of the trachea, larynx and syrinx. Opening and closing of the laryngeal slit or glottis (e.g., when swallowing food) are brought about by two small intrinsic muscles (M. dilator and M. constrictor glottidis). An additional muscle (M. cricohyoideus) connects the larynx and hyoid apparatus. Tracheal muscles show much variation, but one present in most birds is M. tracheolateralis, which adheres closely to the side of the trachea, and inserts on the syrinx. In the highly developed vocal apparatus of passerines (especially oscines), however, a number of additional syringeal muscles are present (see SYRINX).

Neck muscles. The detailed comparative review by Boas (1929) has been the basis for most subsequent studies. Muscles of the vertebral column generally are grouped into an *epaxial* series, situated dorsally, and a *hypaxial*, providing lateral and ventral components. Six neck muscles, originating principally on the first neck segment, are inserted on the skull. Four are of epaxial origin, acting to raise or turn the head; and include M. complexus, which plays an important, if indirect, part in emergance from the egg. Two hypaxial muscles (M. rectus capitis lateralis and ventralis) act as head flexors.

The muscles of the neck proper include some of the most complex to be found in the avian body, spanning many articulations, with individual slips to several vertebrae. The principal epaxial system is that of M. longus colli dorsalis, including long multijoint components as well as shorter ones traversing only one or two vertebrae. Their principal actions are to straighten neck segments I and III, and to flex segment II upwards. Still more intricate is the hypaxial M. longus colli ventralis, the bulk of which consists of long slips arising posteriorly, but each one linked by individual short slips to the vertebrae it passes; its actions are the reverse of M. longus colli dorsalis. Hypaxial muscles also include lateral components, which contribute to lateral bending, as well as providing overall stability; they include both short muscles interconnecting successive vertebrae, notably Mm. intertransversarii and Mm. inclusi, and longer muscles linking 3 or more vertebrae, such as M. cervicalis ascendens.

Muscles of the trunk and tail. Within the body region, spinal mobility is much reduced, and consequently, fewer muscles that interconnect vertebrae are required. However, the axial skeleton of the trunk also provides origin for several muscles of the wing and body wall. The chief vertebral series comprises the epaxial muscles M. longus colli dorsalis, pars thoracicus, and M. iliocostalis et longissimus dorsi, the latter including M. thoracicus ascendens. Some of the slips of M. iliocostalis insert on the posterior surface of the bases of true ribs; upon their anterior faces are inserted the hypaxial series of Mm. levatores costarum. Anteriorly, M. scalenus inserts on the cervicodorsal ribs. From the hypaxial musculature are also derived lateral flank muscles and a rectus sheet enclosing the body wall ventrally. The lateral system is largely supported by the ribs, consisting principally of the internal and external intercostal muscles; in the abdominal region, where ribs are lacking, this system provides the external and internal oblique muscles, and M. transversus abdominis. Ventrally, M. rectus abdominis runs from the pubis to the rear edge of the sternum. Posteriorly, a specialized set of muscles of axial origin controls movements of tail and cloaca.

Muscles of the wing. The rigorous demands of flight impose rather narrow limits on the variability of the wing muscles. As a result, attempts to use these muscles for taxonomic purposes have generally been less fruitful than in the case of the hind limb.

The largest muscle of the wings, and indeed of the whole bird's body, is M. pectoralis, averaging some 15% of the total body weight. It forms the bulk of the fleshy mass on the breast, arising from the body and keel of the sternum and surrounding areas, and attaching by a stout tendon on the crista pectoralis of the humerus. A layered or modified bipinnate structure has been described in many birds. Deep to M. pectoralis is a smaller—but still large—muscle, M. supracoracoideus. It springs also from the keel and body of the sternum, with additional origin from the coraco–clavicular membrane. Its tendon passes through the foramen triosseum, and then over the shoulder-joint to insert on the head of the humerus. Its action is to elevate the humerus, while M. pectoralis depresses it, providing the powerful downstroke of the wing.

Overlying the shoulder prominence are M. deltoideus major and minor, the latter apparently absent in some hummingbirds and cuckoos. M. tensor propatagialis pars longa forms the support for the free margin of the propatagium; receiving slips from various other muscles, its tendon attaches in the carpal region. The muscle also includes a pars brevis, which inserts by various arrangements, often considered of taxonomic significance. Pars brevis is absent in several flightless birds.

On the dorsal side, M. latissimus dorsi, a broad triangular sheet, arises by aponeurosis from neural spines of posterior cervical or anterior dorsal vertebrae, and inserts on the upper side of the humerus. Deep to it lies M. rhomboideus, which originates in a similar way, but inserts on the scapula. The Mm. serrati, arising on anterior ribs, also insert on the scapula. Derivatives of M. latissimus and Mm. serrati act on the metapatagium.

The elbow joint is operated by flexor and extensor groups, the former including M. biceps brachii and M. branchialis, and the latter M. triceps brachii. The presence or absence of a 'biceps slip' (pars propatagialis) has been used in distinguishing major avian groups. Muscles controlling forearm movements include besides M. pronator superficialis and profundus ventrally whose combined action is to pronate the radius and thus depress the leading edge of the wing, and also the dorsal M. supinator which elevates it. In the upper arm region in addition is situated the interesting muscle M. expansor secundariorum, an unstriated muscle of dermal origin, which inserts fleshily on the bases of several proximal secondary quills. Typically it originates by a long tendon from the axillary region via a pulley device, and by a shorter tendon, absent in passerines and several other groups, from the vicinity of the elbow. This muscle has been frequently included in taxonomic diagnoses, but on present evidence is of doubtful value for such purposes.

The humerus also provides origin for some long two- or three-joint muscles acting on the carpus or carpometacarpus. Among these is M. flexor carpi ulnaris, whose long tendon passes through the humeroulnar pulley, a ligamentous loop at the elbow. Finally, muscles operating the digits are of great importance in controlling the movements of primaries and alula in flight; they were inadequately studied prior to Stegmann's (1978) detailed account, which has yielded valuable evidence on the relationships of several major groups.

Muscles of the hind limb. Leg muscles exhibit considerably greater variability than those of the wing, reflecting the wide range of adaptive modifications shown by the hind limb among birds. An excellent functional study is that by Cracraft (1971) on *Columba livia*—a species possessing all but one (M. iliofemoralis externus) of the 'formula' muscles (see below).

One-joint muscles arising on the pelvic girdle and axial skeleton include femoral protractors, such as M. iliofemoralis internus, retractors (such as M. flexor cruris lateralis) and rotators, such as M. ischiofemoralis and M. obturatorius. The two-part M. caud-ilio-femoralis probably functions mainly to produce lateral tail movements. Two-joint muscles with pelvic origin include extensors of the tibiotarsus (e.g., M. iliotibialis, M. ambiens) and flexors (e.g., M. biceps femoris). Muscles originating on the femur itself are predominantly two-joint or multi-joint. Of the former may be mentioned M. gastrocnemius, which acts partly as an extensor of the tarsometatarsus, and M. tibialis cranialis, a flexor. Multi-joint muscles arising from the distal end of the femur all act as flexors of the digits, and are considered in more detail below. The tibiotarsus provides origin for some single-joint muscles such as M. peroneus brevis, which flexes the tarsometatarsus, and M. peroneus longus which acts to extend it, as well as some additional multi-joint muscles acting on the digits. Finally, the tarsometatarsus itself provides origin mainly for a number of single-joint muscles which act as extensors of the digits, and in some cases provide lateral movement as well.

The foundation for taxonomic applications of hind limb myology was laid in the 19th century by Garrod. In the thigh region, he stressed the presence or absence of M. ambiens, and set up a formula in which the presence of components of M. caud-ilio-femoralis and M. flexor cruris lateralis was denoted using letters as symbols. Garrod's original formula, using the letters A, B, X and Y, has been expanded by later workers, and is now made up as shown below. Although most recent pelvic musculature studies use many additional characters, amenable to multivariate or other types of analysis, the formulae are still useful as a shorthand when compiling diagnoses of avian groups. In general, the presence of 'formula' muscles is regarded as a primitive state, and their loss as derived (see CLADISTICS); large complements occur among groups regarded as phylogenetically old (e.g., Galliformes, Gruiformes), while groups of more recent origin mostly show a reduced complement. ACEFMNXY is probably typical of most passerines, while drastic reduction occurs among the Apodiformes (e.g., AEN in *Chaetura pelagica*), related to that of their hind limbs in general.

The 'formula' muscles and their symbols are as follows:

A = M. caudofemoralis
B = M. iliofemoralis
C = M. iliotrochantericus medius
D = M. iliofemoralis externus
E = M. iliofemoralis internus
F = M. plantaris
G = M. popliteus
M = M. fibularis (peroneus) longus
N = M. fibularis (peroneus) brevis
X = M. flexor cruris lateralis, pars pelvica
Y = M. flexor cruris lateralis, pars accessoria
Am = M. ambiens
V = Vinculum between tendons of Mm. flexor perforatus digiti III and M. flexor perforans et perforatus digiti III.

Garrod also drew attention to the variable arrangements of the deep plantar tendons in birds, and these, too, have been much used in systematic studies. There are three principal sets of long flexors each of which may be represented by several muscles, the hallux having but one, digits II and III having three each, and digit IV two. Inserting tendons pass to the bases of 1st, 2nd, 3rd and terminal phalanges of the toes. Those inserting on the proximal phalanx are perforated, just prior to insertion, by tendons inserting on the 2nd and 3rd phalanges and these in turn are perforated by the tendons to the terminal phalanges, so that we speak of flexores perforati, flexores perforantes et perforati and flexor perforans, the latter being tendinous branches of M. flexor digitorum longus.

Mm. flexores perforati digitorum II, III and IV arise in various fashions, separately or partly fused, either from the intercondylar region of the femur or more distally from ligaments around the knee, or the upper part of the tibia and fibula, and from the tendon of M. ambiens. Mm. flexores perforantes et perforati digitorum II and III arise in similar fashion, except for the connection with M. ambiens. In many cases, the tendon to digit III receives a tendinous connection (vinculum) from that of M. flexor perforatus, denoted by 'V' in the muscle formula.

M. flexor digitorum longus ('perforans') is the deepest-lying stratum, with extensive origin on the back of the tibia and fibula. Its stout tendon passes deep to the preceding tendons over the intertarsal joint, and divides into three slips that proceed to the three anterior toes. The hallux has its own deep flexor, M. flexor hallucis longus, also arising distally on the femur; this bifurcates in the metatarsal region, one part forming a vinculum to the adjacent tendon of M. flexor digitorum longus, while the other goes on to insert on the terminal phalanx of the hallux. This vinculum (not to be confused with that between the flexors of digit III) ensures that flexion of the hind toe is automatically accompanied by flexion of the other toes, although these can, through their own deep flexors, contract without involving the hind toe. Where the hind toe is absent, the tendon of M. flexor hallucis longus fuses with that of M. flexor digitorum longus. (W.C.O.H.) P.J.K.B.

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MUSEUM: an institution having nowadays the main function of preserving, for study and display, collections of specimens relating to particular subjects. Study collections of birds are usually to be found in museums or departments of natural history. The size of the museum largely determines its aims. In the largest, these may be to preserve as representative a sample as possible of the birds of the world, and to display every aspect of bird biology suited to display by exhibits; whereas in small museums the object may rather be to show mounted specimens of local species. Such local exhibits often fill in details for which there is no room in the more comprehensive displays.

Public interest is catered for by the education and recreational side of a museum's functions. The objects, captions and graphics of a traditional exhibit allow a visitor wide latitude in depth and speed of study, which is reduced when recorded talks are used. This tendency may be carried much further by reactive displays which put over effectively a limited number of concepts. The information constantly available may be supplemented by guided tours, lectures, demonstrations, classes and film programmes, while portable exhibits may be circulated to schools and other institutions.

While display and teaching are the chief concerns of most museums, the great natural history museums are primarily research institutions in which much more extensive specialized collections, supported by libraries and technical facilities, provide unique opportunities for research by their own staffs and visiting workers. Early collections were mainly received from individuals, since the first 'cabinets of curiosities' were founded by wealthy private collectors; but eggshells are now the only bird specimens subject to the collector's mania, and those who collect other material do so for the furtherance of knowledge. Most private collections have now found their way into museums, and collecting is increasingly purposive, whether as a technique of research or to fill gaps in the museum's own collections. Improving the retrieval of information through better arrangement of the specimens has been a powerful impetus to research into natural classifications (see CLASSIFICATION; SYSTEMATICS; TAXONOMY), which is one of the principal fields for study in natural history museums. Much staff time is spent in protecting the collections from physical and biological injury, which has resulted in the application of new techniques, and in refining their arrangement and documentation for the benefit of research workers.

Research specimens of birds used to consist almost entirely of study skins, simply stuffed in the field and presenting little more than the external appearance, but carrying essential field information on their labels. Though laborious to prepare, skins are easy to transport, store and examine. With their data, they have been of the greatest importance for studies on classification, variation, seasonal changes and distribution; and are still the principal material for investigating relationships at the species level. Other techniques, such as freeze-drying, for producing comparable specimens offer great advantages, but technical difficulties have so far prevented their widespread use in the field.

Since at the species level the classification of birds is uniquely well founded, the emphasis is now on higher classification for which anatomical specimens are more important. Collections of disarticulated study skeletons and of birds preserved in fixatives, though still small in comparison with skin collections, are now growing much more rapidly. New techniques of research (see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA) can involve the formation of what are effectively new types of museum collection, like that of egg-whites at Yale. Archives of recorded bird calls, as at Cornell, are primary research material rather than libraries, and important for taxonomic as well as other studies. The promising new technique of electrophoresis using feather proteins enables the large skin collections to be used for biochemical taxonomy with little damage.

Other types of bird specimen are mainly important to aspects of biology other than taxonomy. Eggshells with their data show where and when a species has bred, and can provide material for the analysis of changing pollution. Nests encapsulate the movements used in building them. Preserved gut contents and gonads contribute to knowledge of diets and of breeding cycles. The maintenance of such a range of collections adds to the problems of curation, yet it may be desirable to maintain parallel collections even for a single type of specimen. For example, TYPE SPECIMENS may be segregated from the general skin collection because of their unique importance to nomenclature, as may the skins of extinct and endangered birds.

Much taxonomic research concerns variation, whether for its own interest or to establish norms. Birds of one population vary individually between age classes and sexes, and from season to season and may also be polymorphic. Populations of most species vary geographically, and sometimes with altitude. Clearly, to be able to provide a reasonable statistical sample of (say) adult males in fresh breeding plumage from each of many sample areas, over the whole range of one of the 9,000 bird species, requires very large total collections. The material in one museum is often insufficient for a particular study, and the natural history museums of the world are continuously engaged in lending specimens for research. Large collections have been made for special studies, but this method may be wasteful and better replaced by the recording of data from birds which are captured and released. Some museums accept extensive data for permanent preservation.

Though anatomical variation is potentially important, its study has scarcely begun because anatomical collections are still comparatively small. Besides their use for modern studies, skeleton collections are essential for the interpretation of older material. Fragments from archaeological sites and Quaternary deposits provide information on former distributions; but it is the rapidly increasing knowledge of bird fossils from the Tertiary which is resulting in fundamental reassessments of evolutionary history and higher classification.

Museums became important as more than mere cabinets of curiosities towards the end of the 18th century, when great national collections such as the Muséum National d'Histoire Naturelle in Paris and the Rijksmuseum van Natuurlijke Historie in Leiden were dominant. In Britain this was the era of the wealthy private collector, and the British Museum's natural history collections (separated as the British Museum (Natural History) about 1881) only gradually achieved pre-eminence as a result of amateur and official collecting throughout the Empire. Today the United States have the bulk of the specimens in the world, held in dozens of national, state, university and independent museums, whose ornithological staffs comprise the majority of all avian systematists. However, there are important collections and active research staffs throughout the developed world, while many developing countries are actively enlarging or founding their own. In numbers of specimens, the largest collections are those of the British Museum (Natural History) and American Museum of Natural History, since they each have about a million study skins, while the United States National Museum of Natural History is actively expanding exceptional anatomical collections.

Several British museums have important research collections of British birds, while for the birds of the world the most important after the BM(NH) are probably the Manchester Museum, Merseyside County Museum, National Museum of Wales, Royal Scottish Museum, and University Museum of Zoology, Cambridge. Some local museums have been designated as biological records centres under a national organization. While some of the functions of this organization are already carried out, for birds, by ornithological and natural history societies, the local centres should make a valuable contribution to planning and conservation. (J.D.M.) I.C.J.G.

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MUSIC, BIRDS IN: regarded here as an avian element in human culture. There are two other articles on this subject: Fisher (1966) and Scholes (1970). These between them list most of the references to birds in the musical repertoire to the end of the 19th century but few more recent ones. This article, therefore, while offering a necessarily selective survey of bird-inspired western music, treats later developments more fully.

Musical inspiration derives from: (1) songs and calls; (2) line and movement; (3) literary sources; and (4) fabulous and mechanical birds. Treatment may be direct sound-imitation; symbolic; impressionistic. In the last few decades, (5) 'concrete' bird music (recorded bird sounds in intact or modified form combined to create musical works) has evolved into a category of its own.

Of the three methods of treatment possible in vocal or instrumental music, direct sound imitation, though present in even the earliest works, has perhaps made the greatest progress and impact in recent years. When birds are used as symbols, there may be no obvious reference but an appropriate 'atmosphere' is generated. Impressionistic treatment, despite its lack of definition, is probably the best vehicle for inducing a felicitous response, especially in the ornithologist who may justifiably be irritated by the inadequacy of human voices and instruments when they attempt to imitate all but the simplest bird calls.

All these three musical approaches have, however, appealed to composers of all periods, whatever the source of their inspiration (apart from the line and movement of birds which can only be treated impressionistically). Indeed, they are often combined in the same work.

The four voices of the 13th century canon 'Sumer is icumen in', the earliest known English secular composition, imitate the Cuckoo's call and it has been musically echoed down the centuries. Janequin's 'Song of the birds' from the early 16th century combines a realistic Cuckoo together with trilled *rrr*'s and fast staccato notes which merely hint at their living sources. Orlando Gibbons, a century later, in his madrigal 'The Silver Swan' takes this mute bird, which dying 'unlocks her silent throat' in wise utterance, as a symbol and the gravely flowing vocal lines mirror the slow, dignified movement of a swan floating on placid water: the beginning of a long tradition of symbolic swan music. Impressionistic use of bird sounds and movement has been continuously represented in instrumental works from, say, Vivaldi's 'Four Seasons' in the early 17th century, to Vaughan Williams's 'The Lark Ascending' and the compositions of Edward Cowie and Trevor Hold in the 20th.

1. Songs and calls. An index of species shows a great variety, with several favourites. The Cuckoo, with its familiar diatonic intervals, is the obvious point of departure for a composer wishing to introduce a pastoral flavour; Beethoven, in his Sixth Symphony, the most notable among them. But the bird also stimulated a number of compositions exclusively devoted to it: Couperin, Pasquini, Vivaldi and Daquin in the 17th and early 18th centuries, for example.

The Nightingale, another favourite but more difficult to represent, had Janequin and Couperin among its early devotees and Rameau (1683–1764) included an 'Air du Rossignol' in his opera 'Hippolyte et Aricie' with both vocal and instrumental imitation. Handel (1685–1759) made the bold attempt to combine Cuckoo and Nightingale in an organ concerto, and these two species and others are thought to be represented in Haydn's (1732–1809) Op. 33, no. 3, nicknamed the 'Bird Quartet'. In the famous Toy Symphony, formerly attributed to Haydn, Quail, Cuckoo and Nightingale figure on the toy instruments. It is now known that this composition is part of a work by Leopold Mozart; the toy instruments added, possibly by Joseph's younger brother Michael Haydn. Later admirers of the Nightingale have included Glinka, Mendelssohn, Liszt, Balakirev, Grieg, Granados, Ravel and Milhaud.

Respighi (1879–1936) arranged some 17th and 18th century works in his orchestral suite 'The Birds' whose subjects are Cuckoo, dove, hen and Nightingale. Doves, specific or unspecified, are numerous (see below) but the domestic hen is less usual, though one of Haydn's symphonies is called 'La Poule'. Humperdinck (1854–1921) in 'Hansel and Gretel' has a cock which diverts us with *ki-ke-ri-ki* in the English translation; he also has a vociferous Cuckoo and a Skylark, but this is a bird of vocal whimsy. Larks, too, go through the centuries from Janequin to Messiaen.

Other passerine species less commonly represented include the Goldfinch (Vivaldi), Linnet (Couperin, Haydn, Rachmaninov), Robin (Lalo and Peter Warlock), Swallow (Dvorak, Pierné, Tschaikovsky), Wagtail (Britten) and, exotically, the Scarlet Tanager (Dvorak's American String Quartet). Remarkably, the Blackbird attracted little attention until the present century. An unpromising species, the Magpie, is the subject of a Mussorgsky song; and the side-drum roll in Rossini's 'La Gazza ladra' could be an imitation of Magpie chatter.

Among non-passerines, there are songs about 'A greedy hawk' and 'Compel the hawk to sit' by William Byrd (1543–1623); and Thomas Weelkes (*c.* 1575–1623) composed the madrigal 'A Sparrowhawk proud'. Haydn has a song about a Blackcock; Beethoven (Sixth Symphony) and Schubert (C major Quintet) have Quails, and Mussorgsky an escaped parrot in the fifth act of 'Boris Godunov'. Prokofiev, in 'Peter and the Wolf', asks an oboe to give a duck squawk. Numerous other non-passerine species used by composers are treated more fully below.

Finally, in this summary of species representation, Boccherini (1743–1805) has a collection in 'The Aviary'—the title of a string quartet.

From the late 19th century to the mid-20th, continental Europe produced several fine composers of large-scale works whose careers overlapped and all of whom to some extent mirrored in their music the countryside of their birth.

The great Austrian symphonist Anton Bruckner (1824–1896) was said to 'reflect . . . the voice of Nature itself' in his Fourth Symphony. The only overt imitation occurs in the first movement; this is a song (more likely two song-types strung together) of a Great Tit. Of all direct imitations of bird song this is one of the most authentic and appealing, yet it emerges as an integral part of the movement, never a mere decorative accessory. But it is true to say, as of others among these composers, that Bruckner's music is informed by natural sounds, including birds, rather than formed from them.

Mahler (1860–1911) made use of birds, although their singing so distracted him when composing that he was known to shoot them. Yet his musical ear appreciated the Chaffinch call *zink zink*, thus transcribed in his own poem for one of his 'Songs of a Wayfarer'. A Cuckoo, singing a perfect 4th rather than the ubiquitous major and minor 3rds, pervades much of his First Symphony along with some unspecified bird song. Another Cuckoo and a somewhat capricious Nightingale turn up in the Third Symphony. The slow section of 'The Drunkard in Spring' from 'Das Lied von der Erde' includes bird calls and chirrups to tell the Drunkard of the arrival of spring and the last movement, 'The Departure', contains music strongly evocative of the natural scene in which the two friends say farewell.

Although Sibelius (1865–1957) was particularly responsive to bird sounds, he made little explicit use of them in his music. Yet he describes the call of the Crane as 'The leitmotiv of my life' and noted on Villa-Lobos's music 'One can hear that he was brought up in a quite different bird world from me' (Levas 1972). His devotion to swans is evident in the enraptured poignancy of his 'Swan of Tuonela' whose long lament is played by the cor anglais.

Most swan music represents the Mute Swan *Cygnus olor*, a species not established in Finland until 1934. 'The Swan of Tuonela' was composed in 1893 and it was the migrating Whooper Swans *C. cygnus* that Sibelius used to greet each year when they were resting on a lake near his home. In the incidental music from Kuolema (where we also find the well-known Valse Triste) there is a 'Scene with Cranes' in which the birds' calls are imitated by two clarinets; and the concert suite from his music for Strindberg's 'Swanwhite' includes 'Peacock' and 'Listen, the Robin sings'.

The Danish composer Carl Nielsen (1865–1931) and Bela Bartók (1881–1945), deeply committed to his native Hungary (though his birthplace is now in Romania), were likewise musicians with an informed appreciation of bird sounds who mostly made implicit rather than explicit use of their carefully studied material. Nielsen chose an unusual avian model in his 'Song of the Siskin' for chorus. 'The First Lark' and 'Springtime on Fyn' are other choral works with bird associations and there is a hint of a Cuckoo in the 'Helios' overture. Basically, however, the loving perception he accords to birds, in his description of their special 'accents' on his native island of Fyn (in his essays 'Living Music'), is transmuted into orchestral colours and time-patterns, especially perhaps in his Wind Quintet.

Bartók produced his most overt nature music only after he had left Hungary for permanent exile in the United States. Biographers testify to his exact knowledge of all natural sounds and his unusually acute hearing. A buzzing, humming sound as of insects is often his way of suggesting a natural background. In 1943, already suffering from his terminal illness, he was sent to relax at Asheville, North Carolina, where he went for long walks and painstakingly noted down the songs of an avifauna that was new to him. When he came to write his last work, the

Third Piano Concerto, this material was transformed (particularly in the second movement) into the seemingly inexhaustible flow of motifs in this splendid work.

In contrast, Olivier Messiaen (b. 1908) brought precise bird vocalizations to the musical masses. A prolific composer and a good ornithologist, he has incorporated the songs or calls of 260 species from six faunal regions in at least 10 of his major works. It is notable, however, that when he contrasts his skilfully contrived overt imitations with impressionistic settings of the habitat—as in the 7-volume 'Catalogue d'Oiseaux' for solo piano—attention and imagination are stimulated. But in those works composed entirely of songs and calls, for example 'Reveille des Oiseaux' for piano and orchestra, attention is taxed to the point of confusion because of the polyphonic nature of the work, wherein as many as 21 species are presented simultaneously at the climax of the dawn chorus.

From such complexity, Messiaen turns to extreme simplicity in his 'Merle Noir' for solo flute with piano accompaniment. This does not aim at complete fidelity: the duration of the pauses between the phrases must be reduced to achieve continuity when there is no answering bird or background song; but it is a distillation of the species' song and a convincing work of art. Messiaen's other works devoted to, or incorporating bird sounds include Oiseaux Exotiques, La Fauvette des Jardins, Chronochromie, Couleurs de la Cité Céleste, Et Expecto Resurrectionem Mortuorum, La Transfiguration and Méditations sur la mystère de la Sainte Trinité. In 1974 Messiaen completed 'Des Canyons aux Etoiles', a 96-minute work which incorporates the songs of 60 species from Utah and the Hawaiian Islands.

There is a long tradition of bird song representation in French music and Messiaen's immediate predecessor and, maybe, his inspirational springboard, Maurice Ravel (1875–1937), has received little credit for his imaginatively unique contribution to it. In the scene 'Lever de Jour' from the ballet 'Daphnis and Chloë', three solo violins, piccolo and flute evoke the unspecified birds who greet the rising sun. They are followed by two shepherds playing pipes (piccolo and E flat clarinet). In no other musical work are we so delicately reminded of the tenuous borderline between avian and human music.

'L'enfant et les Sortilèges', a brief, bewitching opera, ends with a garden scene at night with only a child and the animal denizens taking part. Ravel, master of orchestration, requires a slide flute for his Tawny Owl. He abandons most of the conventional but inaccurate trills dealt out to Nightingales and gives his bird (piccolo) repeated notes and tremolo effects. When a soprano voice sings another Nightingale part there is little attempt at imitation and the bird has a lyrical descant above the other animal voices. In 'Ma Mère l'Oye', a suite of piano duets subsequently extended and orchestrated for a ballet, some unorthodox little birds cheep (complex violin harmonics) as they peck up the trail of crumbs laid by Tom Thumb, and a very orthodox Cuckoo calls in the same piece.

Ravel's most serious essay in bird vocalization is his impressionistic 'Oiseaux Tristes' for piano—an evocation of 'birds lost in the torpor of a forest during the most torrid hours of summer'. No other composer has achieved such a convincing representation of the sounds of birds in conditions where they tend to be vocally quiescent. The only firm evidence about species comes from the report of a friend which tells how Ravel went to the forest to listen to a Blackbird. In this work it sings precisely as Blackbirds do in such circumstances—sporadically and tending to repeat a single phrase. All else is implied, but the pairs of slowly repeated single notes can only be a Turtle Dove: a sudden explosion of alarm calls suggests a Chaffinch, followed closely by a single abbreviated Wren song as elicited by disturbance. Repeated drooping major and minor thirds suggest a slow and indeed a 'sad' Cuckoo. A three-line cadenza near the end of the work hints at subsong from several species and merges finally into the continued murmuring of the Turtle Dove.

Four birds appear in Ravel's song cycle 'Histoires Naturelles'. The noble, if vain, demeanour is depicted in 'The Peacock'; contrary motion black key glissandi represent the spreading tail; and the harsh cry is sung *Léon, Léon* with a properly dissonant accompaniment. 'The Swan' looks back to Saint-Saens' (and Pavlova's) famous bird, but with sophistication and irony. Twenty-three bars of pianissimo writing express the awe and delight of a fisherman whose rod is graced by 'The Kingfisher'. And in conclusion and contrast 'The Guinea-fowl' is conjured up, irascible and raucous, scratching in the soil and bathing in the dust.

Yorkshire-born Frederick Delius (1862–1934) lived not far from Ravel at Grez-sur-Loing. He remarked to Elgar that the song of the birds was the greatest music of all, an explanation, perhaps, for his uniquely tender treatment of the subject of 'On Hearing the First Cuckoo in Spring'. Even greater was his love and sympathy for the pair of Mockingbirds and all that they symbolize in Walt Whitman's 'Sea Drift'. This setting for baritone, chorus and orchestra must be the most extended (24 minutes) eulogy for a living, singing bird and threnody for a dead bird—the singer's mate—ever conceived.

Much bird music has come from the pen of Benjamin Britten (1913–1976). In the children's opera 'The Little Sweep' their voices give vivid renderings of Chaffinch call notes, the Heron, Tawny Owl and Turtle Dove. The Turtle Dove appears again (flutter tonguing on recorder) when Noah launches it from the ark in 'Noyes' Fludde', and yet again in one of Polly's airs in his realization of 'The Beggar's Opera'. In another air the flight of the Swallow is cleverly suggested by the flute. 'The Spring Symphony' has a merry Cuckoo and a quire of birds; piccolos represent the flight of the Skylark in 'A Midsummer Night's Dream'; and the fluttering of an unspecified wagtail comes in 'Winter Words': a cycle of Hardy poems which also includes 'Proud Songsters'. There is music for wild geese in the operetta 'Paul Bunyan' and an evocative reiterated Curlew motif in 'Curlew River'. 'Our Hunting Fathers' contains an angry 'Dance of Death' for Ravenscroft's 'Hawking for the Partridge'.

Amongst British composers, Trevor Hold (b. 1939) has published a study of bird vocalizations and their notation (Hold 1970) and has also used songs and calls, both explicitly and implicitly, in his works. Those in the first category include 'The Unreturning Spring', a song cycle for two voices and small orchestra wherein the Interlude before the final song has a 'mobile' of Song Thrush (flute), Corn Bunting (oboe), Reed Bunting (clarinet), Nightjar (bassoon) and Tawny Owl. Implicit (unspecified) song abounds in his instrumental and orchestral works, notably 'The Blue Firedrake', 'Calendar', 'Time Passes', 'Belfry Music' and 'Clare's Ghost'. In Hold's 'Signs of Winter', based on John Clare's poem, a solo horn represents ducks flying up from a pond.

Edward Cowie (b. 1943) has found inspiration in the environment of north-west Lancashire for several works composed in the 1970s. 'Gesangbuch' (Song book), in two versions, a series of four tableaux for voices and instruments is, in Cowie's words, a response to 'particular aural and visual signals' of these open, often marshy expanses. In one of them, 'Hest Bank' (1974), fragments of bird names and landscape features occur in his own text for the voice parts.

Of contemporary music derived from bird vocalizations obtainable only on disc or tape, outstanding is 'Calling Down the Flevo Spirit' by Kees Hazevoet and Aan Bennink (Snipe Records, 7678, Amsterdam). There is no score because the performers improvise brilliantly and imitate six species with some startling verisimilitude; the titles are Stone Chattin', The Woodcock, King of Saxony, The Roller, Snipe Drumming and Mot-mot.

Beyond Europe, Radio New Zealand leads with a disc (and cassette) of distinction: 'Children of Tane'. Tane is the Maori God of Nature and the birds are his children. Music, words and performance are all by Sydney (Hirimi) Melbourne, a member of the Tuhoe tribes (the people of the mist). Fourteen songs emerge from recordings of the birds' own voices and epitomize native mythology and imitation in the Maori tongue—ideal for the purpose with its many vowel sounds and soft delivery.

2. Line and movement. Sources of inspiration in the shapes and forms of birds at rest, hovering or in flight, and the visual satisfaction they offer, are more difficult to identify than aural sources. Perhaps Vivaldi, in his Flute Concerto 'Il Gardellino', was not as much stimulated by the Goldfinch's twittering, musical song, as by its rapid movements. Certainly Vaughan Williams in 'The Lark Ascending' was particularly sensitive to flight. In some 19th century ballet music, composers (notably Tchaikovsky) were concerned not only to represent birds in movement but to support the dancers when the choreography required emulation of flight. Few can remain unmoved by the artistry achieved by Tchaikovsky and Petipa in the 4-act 'Swan Lake'. But slighter bird works arising from the same composer–choreographer collaboration may arouse even stronger associative feelings on account of their light, delicate texture and the formal scaling down to size and rapidity of movement more compatible with our apperception of birds in general.

In 1964 a one-act ballet was based upon courtship display. Entitled simply 'The Display' its subject is the Lyrebird with music by the Australian Malcolm Williamson (b. 1931), Master of the Queen's

Musick, and choreography by Robert Helpmann. Another recent ballet 'Eagle's Nest' (music by Kamen and choreography by Falco) had its première at La Scala, Milan. The eagle portrayed therein is reminiscent of the magnificent Golden Eagle interpretation by the Indian dancer, Ram Gopal, in the 1940s. These are but a few examples from a field worthy of greater consideration; others will be found in section 4.

Much 'descriptive music', when birds are used as symbols or to create the atmosphere of a woodland, a particular season or time of day, is evidently inspired by visual as well as aural impressions of birds. Most 'swan' music, for instance, derives from the bird's literary and legendary appearances and the solemn atmosphere created by composers as diverse as Orlando Gibbons, Wagner, Ravel, Sibelius and Prokofiev seems to pay homage to the visible majesty of this great bird. Prokofiev's 'White Swan', composed in 1910 but not given its first performance until 1980 in a version edited by Rozhdestvensky, is a setting for female voices, horn and strings of a poem by Konstantin Bal'mont. In a few minutes of grave, gentle music, it presents the swan as 'a serene symbol of feminine beauty'.

Richard Strauss (1864–1949), in his 'Four Last Songs', incidentally illustrates the impossibility of strict categorization of bird-inspired music. In these settings of poems by Hesse and von Eichendorff, two Skylarks rise, hover and ultimately bring 'Im Abendrot' (In the Evening Glow) to a close with their tremulous music and flight. The words of Frühling (Springtime) refer merely to 'bird song'—at which point the vocal line soars above the orchestra in a long melisma.

3. Literary sources. These include all vocal settings of poetry as well as folk tales, legends and stories in which actual (as opposed to fabulous) bird species figure: many works of literary inspiration have been discussed in section 1. Whether poem or legend was the first source of inspiration or whether the composer was attracted to it by an interest in birds is open to argument, or biographical evidence, in individual cases.

After the Bible, the earliest inspirational text is probably 'The Birds' of Aristophanes (455–375 BC), treated by at least seven composers. Many legends have contributed to opera plots or tone poems, and forest or pastoral episodes in an even wider range of operas and ballets demand impressionistic treatment of bird sounds and movement as part of the orchestral scene-setting.

Neatly spanning the main period of European musical development 'The Suffolk Owle', originally a madrigal by Nicholas Vauter (born *c.* 1590), has a modern setting in the cantata 'Voices of Night' by Franz Reizenstein (1911–1968). Cock crows dramatically break into the sombre Passion music in the oratorios of Schütz and Bach and biblical inspiration also evoked bird music in Haydn's 'The Creation'. Handel, in 'Acis and Galatea' and in many pastoral themes in his operas and masques, shows his awareness of bird song, and is said to have 'imported live birds into his operas'. (A 20th century Ashton ballet to music by Messager also brings real birds on stage to supplement the dancers of 'The Two Pigeons'.)

German lieder, so many of them settings of 'open air' poetry, are less productive. Only an occasional hint of bird song, perhaps a grace note in the accompaniment, is used by Schubert and Brahms. Wagner (1813–1883), drawing on medieval legends for his opera plots, gives us the swan symbolism of 'Parsifal' and 'Lohengrin' but it is 'The Ring' cycle and the Siegfried Idyll that bear the strongest testimony to the enrichment of his music by recreated experience of bird sounds.

Liszt (1811–1886) also turned to legend in his pianistic tribute to St. Francis of Assisi preaching to the birds. Trills and arpeggio passages punctuated by brief, often staccato motifs represent the birds which are temporarily silenced by a gentle tenor recitative suggesting the voice of the Saint; this appears in the bass at a climactic point, then a long diminuendo leads back to bird song which drifts into near silence at the close. The impression of song and flight may owe inspiration to the Larks (or in one source the Swallows) which are said to have comprised much of the flock at St. Francis' sermon (see Armstrong 1973).

Dvorak (1841–1904) was constantly and openly inspired by bird song (using it thematically, for example, in two quartets and the 8th Symphony). He was a pigeon fancier but the species of his symphonic poem 'The Wild Dove' (Czech *Holoubek*) must be the Stock Dove, whose persistent cooing above her husband's grave drives an erring young widow to suicide. The complex orchestration—flutes, oboe, high repeated notes on harp and some muffled drumstick strokes on a cymbal—is peculiarly apt, as is Alec Robertson's description of the dove as 'self-righteous'! (Robertson 1964). The Skylark, Cuckoo, Swallow and House Sparrow are subjects of some of Dvorak's songs.

Schoenberg (1874–1951) was also inspired by dove song. The species of his 'Song of the Wood Dove' from the great choral–orchestral work 'Gurrelieder' seems to be the Woodpigeon if judged by the time patterning of fragments in the introduction and coda. But the mezzo-soprano's line is suffused with dove-like conjunct intervals as she declaims the death of Tove, tragic figure of Danish legend. (It appears to be fortuitous that the German *gurren* means to coo.) Schoenberg is again sensitive to birds in his setting of Petrarch's 'When little birds weep'.

Leoš Janáček (1854–1928), from Moravia, was steeped in the music of animal sounds which he notated as meticulously as he did the lines of human speech. Hence it is not surprising that in his captivating nature opera 'The Cunning Little Vixen' birds are prominent: there are a Cuckoo, Raven, woodpecker (xylophone), a Barn Owl, a Jay and a flock of Starlings. A domestic cock presides over his harem which clucks conventionally while their leader astonishes us and, no doubt, her sister hens with egg-inspiring trills and embellishments! 'Katya Kabanova' has bird music which evokes song, flight and the beating of clipped wings. In his last opera 'The House of the Dead' (set in a Siberian prison camp and based on Dostoyevsky's novel) Janáček introduces, ironically, a Cuckoo and, symbolically, an eagle: the Czar of the forest. The captive, wounded bird, its early attempts to fly and ultimate flight to freedom, symbolize the plight and hopes of the prisoners. Among his small choral works are 'The Dove' (Holubička) and 'The Wild Duck'. 'The Screech (Barn) Owl' and 'They Chatter like Swallows' are included in the piano suite 'The Overgrown Path'.

Rimsky-Korsakov (1844–1908), like Janáček, carefully notated bird vocalizations and was so scrupulous as to explain that the song of his pet Bullfinch had to be transposed down a tone 'for the convenience of the violin harmonics'. This bird's song and other bird voices can be heard in his operas 'The Snow Maiden' and 'Mlada'.

Further 20th century illustrations of literary inspiration (apart from the Britten works referred to in section 1) include Carl Orff's 'Carmina Burana', drawing on medieval sources, in which a Swan (again! but this time dead and roasted) finds tenor voice to lament its fate; and, in strong contrast, Peter Warlock's setting of Yeats' poem 'The Curlew' has an evocative flute line as part of the accompaniment.

4. Fabulous and mechanical birds. These are sparse in the musical repertoire wherein Schumann's (1810–1856) 'Prophet Bird' is probably the best known. Oddly, the Phoenix attracted little early attention, though there is an unaccompanied concerto for 4 bassoons by Michel Corrette (1709–1795). In the last 20 years, the bird has given its name to several works, including 'The Phoenix and the Turtle', an opera by Thea Musgrave (b. 1928). A near approach to the Phoenix is Stravinsky's (1881–1971) 'Firebird', composed for Diaghilev's Russian Ballet and choreographed by Fokine. The same composer based his opera 'Le Rossignol' on Hans Andersen's 'The Emperor and the Nightingale'. Subsequently, Diaghilev had it adapted as a ballet 'Le Chant du Rossignol' in which the 'real' Nightingale takes fright at the crude humming of the mechanical bird but ultimately returns to revive the dying emperor with its song.

Rimsky-Korsakov's 'Golden Cockerel', yet another creation for Diaghilev's Russian Ballet, approaches the fabulous (as does Wagner's Forest Bird), in its superavian abilities, although its crowing sounds real enough. Maeterlinck's (1862–1949) play 'The Blue Bird' also inspired works by Humperdinck and Norman O'Neill. In Ravel's opera 'L'Heure Espagnole' there is a fabulous bird 'L'Oiseau des Îles' (played by the piccolo) and a mechanical one: a little toy cock whose diminutive but shrill crowing is reproduced by the reed alone when removed from a sarrusophone. This work, set in a clockmaker's shop in Toledo and concerned with the amorous escapades of the wife of the absent owner, also gave Ravel double-edged scope for Cuckoos, both vocal and instrumental!

In the very different tradition of Brazilian folk music and legend, Deitor Villa-Lobos (1887–1959) composed his early symphonic poem 'Uirapurú': an enchanted and enchanting bird, worshipped as the King of Love. The story, of his own compiling from several legends, tells how the mellifluous nightly song of the bird lures people into the forest in search of it. An arrow-shot through the heart from a beautiful maiden transforms the bird into a handsome young man. But he, shot once again by an ancient Indian nose-flute player, turns back into a bird and flies away, singing, into the forest depths. The rich orchestration, which includes Latin American percussion instruments and violinophone (a violin with a horn attached) exploits fully the dramatic episodes of the story and the peaceful, rippling phrases of Uirapurú's song. In the Paul Schwartz recording this elusive bird has an exquisite and varied song such as Villa-Lobos could not have heard.

5. **Concrete music.** This most recent development, only possible since the advent of the tape recorder, demands a brief separate section because bird voices not only fire the composer's imagination but are the music itself. However, contemporary composers had a predecessor in Respighi who, in his tone poem 'The Pines of Rome', presented an early gramophone record of a real Nightingale song. His treatment is so subtle as to debase neither the music nor the song of the bird.

In America, James Fassett created his 'Symphony of Birds' entirely from recorded vocalizations (Stillwell Recordings, Ficker, USA). Less ambitious is 'Symphony of the Birds' by Johan Dalgas Frisch (MGM Records, New York) which comprises recordings of Brazilian birds, with background music which may or may not please the listener. But predictably Swedish Radio, and the composer Karl-Birger Blomdahl (1916–1968), take precedence with 'Altisonans'. Blomdahl's ideas originated from an observation by the physicist Ludvik Liszka that certain satellite signals exactly resemble the song of the Redwing. The composer then blended unmodified bird voice recordings with 'space' sounds: satellite signals and magnetic storms re-recorded at various playback speeds. The result is impressive and appropriately unearthly. Coincidentally, 'Children of Tane' (see Section 1), otherwise so different in conception, incorporates thunder storms.

Finally, and to solace the mind which may recoil from some contemporary bird music, there is a slender vignette by Percy Buck (1871–1947): 'The Blackbird's Song', a three-part setting for female voices of Henry Kingsley's poem. Only its unashamed romanticism in an age of rampant eclecticism can explain its neglect for, within melodic and harmonic enchantment graced with delicate traces of its song, the bird pleads for the forgiveness of man's sins and in so doing sings itself to sleep. J.H-C. and R.E.J.

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MUSKEG: an environment, consisting of grassy bog, characteristic of much of northern Canada.

MUSOPHAGAE: MUSOPHAGIDAE: suborder and family of CUCULIFORMES (see TURACO).

MUTATION: see GENETICS.

MUTTON-BIRD: local name for various species of petrel (Procellariidae); applied in New Zealand to the Sooty Shearwater *Puffinus griseus*, and on the southern coasts and islands of Australia to the Short-tailed Shearwater *P. tenuirostris* (see PETREL). The young of both species are in these areas collected commercially in large numbers for human consumption. The latter species is known as the Whale-bird in Alaska, which it visits during the northern summer.

MYCTERIINI: see STORK.

MYIASIS, WOUND: the presence of maggots in a wound on a living bird.

MYNAH: substantive name of various Asian species of *Acridotheres*, *Gracula*, and *Sturnus* (see STARLING).

MYOCARDIUM: see HEART.

MYOLOGY: the scientific study of muscles (see MUSCULATURE).

MYTHICAL BIRDS: see FABULOUS BIRDS.

MYZA: substantive name of the 2 species of *Myza* of Celebes (Sulawezi) (for family see HONEYEATER).

MYZOMELA: substantive name of some species of Myzomela, a large genus of Australasian and Pacific island HONEYEATERS.

MYZORNIS: substantive name of *Myzornis pyrrhoura* of south-east Asia (see BABBLER).

N

NAIL: a horny plate-like structure, shaped like a shield, found at the tip of the upper mandible of all species of wildfowl.

NALOSPI: the distance between the forward edge of a bird's nostril and the tip of the bill; term derived from the German NAsenLOch-SPItze.

NAME, COLLECTIVE: see ASSEMBLY, NOUN OF.

NAME, COMMON: sometimes used as an equivalent of 'vernacular name' or 'popular name' (see NAME, VERNACULAR). 'Common name' is subject to the slight ambiguity that it is also the translation of the *nomen triviale* of Linnaeus, which had the meaning of 'specific name' (see NOMENCLATURE).

NAME, ENGLISH: the name ('vernacular name', 'popular name') of a species or category of birds in the English language. English names, especially those of familiar birds, are part of the living language; as with other words, they are thus governed by usage, and this may change with time or differ between one English-speaking country and another. Unlike scientific names, which are based on international agreement among zoologists to accept certain conventions (see NOMENCLATURE), English names can be subject to no fixed rules, and their application may cut across taxonomic boundaries; also, they are usually not of international significance apart from the English-speaking world.

Nevertheless, it is expedient that there should be some approach to uniformity—by consensus of opinion—in the practice of ornithologists with regard to English names, at least during one period of time and in the same country. Clearly, a standard should be sought along the lines of determining the best current usage and of encouraging general adherence to it on the part of ornithologists. Some of these may have strong minority views that it would be improper to stigmatise as necessarily incorrect; but it seems probable that most of the diversity of practice is accidental rather than deliberate. Admittedly, there are in many cases alternative names to those given greatest acceptance by ornithologists—names that have also had substantial currency, and may even have been preferred at earlier dates, or that may be found in poetry or literary prose. There are also dialect names, locally or widely used, that have a place in the popular speech of the countryside and in writings embodying that.

Some ornithologists and others actively seek to influence usage by reviving older names or by introducing new ones because these are considered to be more pleasing or more appropriate. One may think that such attempts to change English names, widely used outside the realm of ornithology, may lead to confusion. On the other hand, it would be unreasonable to deny some latitude in the use of alternative names for which a case can be made (e.g. 'Dunnock').

There are certain tendencies in common usage that may well be encouraged by ornithologists. There is, notably, a welcome trend in the direction of shortening cumbersome compound names, such as the 'Golden-crested Wren' (a misnomer at that) of a few decades ago, now 'Goldcrest'. The prefix 'Common' likewise now tends to be omitted in many instances where it is really unnecessary, and the redundant second term to be dropped in 'Fulmar Petrel', 'Eider Duck', and others. Similarly, ornithologists may help to mould general usage by showing preference for the more appropriate of alternative names both in common use, e.g. 'Willow Warbler' rather than 'Willow Wren'.

In the case of birds familiar on both sides of the Atlantic, it is impracticable in the face of differing common usage to secure complete uniformity in English names as between the British Isles and North America, two areas with many birds in common (see below). Similar considerations apply to names used by English-speaking people in various other parts of the world. On the other hand, many English names have been invented by British ornithologists for birds that are not ordinarily found in their country and that are therefore nameless in common speech. Such names, if unsatisfactory, are more susceptible of deliberate change. In particular, it seems to be good practice to displace such a name in favour of one that is widely current in some part of the world where the bird is well-known; thus what was once the 'Buff-backed Heron' *Bubulcus ibis* of earlier British bird books was known to English-speaking people in Africa and Asia (more appropriately) as 'Cattle Egret' and this has become common usage. Again, in the British Isles, the English names used in North America may well be preferred for species that are merely stragglers from that continent.

Names for species and subspecies. English names are primarily the names of species. This follows naturally from the fact that subspecific forms are usually indistinguishable in the field, except in some cases by skilled observers; they can therefore have no names in common speech. Where it is desired to refer to a subspecies (or race) by an English name, this should consist of the name of the species prefaced by a qualifying adjective or adjectival phrase. Such compounded names for races are nearly all of comparatively recent origin; and indeed the desirable occasions for using them seem to be much fewer than some current practice would suggest. Subspecies can be referred to either by their scientific names, as befits a technical concept, or by such expressions as 'Northern race' in relation with the English name of the species.

There are a few inevitable exceptions, where subspecies are so distinct in appearance that they have acquired separate English names in common speech. If such names are firmly embedded in the language, as where 2 races of *Motacilla alba* are known respectively as 'Pied Wagtail' and 'White Wagtail', it seems impossible to do otherwise than accept the situation. Unfortunately, this means that there is no English name covering the species as a whole; and this in turn involves the invention of additional English names for any forms of it other than the 2 in question.

Initial capitals. Whether or not to use capitals for the initial letters of the English names of species is a controversial point. Ordinary literary usage would prefer small letters, and some ornithological publications follow this. More commonly it is felt that, for scientific purposes, there are advantages in the use of capital letters. For one thing, references to particular species can be more easily picked out on a page. For another, certain ambiguities are avoided; thus, 'a Little Gull' can refer only to *Larus minutus*, whereas 'a little gull' might mean a gull of any small species.

When initial capital letters are preferred, they are used for each main term of the name but not for the second element of a hyphenated compound. Capital letters are in any event not given to English names when these are used in a general rather than a specific sense, e.g. 'gulls'.

Hyphenation. It has in the past been a frequent practice in ornithological publications to hyphenate two elements of a name where this consists of a noun preceded by a noun used as an adjective; but not to insert a hyphen between a true adjective and a following noun. This is a tiresome convention, because it involves e.g., for various tits *Parus* spp., writing 'Marsh-Tit' on the one hand and 'Blue Tit' on the other. Moreover, an exception tends to be made when the adjectival noun is the proper name of a place, as in 'Sandwich Tern', and this further complicates the procedure.

There seems to be nothing in ordinary English usage of the present day to demand such a rule as that mentioned above. 'The hyphen is not an ornament; it should never be placed between two words that do not require uniting and can do their work equally well separate' (Fowler). The present tendency happily seems to favour the suppression of all unnecessary hyphens, including especially those that have been inserted merely because the word before it, used adjectivally, happens to be a noun. A hyphen is unnecessary between any two words of which the second would naturally be used for indexing.

On the other hand, some hyphens are made necessary by the sense, unless the two elements can be written as a single word; 'Oyster-catcher' is a case in point, as 'catcher' here means nothing by itself. Other necessary hyphens are those between elements of a compound adjective, e.g. 'Black-headed'. It seems desirable, however, to encourage a tendency to go further and to make single words out of properly hyphenated pairs when the sense allows. 'The conversion of a hyphenated word into an unhyphenated single one is desirable as soon as the novelty of the combination has worn off, if there are no obstacles in the way of awkward spelling, obscurity or the like' (Fowler). We already have many compound names such as 'Redpoll', 'Bullfinch', and 'Blackbird' that are always spelt as single words; and others that usually or sometimes are, such as 'Oystercatcher', 'Yellowhammer', and 'Hedge-sparrow'. There also seems to be no reason against adjectives such as 'Blackheaded' being written as single words; but there are instances where the result would be aesthetically disagreeable or not immediately intelligible.

A few hyphens are inescapable on account of awkward spelling, notably 'Bee-eater'—to write 'Bee Eater' (indexing as 'Eater, Bee'!) would be wrong; to write 'Beeeater' would be absurd.

Fabricated Names. Where common usage does not operate, ornithologists are free to invent English names (if these are considered necessary in the circumstances); Eisenmann and Poor (1946) have suggested certain principles, as follows. There should be an appropriate name for every species, applicable to the whole species and forming the latter part of the name of each included subspecies. A name should give no false impression of taxonomic relationship. The name of a species should not be formed from a geographical name, or any name from a personal one. The adjectives 'common' (at best of only local relevance), 'least' (or 'little'), and 'great', should be used with extreme care. A name should not be given that is identical with one already well established elsewhere for another species.

American usage. The English names used in the United States and Canada, even without going beyond those currently recognized by the American Ornithologists' Union, show some unavoidable differences from British ornithological practice. The same name may be differently applied; or different names may be used for the same species or group. It may be convenient to draw attention here to the instances over which confusion is most likely to arise.

The following collective names are applied in the respective hemispheres to birds that have superficial features in common but belong to different taxonomic groups: 'vulture', 'quail', 'flycatcher', 'warbler', 'oriole', and 'sparrow'—see entries under the several names and others to be mentioned below. The names 'hawk' and 'bunting' have a wider application in the New World.

Among names for species, applied quite differently, the following are outstanding examples:

	British Application	American Application
Blackbird	*Turdus merula*	*Agelaius* spp.
Robin	*Erithacus rubecula*	*Turdus migratorius*
Redstart	*Phoenicurus* spp.	*Setophaga ruticilla*
Tree Sparrow	*Passer montanus*	*Spizella arborea*

The name 'Great White Heron' is given to *Ardea herodias occidentalis* in America but was until recently applied in British bird books to *Egretta alba*, now designated an 'egret' with varying adjectives. There are of course many instances in which the same name is applied to closely related birds, with or without distinguishing adjectives apt to be omitted in ordinary use. Among unofficial American names, there are such uses as 'buzzard' for vulture (New World family) and 'yellowhammer' for a species of woodpecker.

Special American names for groups include 'loon' instead of 'diver', 'jaeger' instead of 'skua' for *Stercorarius* spp. (not *Catharacta*), 'murre' instead of 'guillemot' for *Uria* spp. (not *Cepphus*), and 'goatsucker' instead of 'nightjar'.

The most important instances of different substantive names for the same species are:

British Usage	American Usage
Long-tailed Duck	Oldsquaw
Goosander	Common Merganser
Hen Harrier	Northern Harrier
Little Auk	Dovekie
Sand Martin	Bank Swallow
Lapland Bunting	Lapland Longspur

There are many other instances in which a different adjectival name is used although the birds are at most subspecifically distinct, e.g. 'Kentish Plover' becomes 'Snowy Plover' in America, 'Grey Phalarope' becomes 'Red Phalarope' (refers to breeding plumage), and 'Common Gull' becomes 'Mew Gull'. Some American names such as 'Duck Hawk' for 'Peregrine' and 'Pigeon Hawk' for 'Merlin' are no longer the official preferences.

Finally, there are many cases in which a species is known in Britain by its substantive name without qualification, but an adjective is added in America for distinction from related species there, e.g. 'Rock Ptarmigan', 'Barn Swallow', 'Winter Wren'.

Other Usages. In the more widely divergent avifaunas of Australia and New Zealand, differences arise chiefly from the use of names familiar in Britain for birds that are not even closely related, e.g. 'chough', 'magpie', 'robin', 'treecreeper', 'warbler', and 'wren'—again see entries under the several names. In other parts of the world, even where English is largely spoken, this tendency is less noticeable; on the other hand, many compound names are merely ornithological fabrications, without roots in common speech and often varying from author to author. Sometimes a name from an indigenous language is adopted and more or less anglicized; or a scientific generic name (currently used or obsolete) does duty as an English substantive name. A.L.T.

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NAME, POPULAR: recognized equivalent of NAME, VERNACULAR.

NAME, SCIENTIFIC: Carl Linnaeus (1707–1778) named many animals in addition to plants. The Swedes have a saying: 'God made the plants and animals, Linnaeus named them'; some scientists and evolutionists may not agree with the first part of this saying, but nobody can disagree with the second part. He was certainly the author of the Binominal (sometimes Binomial) System as in use today, and he proposed there must be two names, in Latin or 'Latinized' Greek so that they could be used throughout the world (see NOMENCLATURE).

Of course many scientific names (popularly known as Latin names) have been given and recognized by zoologists since Linnaeus's time. In some cases the scientific name of an animal has the generic name repeated as the specific name, for example, the Red Kite *Milvus milvus*. This is known as a tautonym, for *tauton* (Gr) the same, and *onoma* (Gr) a name; and has come about because of a change in the generic name; the International Code states that the specific name may not be changed, even though it results in a tautonym. The ruling has been modified for botanical names and tautonyms are not used for plants.

The Wren was among the birds that Linnaeus himself named, and he called it *Motacilla troglodytes*. Under his genus *Motacilla* he included a number of small birds which ornithologists have now split up into several genera, reserving *Motacilla* for the wagtails. In naming the American wren-like birds in the first decade of the 19th century, Vieillot chose the Linnaean specific name *troglodytes* (troglodyte or cave-dweller, by reference to the form of the nest) as a generic name. Later it was found that the European Wren was so closely allied to these that it must go in Vieillot's genus, so it became '*Troglodytes troglodytes*' (Tweedie 1963).

The Code states that the name of the nominate subspecies (race) must have a subspecific name that is the same, i.e. it must repeat, the specific name; the result was that the nominate subspecies of the Wren had to be named *Troglodytes troglodytes troglodytes*, and this ridiculous and lengthy name for such a little bird became something of a joke. Veteran zoologists, who were classical scholars, thoroughly disliked this: there were heated interchanges of correspondence and they refused to use these 'monstrosities'; however they passed from the scene and the rules were finally accepted.

Although Linnaeus used the name *Motacilla* for the wren, he took the name from Marcus Varro, the Roman scholar and author, to whom this Latin word is accredited; Varro died in 27 BC and this name must have been in use since about that time. *Motacilla* does not really mean 'wag-tail', from *motator*, a mover, and *cilla*, a tail, because *cilla* does not mean a tail, and in fact there is no such word. *Motacilla* is a Latin word, using *-illa* a diminutive suffix, and means 'little mover'; when Varro explained this name he said: *Quod semper movet caudam* (which is always moving its tail), when he might have been expected to say: *Quod semper movet cillam*, but he did not; one cannot help thinking that Linnaeus was well aware of this when he used the name for the Wren.

This wrong interpretation must have started long ago, and still persists among some ornithologists; for example we are quite happy to interpret

Haliaeetus albicilla as the White-tailed Eagle; the specific name was supposed to mean 'white-tailed', but it does not.

Names taken from Greek mythology were often used by Linnaeus and later zoologists; the generic name *Halcyon* for a kingfisher is an interesting example. There were strange legends about the kingfishers; the ancient Greeks thought they mated (conceived) at sea and built floating nests, and so at this time the gods favoured them and kept the sea calm. The Greek word for kingfisher, *alkuōn*, is derived from *hals* the sea, and *kuō* I conceive, hence 'halcyon days', calm days, kingfisher days.

An example of an apparently foolish name is a subspecies of the Great Tit, *Parus major minor*. In 1848 Temminck and Schlegel named a new tit from Japan *Parus minor*. Later it was considered to be an eastern member of the 30 or so races of *P. major*, so the subspecific name had to be *P. major minor*. Sometimes in an effort to give a new species a generic name that almost certainly had not already been used, a zoologist resorted to an anagram, for example *Daption capensis*, the Cape Petrel; the generic is an anagram of Pintado, the Portuguese name for this petrel.

The scientific name of an animal might originate from the naturalist who first discovered it, or from a zoologist working in a laboratory, and studying its anatomy; the specific name is quite often given in honour of a well-known person, or the collector who found it. The kiwis have the generic name *Apteryx*, which is derived from the Greek *a-*, a prefix meaning not, or there is not, and *pterux* (Gr) a wing. The wings of a kiwi are rudimentary, hidden by the body feathers, and useless for flight; the Great Spotted Kiwi *Apteryx haasti* was named in honour of Sir Julius von Haast, the New Zealand explorer. Col. R. Meinertzhagen, evidently in a flippant mood, took advantage of the now forbidden hyphen to name a babbler subspecies after his friend William Payn: *Argya fulvus billypayni*.
A.F.G.

Tweedie, M.W.F. 1963. Those Latin names. Animals 2(22): 593.

NAME, SUBSTANTIVE: term used throughout this work for a noun that is the chief element in the English name of a number of species distinguished from each other by qualifying adjectives (including nouns and participles used adjectivally). Either or both elements of the full name may be compound, and each of them, unless written as a single word, should preferably be hyphenated (being indissoluble); on the other hand, the adjectival and substantive names should not be joined by a hyphen. For a few species a single word serves as a complete name, e.g. Brambling, Dodo. In other cases the substantive name may ordinarily be used alone where there is no other species with the same substantive name in the area, but in a wider context an adjectival name must be added. Occasionally there may be two independent (not hyphenated) qualifying names, e.g. Great Crested Grebe, Lesser Spotted Woodpecker. There is a certain analogy between an English substantive name and a scientific generic name, but this must not be pressed; unrelated species may have the same substantive name, and closely related species may have different ones. See NAME, ENGLISH.

NAME, TRIVIAL: see NOMENCLATURE—but also sometimes used in the sense of NAME, VERNACULAR.

NAME, VERNACULAR: 'the name of a taxon in any language other than the language of zoological nomenclature' (International Code)—see NOMENCLATURE; 'popular name' is a recognized equivalent. 'Vernacular name', however, is sometimes used in the restricted sense of a name in a local dialect or in the native language of a country foreign to the writer or speaker; this ambiguity can be avoided by using an adjective denoting the particular language. The vernacular names given in this work are, unless otherwise indicated, 'English names' (see NAME, ENGLISH). For names in other European languages see the works cited below.

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NANDU: alternative name for species of Rheidae (see RHEA).

NAPE: see TOPOGRAPHY.

NARIS: usually in the plural ('nares'), for the paired openings of the nasal cavities in the SKULL. The anterior or external nares (nostrils) pierce the rhamphotheca of the upper mandible at varying distances from its base (uniquely at the tip in kiwis *Apteryx* spp.)—see BILL; the passages continue through apertures in the bones (premaxillae) into the nasal cavities. The posterior or internal nares (also called 'choanae') lead from the nasal cavities into the buccal cavity. For the nasal cavities and their functions see RESPIRATORY SYSTEM and SMELL; for the nasal glands see EXCRETION, EXTRARENAL.

The external nares are of various shapes, from round to linear; sometimes there is a central tubercle in each naris. Usually they are exposed (gymnorhinal); but in some birds they are concealed by frontal feathers, e.g. in crows and grouse. Sometimes each naris is protected by a flap (operculum), which in tapaculos is movable. In the Procellariiformes (Tubinares) the nostrils are carried in a double horny tube on top of the bill. The internasal septum, separating the right and left passages, is imperforate in most birds but perforate in a few. Although the nostrils remain open (pervious) in most birds, they are or become secondarily closed (impervious) in some Pelecaniformes; in such cases, entry to the nasal cavities is only from the mouth through the choanae, which may be quite large, and respiration is through 'secondary external' nares at the angle of the mouth.

The shape of the *bony* aperture of the nostril has been used as a taxonomic character. It is 'holorhinal' when the posterior margin is rounded, 'schizorhinal' when it forms a slit; 'pseudoschizorhinal' is a term applied to a modification of the holorhinal type; and 'amphirhinal' signifies that there are two bony apertures (one behind the other) on each side. In Sulidae (see above) even the bony aperture is blocked.

NARROW FRONT MIGRATION: see MIGRATION under Flight performance.

NASAL: a paired bone of the SKULL.

NASAL CAVITY: see NARIS; RESPIRATORY SYSTEM; SKULL; SMELL; and EXCRETION, EXTRARENAL.

NATIVE COMPANION: alternative name for the Australian Crane *Grus rubicunda* (see CRANE).

NATIVE HEN: substantive name, in Australia, of *Tribonyx* spp. including the flightless Tasmanian Native Hen *T. mortieri* (for family see RAIL).

NATURALIZED BIRDS: species that have been introduced by human agency, direct or indirect, into areas where they either had not yet spread by natural means or had become extinct, and that have successfully established themselves and are now breeding regularly as wild birds. Mere acclimatization in captivity, or even the casual escape of captive individuals, is excluded from the definition.

Extensive man-made changes have taken place in the world distribution of certain bird species within the past hundred years or so. The House Sparrow *Passer domesticus*, for instance, was a native of Europe and parts of Asia and North Africa but has been spread to the remaining continents by human agency. It now occupies almost the whole of North America, large parts of South Africa, as well as New Zealand, Cuba, Hawaii, New Caledonia, the Falklands, and many other islands. It has been estimated that within the past century largely man-made extensions have doubled the natural world range of the House Sparrow, which was over 15,000,000 km^2, so that it now occupies one-quarter of the earth's surface. The Starling *Sturnus vulgaris* has been artificially spread almost as widely, as will be further mentioned.

Introductions may be either deliberate or more or less accidental. Deliberate introductions have been made for three main reasons. In western Europe and in North America excessive shooting of game stocks has led to widespread and prolonged introductions of game-birds; this has sometimes, as with the Grey Partridge *Perdix perdix* from Hungary to Britain, been to supplement stocks of native species, but more often, as with the Pheasant *Phasianus colchicus* in both Europe and North America, to diversify the native game stocks with completely alien birds. Nostalgia for the sights and sounds of the home country led to large-scale and often highly successful introductions of western European song-birds into North America, South Africa, Australia, and New Zealand. In the

British Isles especially, the desire to increase the amenities of country estates led to the importation of large numbers of ornamental waterfowl, the progeny of which have sometimes been neither pinioned nor wing-clipped and have thus escaped to found feral populations. Some more or less domesticated birds have also been able to escape from captivity and establish themselves in the wild. In the British Isles, despite attempts to introduce upwards of 100 bird species (mostly during the past hundred years), only 4 completely alien birds have become thoroughly naturalized over a wide area; the Pheasant from various parts of Asia, the Red-legged Partridge *Alectoris rufa* from southern Europe, the Little Owl *Athene noctua* from western Europe, and the Canada Goose *Branta canadensis* from North America. In addition, the Mandarin Duck *Aix galericulata* and the Golden and Lady Amherst's Pheasants *Chrysolophus pictus* and *C. amherstiae*, all 3 from China, and the Ruddy Duck *Oxyura jamaicensis* from North America are naturalized in limited areas; the Capercaillie *Tetrao urogallus*, after becoming extinct in the Scottish Highlands about 1785, was successfully reintroduced there from Sweden in 1837–39; the Gadwall *Anas strepera* became naturalized in two small areas in south-eastern England at the same time as an apparently natural colonization from the Continent took place in Scotland; and the widespread present-day populations of both the Mute Swan *Cygnus olor* and the feral domestic pigeon *Columba livia* var. represent escapes from more or less domesticated stocks. Of these 12 species, 5 were introduced to supplement game stocks, 4 were ornamental waterfowl, 2 were formerly kept for food, and the Little Owl was introduced as an aesthetic whim of a handful of bird-loving 19th century landowners. The Ring-necked Parakeet *Psittacula krameri*, an escaped cage bird, appears to be established in one or two British localities, as it is in parts of the Middle East and Lower Egypt.

In France, on the other hand, the numerous introductions of birds over the past hundred years have resulted in only one additional species becoming established—Reeves's Pheasant *Syrmaticus reevesii* joining the already naturalized *Phasianus colchicus*. This is no doubt largely due to the fact that a continental area tends to have fewer vacant ecological niches than an island.

In North America the 2 most successful and widespread naturalized birds have been the House Sparrow and the Starling from Europe. The House Sparrow has now occupied the whole of the cultivated area of the United States and Canada. The Starling has spread, since 1891, over the whole continent north to the Gulf of St Lawrence and west to the Rocky Mountains; it also occurs in Jamaica as a result of a separate introduction in 1903. Small local populations of naturalized Grey Partridges, Pheasants, Goldfinches *Carduelis carduelis*, and Tree Sparrows *Passer montanus* from Europe have also been added to the avifauna of North America. More recently the Monk Parakeet *Myiopsitta monachus* from southern South America and the Mexican House-finch *Carpodacus mexicanus* have become widely naturalized and a number of escaped cage-birds, especially parrots and doves, have become locally naturalized around Los Angeles, California, and Miami, Florida. Honolulu, Hawaii, has its own special constellation of introduced species. The Greater Bird-of-paradise *Paradisaea apoda*, of the Aru Islands and New Guinea, was successfully introduced into Little Tobago, West Indies, in 1909.

Of the numerous European song-birds introduced into Australia and New Zealand by homesick emigrants, mainly in the 1860s, 8 are now naturalized in Australia and 13 in New Zealand. The Skylark *Alauda arvensis*, Song Thrush *Turdus philomelos*, Blackbird *T. merula*, Greenfinch *Carduelis chloris*, Goldfinch, House Sparrow, and Starling are found in both countries today. In New Zealand an interesting by-product has been the interbreeding of subspecies of the Redpoll *Carduelis flammea* from different parts of Europe, and perhaps also of the Yellowhammer *Emberiza citrinella*.

Asian birds naturalized in Australia include the Indian Spotted Dove *Streptopelia chinensis suratensis*, the Common Myna *Acridotheres tristis* (also naturalized in Hawaii and New Zealand), and the Red-whiskered Bulbul *Pycnonotus jocosus*. All the birds of the last-named species now at large in New South Wales and Victoria are said to derive from some that either escaped or were liberated from an aviary in Sydney, a city where they are now plentiful in the parks and threaten to become a pest to fruit-growers. From Africa, the Ostrich *Struthio camelus* was introduced into South Australia under domestication and has become feral in one or two areas. Non-European birds naturalized in New Zealand, in addition to the Common Myna, include the California Quail *Callipepla californica*, the Canada Goose, which is now locally abundant, the Black Swan *Cygnus atratus* from Australia, and the White-backed Magpie *Gymnorhina hypoleuca* (Cracticidae) also from Australia.

Success in deliberate attempts at naturalization is quite haphazard, as the British record shows. Animal species are well adapted to their native environment but, if they are to establish themselves firmly in a completely different part of the world, a whole complex of factors, such as climate, food supply, and cover for both nesting and roosting, must be suited to them; nor must pressure from predators be too great. A.C. Twomey has pointed out that imported European birds became naturalized in the United States only in regions with temperature and rainfall corresponding to those in their native breeding places. In New Zealand the introduced European species have completely supplanted native birds over most of the cultivated area, being for the most part pre-adapted to the habitat created by the destruction of the native vegetation and the substitution of imported crop plants. No doubt the native New Zealand birds would in time have adapted themselves to the areas cultivated by man, but the presence of the European birds has deprived them of the chance.

Several other island archipelagos also have their inhabited and cultivated areas dominated by introduced species, notably the Seychelles in the Indian Ocean, where the 3 commonest land birds are the Common Myna, the Peaceful Dove *Geopelia striata*, and the Cardinal or Madagascar Fody *Foudia madagascariensis*. The dove, called also Barred Crown Dove and Zebra Dove, has a very involved history. A native of South-east Asia and Australia, it was first introduced to Mauritius (where it is still common) by Indian traders, and thence to the Seychelles. Some 30 introduced species of birds are also at least locally established in the Hawaiian archipelago, out of well over 100 that have been liberated at one time or another.

Theoretically, its own fecundity is the only limit to the increase of an introduced bird population in a suitable new habitat, until it comes up against the natural ceiling that the environment imposes on it. The expansion of the Starling and House Sparrow populations in North America bears this out well; so does the increase, from 2 cocks and 6 hens to 1,898 birds in 5 years, of a population of Pheasants on a small island off the western coast of North America.

When populations build up to their natural ceiling on an island, the surplus may attempt to spread oversea, as is suggested by the fact that, as Williams (1953) has shown, many of the small birds naturalized in Australia and New Zealand began to appear by the end of the century on the small islands that lie mostly 320–880 km to the southward of the two main landmasses. There can be little doubt that most of them were blown there by the wind. Campbell Island, for instance, 700 km south of Dunedin, now has breeding Blackbirds, Song Thrushes, Starlings, Redpolls, Chaffinches *Fringilla coelebs*, and Dunnocks *Prunella modularis*, all almost certainly self-introduced—but from stocks naturalized in a secondary area.

No highly migratory species have succeeded in keeping their migratory habit while becoming naturalized in a new country. Most of the European birds that have been so successful in other parts of the world are at most partial migrants in Europe. The Canada Goose in Britain, however, provides an instance of a migratory bird population that has lost its urge to migrate during a period of captivity and has become wholly sedentary in its secondary home, apart from a moult migration between some English breeding populations and the Beauly Firth in Scotland. The Pheasant, on the other hand, is normally a wholly sedentary bird but has shown some signs of acquiring a migratory habit in the harsher climate of Sweden, while Swedish Canada Geese winter in Germany and the Netherlands.

Bird introductions have on the whole proved less disastrous than introductions of mammals and insects, but the examples of the Starling in North America and perhaps of the Red-whiskered Bulbul in Australia are there to point the dangers of irresponsible introductions. R.S.R.F.

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NATURAL SELECTION: all those factors that lead to systematic differences between various genetic forms in a population in their rates of survival or reproduction. Such differences lead to differences in fitness—the relative contribution each genotype makes to the next generation. Natural selection is the main factor bringing about evolution, as first suggested by Darwin and Wallace and confirmed by subsequent studies, particularly in genetics and ecology, and by the development of the mathematical theory of population genetics.

Genetical variation within populations is the pre-requisite of natural selection. Such variation is abundant. Although about two-thirds of the genetic material carried by each individual is identical in most members of the majority of animal and plant populations, the remaining one-third varies from individual to individual—i.e. the alleles at each locus are not the same in all members of the population (see GENETICS). This variation may be manifest in various ways in the characters of the organism. A characteristic may vary continuously from one extreme to another, with no division into distinct classes (e.g. body-weight) or with such division being imposed merely by the integral nature of the characteristic (e.g. CLUTCH-SIZE). Alternatively, variation may be discontinuous, with sharply distinct classes (e.g. the bridled and unbridled forms of the Guillemot *Uria aalge*. See POLYMORPHISM). Variation is found in all types of characters (morphological, physiological, biochemical, behavioural) and all types may be subject to natural selection.

Natural selection in birds was first clearly demonstrated by H.C. Bumpus in 1898. He studied 136 House Sparrows *Passer domesticus* found exhausted after a severe snowstorm: 72 survived and 64 died. The mean total length of the survivors was 158.7 mm, while that of those that died was 160.5 mm. Thus there was strong and significant selection against longer birds.

Studies of predation by birds on the peppered moth *Biston betularia* provide an illustrative example of natural selection. This species is typically pale in colour with darker markings that render it highly cryptic on the lichen-covered tree-trunks on which it rests by day. There is a melanic variety of the species that is conspicuous in such locations. Direct observations of moths on tree-trunks show that birds tend to find the melanic variety much more readily that the typical form. As a result, the survival rate of melanics is much less than that of the typicals. Converse results have been obtained in areas affected by atmospheric pollution. There the tree-trunks present a dark background, having few epiphytes, and the melanic moths appear less conspicuous than the typicals. As expected, birds find the typicals more easily than the melanics in such places and the resultant mortality rate of the typicals is higher than that of the melanics.

Natural selection often results in the maintenance of the *status quo* with regard to the genetical constitution of populations. Thus most *Biston betularia* of rural areas are of the typical form. Melanics occur, as a result of mutation (see GENETICS) or of immigration from polluted regions, but their frequency is kept extremely low because the birds find them more easily than they find the typical ones. Another example of stabilizing selection is found in Bumpus's study of House Sparrows. Humerus lengths were significantly more variable among the dead birds than among the survivors, though the mean lengths were the same: this means that birds with extreme humerus lengths, whether long or short, survived less well than birds with humeri of average length. Such elimination of the extremes is commonly found in studies of selection acting on continuously varying characters. In general, stabilizing selection is likely to occur whenever a population has been living in a fairly constant environment for some time.

When environmental conditions change, the relative fitnesses of the genotypes in the population may change. A form which previously survived relatively well may survive relatively poorly in the changed conditions. The result of this will be that its frequency in the population will decline. The resultant gradual change in the genetic composition of the population is the basis of evolution. Thus prior to the industrial revolution most areas that now suffer atmospheric pollution did not do so and the trees growing in them supported abundant epiphytic lichens. At that time, melanic *B. betularia* were universally rare. The pollution consequent upon industrialization killed the lichens and so changed the direction of selection, the melanics subsequently surviving better than the typical moths. As a result, the frequency of the melanics rose from about 0% to over 90% in 50 years in many industrial centres in Britain.

At first sight one might expect that selection would tend to eliminate all genotypes except the one with the highest fitness and thus give rise to genetic uniformity. That this is not always true is demonstrated by the large amount of genetic variation to be found within natural populations. This variation originates by mutation and by the continual production of new combinations of genes that results from sexual reproduction (see GENETICS). It is maintained in populations by various forms of natural selection. One such form is selection in which rarer genotypes have relatively high fitnesses by virtue of their rarity. Such selection may arise in various ways. For example, experiments with various birds and other animals have shown that when they are feeding on food of more than one type, they tend to overlook the rarer forms of food, so that they not only take an absolutely larger number of the commoner forms but also a disproportionately larger number. In nature, if the different forms of food are the different genotypes of a single species then, because each genotype is selectively advantageous when rare but disadvantageous when common, a variety of genotypes is preserved in the population. FREQUENCY-DEPENDENT SELECTION of this form may be of great importance in the maintenance of genetic variation.

Selection may vary with frequency in ways that do not conserve genetic variation. If the fitness of each genotype is greater when that genotype is commoner, then rare genotypes are rapidly eliminated and eventually only a single type remains. This occurs when some birds feed on prey which are packed closely together, such as Goshawks *Accipiter gentilis* feeding on flocks of Domestic Pigeons *Columba livia*: they take more light birds from flocks that are mainly dark and vice versa.

Selection is measured as fitness, which may be most precisely defined by example. Suppose that one has a population in which there are simply two genotypes, A and B. Consider the newly-fertilized eggs of one generation and the birds developing from them: some will not survive long enough to reproduce themselves; of those that do survive, some may have only a few offspring while others may have many. Suppose that the average number of newly-fertilized eggs of the next generation to which an egg of this generation contributes is a if the egg is of genotype A and b if it is of genotype B. Suppose that A is the fitter genotype, i.e. a is greater than b. Then, by convention, the fitness of genotype A is 1 and the fitness of genotype B is b/a. Thus the fitness of a genotype is the average contribution made by an individual of that genotype to the next generation, measured relative to the fitness of that genotype which contributes most (which has a fitness of 1 by convention), with the point of measurement in each generation being the newly-fertilized egg stage.

The definition of fitness in terms of average contributions of genotypes clarifies an important point. To say that natural selection, in the form of predation by birds, favours melanic *Biston betularia* over typicals in industrial areas means not that the birds eat none of the melanics and all of the typicals but that they eat a higher proportion of the typicals. Nor is the fact that many of the deaths are 'accidental', i.e. unrelated to the genotype of the individual, important: so long as there is some systematic difference in average rates of survival and reproduction, natural selection is occurring.

Since fitness is a relative measure, based on comparisons within a single population, one cannot validly speak of the fitness of a whole population. The mean fitness of a population is a mathematical abstraction, quite unrelated to the potential growth-rate, size, or competitive ability of the populations. It cannot, therefore, be used for comparing the probability of survival of different populations.

A source of confusion is that 'fitness' is a technical term with a precise meaning but is also a word in general use with other meanings. An Olympic athlete may be fit in the evolutionary sense, but not necessarily: 'physical fitness' is only one factor in genetic fitness. In evolutionary biology, the latter is of prime importance, so 'fitness' should only be used in its technical sense in evolutionary discussions.

The fitness of the individual is an insufficient explanation for the phenomenon of parental care, manifest more in birds than in any other class of animals. A genotype that produced large numbers of eggs but which failed to care for them, so that none survived, would rapidly disappear from a population. Genotypes that produced fewer eggs but which cared for them, so that some survived to adulthood, would prevail in evolutionary time. Thus it is not just the fitness of the individual that must be taken into account but the fitness of its offspring. However, because of the biparental nature of sexual reproduction, only half of the genetic material in an offspring is received from each of its parents. Thus, for the potential genetic contribution to future generations, the fitness of an individual's offspring is only half as important as the fitness of the individual itself. To take an extreme and simplified example, a genotype that lays down its own life to ensure the survival of more than two offspring to reproductive age will tend to prevail in evolution whereas a genotype that lays down its life to ensure the survival of less than two offspring to reproductive age will not.

Individuals share part of their genetic endowment not only with their offspring but also with all their relatives: brothers and sisters have half their genetic endowment in common, full first-cousins have one-eighth in common, half-brothers have one-quarter, etc. Thus genotypes that have characteristics benefitting their relatives will prevail in evolution, so long as the characteristics do not cause too great a loss of fitness to the individual. The DISTRACTION BEHAVIOUR of ground-nesting birds provides an example of this: it increases the probability of survival of the eggs or chicks without involving a great risk to the parent. W.D. Hamilton has analysed the theory underlying this idea and has shown that the important factor, in terms of evolution, is the 'inclusive fitness' of an individual—i.e. its own fitness (defined as above) plus the fitnesses of all its relatives, weighted according to their degree of relatedness.

In mobile species in which individuals have no great tendency to live near their relatives, the characteristics of an individual will be largely irrelevant to the fitness of its relatives. Thus only offspring need to be considered in calculating inclusive fitness. But in species where individuals tend to associate with their relatives, inclusive fitness in a broad sense is important and selection must be considered in terms of the relatives of the individual as well as the individual itself—KIN SELECTION. The Tasmanian Native Hen *Tribonyx mortierii* provides an example. The sex-ratio is biased, with an excess of males. Some birds breed in pairs but others form trios of two males and a female, each male obtaining about half the copulations and probably fathering about half the offspring. Such an arrangement is extremely rare: in most species two males display or fight until one gains sole possession of the female. The wife-sharing in *T. mortierii* is facilitated by the two males usually being brothers. Thus although each male only fathers half the offspring, he is uncle to the other half. This reduces the selective pressure on males to fight for sole possession of the female.

Competition between members of one sex for access to members of the other gives rise to a particular type of natural selection known as SEXUAL SELECTION.

As a result of natural selection, organisms have characters which aid their survival in their particular ecological niches—they are adapted to their environments. The study of adaptations is a key area of evolutionary biology. In studying the evolutionary forces that have resulted in a particular character, one is in a sense studying the function of the character (without implying that the evolution that produced it was orientated to the goal of producing it). The study of adaptation has, therefore, been named teleonomy by analogy with, and to distinguish it from, Aristotelian teleology. The particular form of any teleonomic study depends on the character being studied but the aim is always to identify, and if possible measure, the selection pressures responsible for the evolution and maintenance of the character.

The evolutionary forces responsible for the origin of a character may be considered the 'ultimate causes' of that character, in contrast to the processes occurring during the individual's development that result in the character being formed, the 'proximate causes'. Thus the ultimate cause of flipper-like wings in penguins is that penguins use their wings for submarine locomotion; the proximate cause is that the developmental pathway of the penguin's wing is deflected somewhat from that found in typical birds. The existence of two levels of causative explanation, as a result of evolution by natural selection, is one of the unique features of biology. (A.J.C.) J.J.D.G.

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NAVIGATION: here used in the sense that a bird may be considered to have navigational ability if it is able to orientate its flight path in the absence of landmarks previously known to it. The orientation may be simply in a fixed compass direction, or towards a particular area (homing), from any direction.

Many birds appear simply to shuttle back and forth between summer and winter quarters. To reach the latter the only requirement for the young, naive bird, when not accompanied by experienced adults, is for it to be innately programmed to fly for a certain distance in a given direction, distance-and-bearing navigation in sailors' parlance.

If young migrants are held captive in an unchanging, artificial environment when they would normally be migrating, they show periodic bouts of fluttering and hopping, migration-restlessness. It is found that long-distance migrants continue to show this activity for much longer than closely related species migrating only short distances. Since the time spent in flying (if they were free) would determine the distance covered, one element of the migration programme is thus established. See MIGRATION.

The restlessness of caged migrants also has a directional component which can be automatically registered on a circle of pressure-sensitive perches. The scatter this produces about a mean direction is generally wide, but if the mean of each day (or night) is calculated and the means over, say, a month are examined, they are found to cluster in the general direction of the seasonal migration. Anomalous directions may also be taken up and these 'nonsense orientations', unrelated to migration or home direction, have been studied especially in Mallard *Anas platyrhynchos*, using free-flying birds and examining the cluster of bearings on which individually released birds vanish from sight when observed through powerful binoculars.

The sun is the primary basis for compass-orientation, with an element of time-compensation to allow for its apparent movement round the sky. Caged birds change orientation as the sun position is deflected by mirrors, change their angle to a fixed, artificial sun throughout the day and switch through 90° if their internal 'clocks' are shifted by 6 hours by being kept in an artificial day out of phase with the normal (see RHYTHMS AND TIME MEASUREMENT). A 12-hour shift produces a 180° switch when the artificial and normal days overlap. If the birds are released by day when their shifted clocks register night-time, various directions are taken up. These have been interpreted as showing that the mechanism changing their flight angle to the sun by 15°/h during the day goes into reverse during the night.

There are indications that the position of sunset is an important clue to birds migrating later in the night. But Mallard, released long after the sunset glow has gone, orientate well if the moon is the only visual clue (the stars being obscured by cloud). Time-shifting modifies this orientation, but it is not clear if the same 'clock' is involved as for sun-compass orientation.

If the stars alone are visible, compass orientation is shown which is not influenced by imposed time-shifts. This leads to the interpretation that it is the shape of the constellations and their relation to the fixed point (north) marked by *Polaris* that are the clues used. This concept has been explored in detail using caged passerines under the domes of planetaria. The naive young bird learns firstly the point of least rotation in the night sky and the relation constellation patterns (which need not be ones occurring in nature) bear to this. Subsequently the constellations themselves are used to find the north, much as we do ourselves. The circumpolar constellations which are above the horizon at night throughout the year are the important ones. The constellations farther from the pole can be blotted out without loss of orientation. Seasonal changes, in which different non-polar constellations become visible at night, do not determine the migratory direction taken up. This depends on the bird's physiological condition, governed primarily by photoperiod.

Migration predominately occurs under clear or partly-clouded skies. However, field evidence, particularly from radar observations, has shown that well-orientated flights occur when astronomical clues are not available, even when birds are flying between cloud layers. This has re-awakened interest in orientation with reference to the earth's magnetic field. Marginal orientations in the appropriate migratory directions have been shown by caged migrants confined in closed rooms. These orientations have been switched by artificially moving the magnetic pole. Moreover birds appear to determine the direction of the magnetic field through its tilt from the horizontal, the downward pole being taken as north. Some evidence suggests that the magnetic compass is actually used to calibrate the sun-compass and the constellation compass, i.e. it is the 'primitive' compass. The mechanism whereby the magnetic field could be detected is baffling, though crystals of magnetite, found in the heads of birds, may be the intermediary. Great difficulty has been experienced in demonstrating a direct sensitivity to magnetism, one exception being a training experiment in which pigeons had to make their choices while actually in flight.

When migrants have been displaced laterally, by wind drift or by experiment, the young birds on their first migration tend to proceed in the programmed direction. Older birds, with experience of at least one migration, tend to correct for the displacement and 'home' to the normal winter-quarters. This implies a much more advanced form of navigation than a simple distance-and-bearing procedure.

Most homing experiments have been carried out on breeding birds, since their urge to return is strong and only a small area round the nest need be kept under observation. Those breeding in colonies offer obvious advantages in this respect. Many migratory species have homed from remarkable distances. The longest flights on record are those of a Manx Shearwater *Puffinus puffinus* which homed 4,910 km in 12½ days, and of Laysan Albatrosses *Diomedea immutabilis* which covered 5,150 km in 10 days and 6,630 km in 32 days. These, and many shorter journeys, are done in times indicative of more or less straight line flight rather than of random wandering in search of known landmarks. Homeward orientation has also been demonstrated while the birds are still in sight of the observer. Indeed the bulk of experimental work has concentrated on the scatter of vanishing points of individually released birds. The distance to which birds may be followed has been increased, in some researches, by the attachment of minute radio-beacons on their backs. Overwhelmingly the domestic pigeon *Columba livia* has been the preferred species, because of the ease with which large numbers can be reared and kept under precisely known conditions. Although originating from non-migratory stock, pigeons have been selected over many generations to the point that many will home rapidly from hundreds of kilometres away. It is argued that if pigeons can undertake some navigational task, long-distance migrants could surely do better.

Homeward orientation within a few kilometres of the home site may reasonably be ascribed to visual recognition of previously known landmarks, though there is some argument about this. Farther away from home, several workers have found a zone of disorientation and it is not until about 80 km that consistent homeward orientation reappears, possibly improving with distance thereafter. This apparent requirement for a minimal displacement has led to the concept of a navigational 'grid' (or, as some would have it, 'map'). This visualizes at least two physical features varying more or less regularly in a quantitative way across the earth's surface, but with their gradients crossing each other. The values of these factors at the release point (if sufficiently far away) will be detectably different from those at home and so indicate their relative positions on the 'grid', and thus the direction in which the bird must fly to regain home. The bird will also need to know how the 'grid' relates to local topography—the grid may indicate home is to the north but it must know which direction is north. The compass mechanisms discussed earlier would suffice for this; the real problem is what are the bases for the 'grid'.

The common observation that homeward orientation, and homing, were much better in conditions of broken cloud, led to the examination of possible astronomical bases. Homeward orientation has not been demonstrated in free-flying birds under a night sky and some supposedly positive evidence from caged migrants is now treated with caution. A vast amount of experimentation has been undertaken to test whether a sophisticated interpretation of the sun's position in the sky is open to a bird, much as it is for human navigators. The simplest method would be to observe the sun at its highest point (local noon) enabling a time comparison to give the change in longitude. The sun's angle of elevation at that time, and comparison with the home value, would give the change in latitude. However, birds can orientate towards home at various times of day, not only at noon. They would therefore have to detect the movement of the sun and, in effect, compare with the remembered condition at home at that time. Alternatively the bird might extrapolate the observed portion of the sun arc to guesstimate the highest elevation and make comparison at that point. This would require much less of its memory.

Most field experiments have indicated that the sun's only role in the homing process is as a compass, though there are some exceptions. The most positive support has come from experiments with pigeons held rigidly and exposed to variations in the position of an artificial sun or to the real sun being apparently shifted by the use of prisms. The birds' responses indicated that they could detect movement slower than that of the normal sun, remember its position to within half a diameter for 24 hours, and react to changes in its elevation as if they were due to changes in latitude. The evidence for time-comparison ability is much more nebulous. However, biological clocks with very precise periods (±2 min in 24 h) have been demonstrated. Mostly these have periods slightly more than or less than 24 hours and so slide out of phase if not subject to regular checks against sunrise/sunset. But for a really constant 'chronometer', natural selection has only to favour a 24.0 hour clock-period.

Where pigeons experience prolonged overcast conditions and are only flown in such conditions, homeward orientation is demonstrated in the absence of astronomical clues. Homeward orientation has also been found in pigeons where eyesight has been severely restricted by cloudy contact lenses. These results have led to the search for other possible components of the navigational grid, especially those concerned with the earth's magnetism. Homeward orientation of pigeons flying below overcast is disrupted by attached magnets and can be turned about by changing the tilt of the field imposed by electrical coils mounted on the birds' heads. But this evidence does not suggest that more than a magnetic compass is involved. Some disruptions of orientation by magnetic anomalies or storms are slightly more indicative of a magnetic grid.

A long range of experiments, mostly in Italy, suggests that olfaction may play a part in homing. This was affected by surgical or other interference with the nerve tracts and olfactory organs, or by diverting the direction of the winds impinging on the birds at home. The theory is that the pigeon builds up an olfactory map around home, associating one smell with one direction, another with the opposite, and so forth. There is conflicting evidence, and at best such a system could not be effective any great distance from home.

Inertial navigation, whereby every change of direction and acceleration during the outward journey is recorded and integrated to give the overall angular displacement from home, has often been proposed. But imposition of highly complicated, irregular accelerations, in a revolving drum, had no effect on homing ability. Nor did surgical interference with the inner ear mechanism, most likely site of such a mechanism. Experimenters should remember that the whole bird is the flying machine and that it is capable of flying skills that would defeat a human aviator.

In summary then, there are two main forms of navigation shown by birds; a simple distance-and-bearing type programmed innately in inexperienced birds, and a more complex displacement-correcting mechanism in older, experienced birds. The compass element in the former can be based on clues from sun, moon, stars and the earth's magnetism. The 'grid' needed in the latter may involve the sun's position (at least its elevation), magnetic information or even olfactory clues, but the evidence is still far from clear. G.V.T.M.

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NEARCTIC REGION: the usual designation in zoogeography for North America north of the tropics (see DISTRIBUTION, GEOGRAPHICAL). The borders are the Arctic Ocean in the north, the Bering Strait and the Pacific Ocean in the west, and the Atlantic Ocean in the east. A border in the south is more difficult to draw; it is usually placed through Mexico, along the northern edge of the tropical rain-forest (see NEOTROPICAL REGION). Thus defined, the Nearctic Region extends from about 83°N to about 20°N.

Physiography. In this vast area almost the entire range of possible climates is encountered. The major geographical features of North America, in contrast to Europe, extend longitudinally. The west consists of parallel mountains, the Rocky Mountains and related chains, extending from Alaska southward into Mexico and Central America and continuing into the Andes of South America. The interior of North America is occupied by plains extending from the Gulf of Mexico northward into Canada, where they comprise the vast Canadian Shield. In the east a minor chain of mountains, the Appalachians, extends from Georgia and Alabama into Pennsylvania and continues in several more or less isolated mountain ranges in New York, Vermont, New Hampshire, Maine, and the Maritime Provinces of Canada. This essentially longitudinal arrangement of the major geographical features is, to a large extent, responsible for some of the otherwise puzzling features of the North American bird-life.

Many attempts have been made to subdivide the Nearctic Region into local provinces, from the life zones of Merriam to the biotic provinces of recent authors. Since all these zones intergrade insensibly, none of the attempts can be considered fully successful. On the whole, bird-life and landscape change latitudinally, with the climatic and vegetational belts becoming increasingly better defined northward. A circumpolar tundra belt north of the tree-line is well defined. A 'Canadian' coniferous belt with its characteristic avifauna is fairly well defined. Both extend southwards along the mountains. Farther south there is a less well defined series of belts of deciduous forest, limited to areas of higher rainfall. Between the Mississippi Valley and the Rocky Mountains lie extensive plains ('prairies'); and in northern Mexico and the south-western states are extensive arid areas, some of them true deserts. The bird-life of each of these vegetational areas differs more or less drastically from that of other areas.

History of the avifauna. The composition of the North American bird fauna is best understood in the light of its history. The North American continent was connected with Europe (via Greenland) in the early Tertiary when the Atlantic Ocean was much narrower; it has had intermittent connections with Asia across the Bering Strait bridge; and it was separated from South America, at least from the early Eocene to the late Pliocene, by a series of Central American water-gaps cutting through what are now Nicaragua, Panama, and north-western Colombia. This history of the North American landmass explains the composition of its avifauna. After the late Eocene separation from Europe the fauna evolved in isolation from both Eurasia and South America, but there has been opportunity for a limited amount of faunal exchange across the Bering Strait bridge and the 'stepping-stones' in the Panamanian gap.

During the first half of the Tertiary the southern half of North America was humid and tropical as far north as latitudes 38°–40°, as shown by the palaeo-botanical record. This permitted the evolution of a tropical North American fauna rather distinct from the tropical fauna of South America. The two tropical faunas intermingled when the Panamanian land-bridge was established near the end of the Tertiary (late Pliocene). In the meantime there had been a steady process of cooling and reduction of rainfall in North America, in part caused by the rising of the mountain ranges in the western parts. This resulted in the development of deserts, subsequently populated by colonists from the adjacent, more humid habitats.

In addition to sea birds and world-wide taxa, the North American avifauna consists essentially of four elements: (1) an old indigenous one that developed during the Tertiary isolation; (2) a less old Holarctic element dating back to the Eocene trans-Atlantic connection with Europe; (3) more recent Holarctic immigrants from Asia; and (4) immigrants from South America. The fauna as a whole is thus somewhat intermediate between that of South America and that of Eurasia. Even though there is some ambiguity in any faunal analysis, it is fairly easy to determine to which of the four stated faunas most genera and families of North American birds belong.

Indigenous elements. Five families of songbirds can be considered indigenous North American elements. The wrens (Troglodytidae) have more genera north of the Tertiary gap through Central America than they have in South America, but more species south. The large number of endemic species and genera in the arid, subtropical zone of Mexico and the south-western United States is further proof of Nearctic origin. A single species, the well-known Winter Wren *Troglodytes troglodytes*, has crossed into Eurasia. Other well-known North and Central American species are the House Wren *Troglodytes aedon*, the Carolina Wren *Thryothorus ludovicianus*, the Marsh Wren *Cistothorus palustris*, and the Rock Wren *Salpinctes obsoletus*. Wrens are found in nearly every habitat from the most desolate desert to marshes and the tropical rain-forest.

The mocking-thrush family (Mimidae) contains many well-known North American birds of gardens, woodlands, and open country, such as the Gray Catbird *Dumetella carolinensis*, the Brown Thrasher *Toxostoma rufum*, and the Mockingbird *Mimus polyglottos*; the family is restricted essentially to the areas south of the coniferous forest belt. The vireos (Vireonidae), a family of small, mostly greenish, insect-eating birds of the leafy canopy of trees and bushes, are particularly well represented in the southern United States, Central America, and the West Indies, but there are also many South American species; the Red-eyed Vireo *Vireo olivaceus* is perhaps the most common North American woodland bird, the polytypic species extending as far south as southern South America. The American wood-warblers (Parulidae) are a group of colourful but structurally little diversified warbler-like birds well represented also in the northern coniferous belt, and 2 species have indeed crossed over into eastern Siberia; the northern species are highly migratory, and their passing through the United States in spring and fall, in enormous numbers, is one of the most spectacular aspects of bird-life in North America. Although the general pattern of distribution, as well as the number of endemic genera, indicates that tertiary North America was the home of these 4 families, all of them have crossed over into South America rather early, and have there produced a secondary radiation of species.

The fifth family consists of the buntings or American sparrows (Emberizidae). This family is highly diversified in the New World, so much so that it is difficult to delimit it against the tanagers (Thraupinae) and other finch-like birds. Well-known North American species are the Song Sparrow *Melospiza melodia* with over 30 subspecies extending from the Aleutians and Alaska south to Mexico, the Field Sparrow *Spizella pusilla*, the White-throated Sparrow *Zonotrichia albicollis*, and the Rufous-sided Towhee *Pipilo erythrophthalmus*. These buntings, like their Eurasian counterparts, are largely birds of the open country, from deserts to prairies and marshes; but many other species are typical of the undergrowth of the forest, particularly in the tropics.

Some small families or subfamilies that are presumably indigenous North American elements are the dippers (Cinclidae), the gnatcatchers (Polioptilinae), the waxwings (Bombycillinae), the silky flycatchers (Ptilogonatinae), the mostly tropical motmots (Momotidae), the West Indian todies (Todidae) (known from North America as fossils), and the Palmchat (Dulidae). Several families of non-passerine birds are perhaps indigenous North American elements, such as the New World vultures (Cathartidae) represented by the Turkey Vulture *Cathartes aura*, Black Vulture *Coragyps atratus*, and California Condor *Gymnogyps californianus*. The American quails (Odontophorinae) are derived from the pheasants and partridges (Phasianinae) of the Old World. Two species of turkey (*Meleagris*) are the most spectacular gallinaceous birds of the New World.

Old World element. Since North America and Europe were a single continent up to the Eocene, permitting considerable faunal interchange across the transatlantic connection, it is impossible to determine the exact area of origin of the older Holarctic element, such as cranes (Gruidae), pigeons (Columbidae), cuckoos (Cuculidae), certain owls and nightjars, kingfishers (Alcedinidae), the bluejay group (Corvidae pt.), Cardueline finches, and certain thrushes (Turdidae). The grouse subfamily (Tetraoninae), with numerous woodland species but also birds of the open country such as the extinct Heath Hen (an eastern subspecies of the surviving Greater Prairie Chicken *Tympanuchus cupido*) and the spectacular Sage Grouse *Centrocercus urophasianus*, apparently originated in the Old World, but had a rapid radiation in North America in the late Tertiary. A more recent Palearctic element evidently came across the Bering Strait bridge. This includes larks (*Eremophila*), creepers (*Certhia*), pipits (*Anthus*), nuthatches (*Sitta*), wrentit (*Chamaea*), some Corvidae (*Perisoreus*, *Pica*, *Corvus*, *Nucifraga*), Paridae (*Parus*, *Auriparus*, *Psaltriparus*), kinglets (*Regulus*), Barn Owl *Tyto alba*, and some Hirundinidae (*Riparia*, *Hirundo*, *Petrochelidon*). E.M.

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See also Neotropical Region.

NECK: see TOPOGRAPHY.

NECTAR-FEEDERS: birds that feed on the sugary liquid in the calyces of some flowers. The habit has been evolved in several unrelated families in different parts, mainly tropical, of the world. The principal groups are the hummingbirds and honeycreepers of the New World, the sunbirds of Africa and southern Asia, the honeyeaters and flowerpeckers found chiefly in Australasia, and the Hawaiian honeycreepers (Drepanididae).

NECTARINIIDAE: a family of the PASSERIFORMES, suborder Oscines, SUNBIRD.

NEDDICKY: name, in South Africa, of *Cisticola fulvicapilla* (for family see WARBLER (1)).

NEGRITO: substantive name of *Lessonia rufa*, a South American tyrant-flycatcher (see FLYCATCHER (2)).

NEGRO-FINCH: substantive name of *Nigrita* spp. (see ESTRILDID FINCH).

NEMATODE: see ENDOPARASITE.

NE-NE: Hawaiian vernacular name, widely adopted, for the Hawaiian Goose *Branta sandvicensis* (see under DUCK).

NEOGAEA: see under ARCTOGAEA; DISTRIBUTION, GEOGRAPHICAL.

NEOGNATHAE: a superorder (see under CLASS).

NEOGNATHOUS: see PALATE; SKULL.

NEOMORPHINAE: see CUCKOO.

NEONATE: a newly hatched bird.

NEONTOLOGY: the study of geologically recent forms of life (contrasted with PALAEONTOLOGY).

NEORNITHES: a subclass (see under CLASS).

NEOSITTIDAE: a family of PASSERIFORMES, suborder Oscines, SITTELLA.

NEOSSOPTILE: term applied to the natal down plumage (where present), as contrasted with 'teleoptile' (see PLUMAGE).

NEOTENY: persistence of embryonic characters into adult life.

NEOTROPICAL REGION: usual designation in zoogeography for tropical America and the non-tropical parts of South America, together with the West Indies and other islands near South America (see DISTRIBUTION, GEOGRAPHICAL). South America is the real home of the Neotropical fauna, while Central America and the West Indies occupy a special position discussed below. The Neotropical Region extends from the northern edge of the tropical rain-forest in Mexico, about 20°N (see NEARCTIC REGION), south to Cape Horn, in about 57°S.

Physiography. South America is characterized by numerous geographical superlatives. The Andes, forming the western edge of the continent throughout its length, are the longest mountain range in the world, extending through 80° of latitude. The Amazon is the world's greatest river. The region is dominated by tropics and subtropics, and the southern third of the continent is so narrow that it leaves only little space for a temperate zone fauna. There are two areas of mountains east of the Andes—the isolated Guiana-Venezuela highlands (with Mt Roraima and Mt Duida), and the eastern Brazilian mountains. There are some extensive savannas ('llanos') north of the River Amazon, particularly in the upper Orinoco basin of Venezuela and north-eastern Colombia, and more extensive ones from the Matto Grosso south into Patagonia. Very arid country, some of it true desert, extends from the Pacific coast of southern Ecuador south through coastal Peru and Chile to about Valparaiso, southwards extending increasingly far into the mountains and encroaching in northern Argentina beyond the foot of the eastern Andes. As Wallace said, the Neotropical Region 'is distinguished from all the other great zoological divisions of the globe by the small proportion of its surface occupied by deserts, by the large proportion of its lowlands, and by the altogether unequalled extent and luxuriance of its tropical forests'.

History of the avifauna. The avifauna of South America not only is the richest in the world but is also remarkably uniform throughout the continent. There are no latitudinal barriers anywhere east of the Andes, and the Andes themselves have served as a distributional pathway, permitting the colonization of the lower latitudes by many temperate zone elements. The south temperate avifauna is characterized more by the paucity of its elements than by its distinctiveness. There are, however, a number of endemic genera, some of them, such as the seedsnipe (Thinocoridae), forming an endemic family. The Rhinocryptidae are of largely temperate zone distribution.

Although South America is now in land connection with North America across the isthmus of Panama, the two continents were isolated for most of the Tertiary Period and perhaps for much longer. Three major water-gaps ('portals') are known to have existed during this period; one across Nicaragua, one across Panama, and the third across north-western Colombia. These water-gaps were bridged by insular 'stepping-stones' for those faunal elements capable of island-hopping. The last of the portals (between Panama and Colombia) did not close until the Pliocene, presumably about 3 million years ago. There is no ornithological evidence for any connection with Africa. Prior to the break-up of the Gondwana plate South America was connected (directly or by stepping-stones) with Antarctica-Australia. The ratites are the only element in Australia clearly a remnant of this former connection. South America has acquired several species from Africa by recent transoceanic colonization such as that demonstrated by the Cattle Egret *Bubulcus ibis*, the Green-backed Heron *Butorides striatus*, 2 whistling ducks *Dendrocygna* spp., and a pochard *Netta erythrophthalma*.

Indigenous element. The old indigenous South American element includes a number of small families (the number of included species is indicated in parentheses), such as the rheas (Rheidae) (2), screamers (Anhimidae) (3), hoatzin (Opisthocomidae) (1), trumpeters (Psophiidae) (3), sunbittern (Eurypygidae) (1), seed-snipe (Thinocoridae) (4), potoos (Nyctibiidae) (5), and oilbird (Steatornithidae) (1). Fossil rheas are known as far back as the Eocene, while for the 8 other families the assumption of a South American origin is based on inference (absence from all other continents, either living or as fossils). Five other non-passerine families are much richer in species in South America than anywhere else, and for them a South American origin is hardly in doubt: tinamous (Tinamidae) (47), hummingbirds (Trochilidae) (300), puffbirds (Bucconidae) (33), jacamars (Galbulidae) (14), and toucans (Ramphastidae) (37). They include some of the most characteristic elements of the South American avifauna.

South America is characterized, even better than by these non-passerines, as the home of the Clamatores (= suborder Tyranni) the true mesomyodian passerines. All the families of this suborder are Neotropical (except for a few Old World genera with simplified syringeal musculature, which may well have acquired this similarity by convergence). The South American Clamatores are divisible into two main branches, the Tracheophonae (= Superfamily Furnarioidea) and the Haploophonae (= Superfamily Tyrannoidea). The Tracheophonae, in which the syrinx is entirely tracheal, consist of the tapaculos (Rhinocryptidae) (26), gnateaters (Conopophagidae) (10), antbirds (Formicariidae) (221), ovenbirds (Furnariidae) (212), and woodcreepers (Dendrocolaptidae) (47). This group, including more than 500 species, forms a dominant element in the South American avifauna. The antbirds are particularly characteristic of the undergrowth in the tropical rain-forest, while some of the genera of ovenbirds contribute conspicuous species to the temperate zone fauna of the continent, both in the southern latitudes and at the higher altitudes of the Andes.

In the haploophone Clamatores, the syrinx muscles are tracheobronchial, but are attached only at one end of the bronchial rings. This includes the tyrant-flycatchers (Tyrannidae) (366), the manakins (Pipridae) (51), cotingas (Cotingidae) (61), and the plantcutters (Phytotomidae) (3). This group thus comprises nearly 500 species. Indeed, the 2 groups of Clamatores combined contain nearly one-eighth of all the known species of birds of the world.

Most of the indigenous South American bird families, like their mammalian counterparts, have been poor colonizers. Only the hummingbirds and the tyrant-flycatchers, among the truly South American elements, seem to have colonized North America across the Central American stepping-stones to develop subtropical and temperate zone representatives in the North American fauna. The other families crossed into Central America late in the Tertiary, most of them apparently only after a complete land connection had been established.

Nearctic element. The stepping-stones between North and South America were used much more actively by North American elements to carry on a steady colonization. The earliest of these immigrants—the tanagers and honeycreepers (Thraupinae), cardinals (Cardinalinae), and troupials (Icteridae)—settled there such a long time ago that, except for their evident relationships with North American elements, they have acquired all the characteristics of South American families. The Emberizidae should perhaps be included in this group. Much of the adaptive radiation of these families took place in South America.

Other immigrants radiating secondarily in South America were contributed by such pantropical groups as the parrots, the trogons, the barbets, and one or two smaller groups. Other somewhat later arrivals from North America include the guans (Cracidae), the American quail (Odontophorinae), pigeons (Columbidae), jays (Corvidae), and thrushes (Turdidae). Typically North American families, such as the wrens (Troglodytidae), vireos (Vireonidae), wood warblers (Parulidae), and motmots (Momotidae), invaded South America presumably prior to the closing of the water-gap, because certain genera speciated there quite actively, having now more species in South America than in North America. The Andean chain, through Central America in almost continuous mountainous connection with the North American Rocky Mountains, has permitted the immigration of some typically Holarctic elements into South America, such as pipits *Anthus* spp., the Horned (or Shore) Lark *Eremophila alpestris*, and the Short-eared Owl *Asio flammeus*.

Needless to say, the South American continent has a rich fauna of fresh-water birds, consisting essentially of cosmopolitan families but with many endemic genera and species. Among the more characteristic of these the following may be mentioned: torrent ducks *Merganetta* spp., the Coscoroba Swan *Coscoroba coscoroba*, the South American sheld-geese *Chloephaga* spp. and the steamer ducks *Tachyeres* spp. (mostly salt water).

Subdivisions and Islands. Attempts to subdivide the Neotropical Region into subregions have been unsuccessful as far as the area south of Panama is concerned. The 'Guianan' and 'Brazilian' districts are occupied by some different species and genera, but the total character of the local faunas depends more on climate and vegetation than on historical features.

Central America, 'tropical North America' as Wallace quite rightly called it, contains a strongly mixed fauna—an old indigenous element and numerous post-Pliocene invaders from South America. The West Indies have an unbalanced and impoverished avifauna, indicating that they received their fauna by transoceanic dispersal; this is confirmed by studies of mammals, reptiles, fishes, and insects. Most of the avian immigrants came from tropical Central America, for a long period before and after the closing of the Panamanian gap. Typical for the West Indies are certain thrushes, mocking-thrushes (Mimidae), vireos, wood warblers, tanagers, finches (Fringillidae), icterids, and the peculiar Palmchat *Dulus dominicus* (related to *Bombycilla*), some tyrant flycatchers, the endemic family Todidae, some trogons, some hummingbirds (including the smallest bird in the world), some parrots, pigeons, and some hawks, to mention the more important. Other islands, such as the Galapagos, the Falklands, and the Juan Fernandez group, received most of their fauna from the adjacent parts of South America. E.M.

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NEOTYPE: see TYPE SPECIMEN.

NEPHRON: an excretory unit of the kidney (see EXCRETORY SYSTEM).

NERVOUS SYSTEM: in birds, built on the same plan as in vertebrates generally; it resembles that of reptiles, especially the Crocodilia and certain lizards, very closely. The difference from reptiles is chiefly one of relative size; in a bird the brain is 10 or more times larger than the brain of a reptile of similar body weight. See also DEVELOPMENT, EMBRYONIC; GROWTH.

Central and peripheral systems. The nervous system consists of a central nervous system (C.N.S., the brain and spinal cord) and a peripheral nervous system (the cranial and spinal nerves, and the visceral or autonomic nerves and ganglia). The peripheral nerves are made up of nerve fibres that can be divided into two main categories; those that conduct impulses from the special sense organs such as eyes or from the skin and deeper tissues to the C.N.S. (afferent or sensory fibres); and others that conduct impulses from the C.N.S. to the muscles, causing them to contract and produce movements (efferent or motor fibres)—see also MUSCULATURE. Viscera such as the heart, blood-vessels, glands, and the alimentary canal are supplied by efferent nerve fibres that are classed as autonomic or visceral and are further subdivided into sympathetic and parasympathetic. Viscera usually have a double nerve supply, sympathetic and parasympathetic; these are in general functionally antagonistic—for example, parasympathetic stimulation slows the rate of the heart beat, whereas sympathetic causes acceleration. Viscera are also supplied by many afferent fibres.

Functions. It is the general function of the C.N.S. to integrate the information reaching it in the form of afferent or sensory impulses from all parts of the body and from the outside world, into patterns significant in the life of the animal. It must also be capable of storing this information selectively, so that it can form the basis of memory and learning; but the physical form in which information is stored in the C.N.S. is not known. The C.N.S. must also have motor functions; on the basis of the information reaching it at any particular time, combined with what has been stored from previous experiences, it must integrate or co-ordinate outgoing efferent impulses to the muscles and viscera so that useful movements and patterns of behaviour result.

To a large extent the particular kind of behaviour that can be integrated by the nervous system depends on its intrinsic structure, its 'built-in' characteristics (which are inherited). Such behaviour is activated automatically in response to appropriate sensory stimuli and is called reflex or instinctive. The extent to which it can be modified or added to as a result of experience varies in different vertebrates (see LEARNING). In birds it is limited, and much avian behaviour consists of complex but relatively stereotyped patterns, as is well seen in the reproductive cycle (mating, nest building, and so on). Patterns of behaviour depending on inherited structure are not so conspicuous in mammals, where the nervous system is less rigidly organized and shows greater plasticity in its functions: behaviour in consequence depends to a larger extent on learning and the storage of information. However, the learning ability of birds is certainly superior to that of many mammals: pigeons, for example, in some circumstances perform rather better than domestic cats. These differences between birds and mammals are reflected in fundamental differences in the structure of the nervous system, particularly in the part called the fore-brain (see below).

The functions of the nervous system in co-ordinating and activating patterns of behaviour can also be strongly influenced by chemical substances, hormones, circulating in the blood. These are produced by the endocrine glands (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM), some of which (the pituitary and the suprarenal glands) are closely associated anatomically with the nervous system. The effect is well illustrated in sexual behaviour. When, as in the male animal, male sex hormones are predominant, the behaviour integrated by the nervous system will be that appropriate for the male; experimentally the same nervous system can be shown to be capable of integrating female sexual behaviour under the influence of female sex hormones. Although such effects can be demonstrated in mammals, they are particularly characteristic of birds, where 'built-in' mechanisms form a more important part of the nervous system.

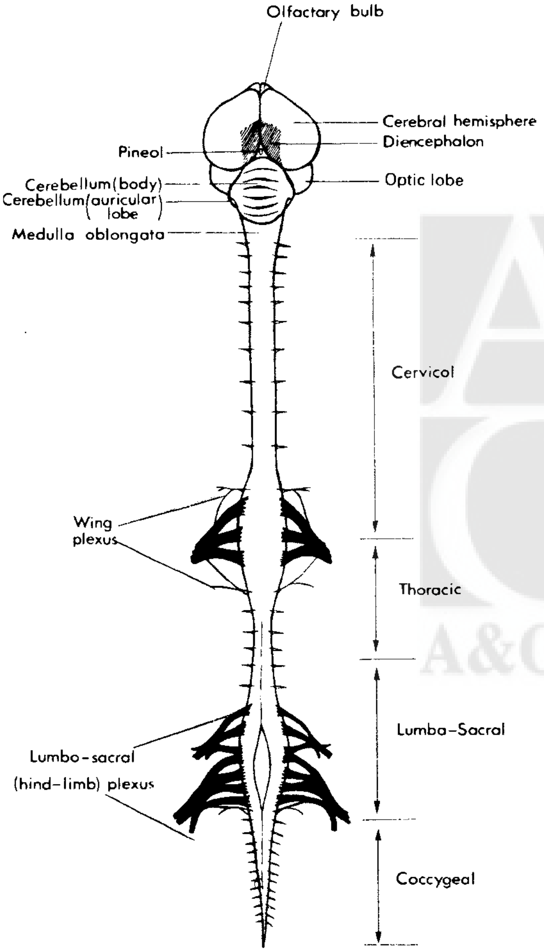

Fig. 1. Diagram of the nervous system of a bird (*Columba*). (Modified from Kappers, Huber & Crosby 1936).

Spinal cord. The spinal cord (Fig. 1) is co-extensive with the vertebral column, as in most other vertebrates except mammals, and contains a narrow channel throughout its length known as the 'central canal'. The cervical and lumbo-sacral regions are long, the thoracic and coccygeal relatively short; there are well marked cervico-thoracic and lumbo-sacral enlargements where the nerves to the wings and legs arise. A feature peculiar to birds is the 'rhomboid sinus'; this is a mass of gelatinous tissue, rich in lipids and glycogen, which separates the dorsal parts of the lumbo-sacral region of the spinal cord (Fig. 2); its significance is unknown. In the same region collections of nerve cells situated superficially on the lateral aspects of the cord form the 'nuclei of Hoffmann'. Somewhat similar but less conspicuous marginal nuclei are present in reptiles. The spinal cord is connected by well developed ascending and descending tracts with the medulla oblongata (see below) and the cerebellum; the latter is largely concerned with the maintenance of equilibrium, a particularly important function during flight. Other connections with the brain are much less well developed, and the spinal cord possesses considerable autonomy. It is able to co-ordinate the movements of the wings in flight, or the legs in running, with little assistance from the brain; it is well known that movements of this kind are often carried out actively for a short time after decapitation.

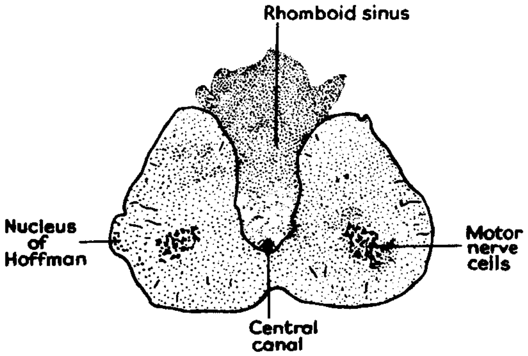

Fig. 2. Transverse section through lumbo-sacral region of the spinal cord of a pigeon *Columba* to show the rhomboid sinus. (Modified from Kappers, Huber & Crosby 1936).

Brain stem. As the spinal cord enters the skull it enlarges to form the medulla oblongata, from which most of the cranial nerves arise (Figs. 1, 3, and 4). In the same region the central canal enlarges to form a cavity called the 4th ventricle. The parts of the brain stem surrounding this ventricle belong to a subdivision of the vertebrate nervous system known as the hind-brain; it includes the pons in mammals (small in birds) and the cerebellum (see below) as well as the medulla oblongata. Except in detail the medulla oblongata of birds does not differ markedly from the usual vertebrate pattern. Its expanded cranial end is continuous with the next part of the brain stem, the mid-brain, which is characteristically specialized. It possesses two more or less spherical swellings, the optic lobes, which develop on its dorsal aspect and remain in that situation in all other vertebrates; in birds they are displaced laterally and ventrally by the backward enlargement of the cerebral hemispheres (Figs. 1, 3, and 4).

Cerebellum. The cerebellum (Figs. 1 and 3) is large, and situated on the dorsal aspect of the hindbrain. The main part, the corpus or body, is somewhat compressed from side to side and elongated cranio-caudally; it corresponds with the vermis in mammals and there is only rudimentary representation of the lateral extensions that form the mammalian cerebellar hemispheres. The body is divided by transverse furrows into anterior, middle, and posterior lobes, corresponding closely with the same subdivisions in mammals. These lobes are further divided by secondary furrows into folia; the most caudal of these is the nodule, and, strictly speaking, should not be included in the body of the cerebellum. On each side the nodule gives rise to a lateral extension which varies in size in different birds. This is the auricular lobe (Fig. 3), corresponding to the

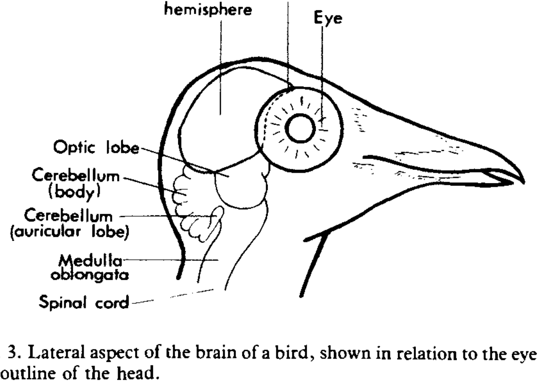

Fig. 3. Lateral aspect of the brain of a bird, shown in relation to the eye and the outline of the head.

flocculus of mammals. The whole complex (the nodule with its lateral extension) is called the auriculo-nodular lobe, corresponding to the mammalian flocculo-nodular lobe, and is a primitive part of the cerebellum that receives many connections from the vestibular division of the 8th cranial nerve.

Functionally the cerebellum is essential for the maintenance of posture and equilibrium and for regulating the range and force of movements. It may be thought of as acting like an 'automatic pilot', maintaining stability and direction during flight, and it is noteworthy that the tracts connecting it with the centres in the spinal cord through which bodily movements are controlled are well developed in birds. The absence of cerebellar hemispheres is also understandable; they are a characteristic feature of the mammalian brain, where they are concerned in the regulation of learnt skilled movements, particularly of the limbs, and movements of this kind play little part in the behaviour of birds.

Fore-brain. The cranial end of the brain stem, the mid-brain, is continuous with a complex mass of nervous tissue, the fore-brain. This consists of a median part, the diencephalon, directly continuous with the mid-brain, and bilateral expansions forming the cerebral hemispheres (Fig. 1). The whole forebrain is hollow, the median cavity of the diencephalon being called the 3rd ventricle. It is continuous caudally through the mid-brain and the 4th ventricle of the hind-brain with the central canal of the spinal cord. On each side the cavity of the 3rd ventricle extends into the cerebral hemisphere to form small lateral ventricles (Fig. 4).

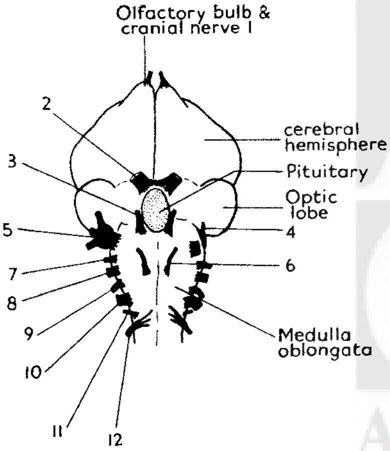

Fig. 4. Ventral aspect of the brain of a pigeon, to show the roots of the cranial nerves.

The median diencephalic part of the fore-brain is concealed from view by the cerebral hemispheres (Fig. 1). On each side it contains complex masses of nerve cells, the thalami, which are similar in their organization to the same parts in reptiles. Ventral to the thalami and forming the floor of the 3rd ventricle is the hypothalamus, another complex of nuclei, connected by a thin stalk to the pituitary gland (Fig. 4). On the dorsal aspect of the diencephalon the pineal apparatus is found; it is vestigial, and no parietal eye is present as in some reptiles.

The cerebral hemispheres are rounded and smooth, lacking the convolutions characteristic of the mammalian brain. The olfactory bulbs (Figs. 1 and 4) attached to the anterior poles of the hemispheres are generally small and sometimes fused together. The olfactory sense is correspondingly poorly developed, so that most birds are classed as microsmatic; most vertebrates have a well developed sense of smell and are classed as macrosmatic. In a number of avian species, however, e.g. ducks, the domestic fowl, and most markedly the kiwis *Apteryx* spp., the bulbs are quite well developed; but, with the possible exception of the kiwis, it is doubtful if any birds could be described as macrosmatic (see SMELL).

In all vertebrates the cerebral hemispheres are divided into dorsal and ventral parts forming the roof and floor respectively of the lateral ventricles. In the dorsal part the extensive superficial cortex so characteristic of mammals is formed; the ventral part forms the basal ganglia of the hemisphere.

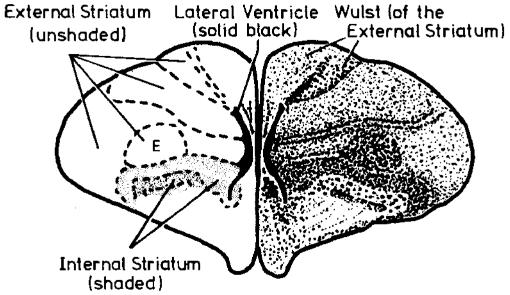

Fig. 5. A section through the cerebral hemispheres of a pigeon. On the left, the subdivision of the basal ganglia into internal and external striatal segments is indicated. On both sides, the complicated subdivision of the external striatum is easily seen. 'E' is the ectostriatum.

In birds the most immediately striking features are the small and rudimentary character of the cortex proper, and the relatively enormous development and complex differentiation of the basal ganglia (Fig. 5). This appearance is, however, deceptive. The 'basal ganglia' of birds can in fact be divided into two parts, the internal striatum and the external striatum. The smaller of these, the internal striatum, corresponds to the corpus striatum of mammals and is concerned with the control of movement. The larger external striatum is more sensibly grouped with the rudimentary cortex, since, like the cerebral cortex of mammals, it receives sensory information (especially from the eyes, the ears and, to a lesser degree, that related to the sense of touch) relayed, just as in mammals, through the thalamus of the diencephalon. A part of the external striatum may correspond to the mammalian 'motor cortex', in as far as it sends nerve fibres directly to the spinal cord. It seems that during evolution birds, like reptiles, failed to find the mechanism for expanding these forebrain masses into a sheet-like cortex. This evolutionary failure perhaps accounts for the lesser evolutionary success of birds in the production of types capable of the very flexible and adaptable behaviour patterns characteristic of higher mammals. In one respect though, birds outdo mammals in this all-important area of plasticity: in song birds there are collections of neurons in the external striatum which control the production and pattern of song. These neurons are remarkable in that they change their structure with the seasons and circumstances, corresponding to the natural seasonal variation of song pattern in these species. There is no doubt that the large basal ganglia are functionally concerned with the integration of the instinctive behaviour of birds, and it is probable that the hyperstriatum is of particular importance in relation to the activities of the breeding cycle. These neural mechanisms are very sensitive to facilitation or inhibition by hormones.

The hypothalamus of the diencephalon is closely associated with the pituary gland. It is mainly concerned in the integration of visceral and metabolic activities and has been described as the head ganglion of the autonomic nervous system. In mammals its functions are not purely neural, and it can secrete hormones that pass down the stalk to the pituitary, so that it is very closely associated with the endocrine system; it probably has similar functions in birds. Centres for the regulation of the excretion or retention of water, for temperature regulation, for a general inhibition resulting in sleep, and a number of other functions have been identified in the hypothalamus, which is a very important part of all vertebrate brains.

Cranial nerves. The 12 pairs of cranial nerves (Fig. 4) characteristic of higher vertebrates are all present in birds. The 1st (olfactory) are slender (see above). The 2nd (optic) are particularly large and decussate completely in a chiasma or crossing. They discharge to the optic lobes of the mid-brain, which contain what is probably the most highly differentiated neural tissue in the avian nervous system. The size of the nerves and the complexity of the optic lobes is associated with the great importance and high degree of development of the visual sense in birds (see VISION).

The visual system is organized in the same way as that of all vertebrates: the optic nerves discharge directly to both the optic lobes of the midbrain and to the thalami of the fore-brain. The optic lobes also send information to the thalami, and from this structure all the visual information passes to the cerebrum. In mammals, the connection from the eyes to the midbrain is relatively smaller than that made directly with the thalami: the ultimate target for the information is the cerebral cortex.

In birds, although the main visual centres are undoubtedly in the midbrain (the optic lobes send fibres to the brain stem and so are able to control many motor responses to visual information in a reflex way), optic nerve fibres certainly do run directly to the thalami. There is evidence that the appreciation of the nature of seen objects requires the cooperation of those parts of the avian external striatum (the Wulst or hyperstriatum, and the ectostriatum—E in Fig. 5) which are the destination of visual informmation from the thalami. The 3rd (oculomotor), 4th (trochlear), and 6th (abducens) nerves are all purely efferent and supply the ocular muscles as in vertebrates generally. The 12th (hypoglossal) is also efferent and supplies the tongue muscles; it gives a branch to the muscles of the syrinx, which are therefore not comparable with laryngeal muscles (supplied by the vagus)—see SYRINX. The 5th (trigeminal), 7th (facial), 9th (glossopharyngeal), 10th (vagus), and 11th (accessory) form the usual series of branchial or visceral arch nerves. They contain, of course, no component from lateral line organs as in aquatic vertebrates, and only a few special avian features need be mentioned. The 5th nerve is well developed and supplies complex sensory corpuscles, such as those of Grandry and Herbst, which are often associated with the bill; while usually considered to be tactile, their function is not fully understood (see TOUCH). Fibres serving the sensation of taste are present in the 7th and possibly in the 9th nerves, but are very few in number on account of the poor development of this particular sense in birds (see TASTE). The 11th nerve (accessory) is small and constitutes one of the caudal roots of the vagus; there is no spinal component as in mammals. There remains only the 8th nerve, which has both auditory and vestibular divisions with connections in the brain stem resembling those of mammals rather closely. The auditory division (from the lagena) is comparatively small, but the vestibular is well developed, as would be expected in animals where the maintenance of equilibrium is a particularly important function (see HEARING AND BALANCE).

Spinal and autonomic (sympathetic and parasympathetic) nerves. These are arranged on the same general plan as in mammals and reptiles, but there are many detailed differences related to the different proportions of the parts and organs of the body.

The roots of the spinal nerves are shown attached in series to the spinal cord in Fig. 1. They are enlarged opposite the wing and the hind limb, where they form the brachial (wing) plexus and the lumbo-sacral plexus respectively, as in all tetrapoda. Autonomic nerves are not shown: they arise from ganglia (collections of nerve cells), outside the C.N.S., that are classified in two categories, sympathetic and parasympathetic (see above). The former are arranged in two regular chains, approximately one pair of ganglia for each segment of the body, on each side of the vertebral column; the latter are more irregularly scattered, usually close to the viscera they supply. Both sympathetic and parasympathetic ganglia are connected to the C.N.S. through spinal or cranial nerves, so that their activity is centrally regulated and integrated.

Differences among Birds. There are great variations among birds in the size of the brain and in the proportions between its parts. In general the gallinaceous birds show primitive characteristics, with relatively small cerebral hemispheres and well developed olfactory bulbs, and the same may be said of pigeons and plovers. Crows, owls, and parrots are at the opposite extreme, with particularly large cerebral hemispheres. (In all birds the cerebral hemispheres comprise a relatively larger part of the brain than in reptiles. Indeed, in this feature birds vie with many mammals.) The 'ratite' birds tend to have relatively large olfactory bulbs, and among them the kiwis have already been mentioned as possibly macrosmatic; these birds also have the large cerebellum typical of birds generally, suggesting that they are descended from ancestors able to fly (see EARLY EVOLUTION OF BIRDS). In the fossil *Archaeopteryx*, the earliest known bird, the endocranial cast indicates that the brain was essentially reptilian in form; the cerebral hemispheres were elongated, possibly with long olfactory peduncles as in a typical lacertilian brain, and there is no evidence of enlargement of the cerebellum or of ventral displacement of the optic lobes (see ARCHAEOPTERYX). The evidence from endocranial casts of fossil forms is always to be accepted with caution, since it cannot be known with certainty how completely the cranial cavity was filled by the brain. In modern birds (unlike reptiles) the cranium does in fact fit closely around the brain, so that a cast gives an accurate representation of its form and proportions. It is of interest that in the fossil flying reptiles (Pterosauria) there seems to have been a similar close relationship between the cranium and the brain, which is shown by endocranial casts to resemble that of modern birds closely, perhaps more closely than is the case with *Archaeopteryx*.

Some small birds, notably the hummingbirds, have a particularly large brain/body weight ratio. In spite of this, the cerebral hemispheres are very primitive and reptile-like, so that their claim to be neurologically advanced depends chiefly on the cerebellum and mid-brain. Most of the differences between the brains of different birds can be related to differences in their mode of life; they do not seem to have much systematic relationship to taxonomic subdivisions, since quite large differences may be found between birds not widely separated in taxonomy. (F.G.) K.E.W.

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NEST: popularly the word 'nest' implies a structure, made by a bird, in which eggs are laid and incubated; it is perhaps usually thought of as shaped like an open bowl; to ornithologists this meaning is inadequate. Many birds make no nest; others excavate or use holes without nest material; still others make structures but do not incubate the eggs. Further, though eggs are normally incubated in one spot till they hatch, the Black Vulture *Coragyps atratus* of the New World may move its eggs for appreciable distances during incubation, as may some nightjars. Thus, a comprehensive definition of 'nest' would be: a structure built or excavated by a bird or already in existence, or a spot or area, in which eggs are laid and remain till they hatch (after incubation by the species concerned or by some other means). The only exceptions are brood-parasites, such as Old World cuckoos (Cuculidae), cowbirds (Icteridae) of the New World and some others that make no nests of their own (see BROOD-PARASITISM), and some penguins, e.g. Emperor *Aptenodytes forsteri* and King *A. patagonicus*, that incubate the single egg between belly and tarsi or feet and may move about with it thus held, so having nothing that can be called a nest. (See also NEST BUILDING; NEST FUNCTION; NESTING ASSOCIATIONS.)

Nests are often specifically distinct in materials or site or both. For instance, the tyrant-flycatcher *Tachuris rubrigastra* of Argentina makes a beautifully felted cup of yellow plant-down attached to a single reed; the Paradise Riflebird *Ptiloris paradiseus* of Australia often decorates its nest with a discarded snake-skin; and the Crested Bellbird *Oreoica gutturalis*, also of Australia, customarily puts hairy caterpillars on the rim of, or inside, its nest. Moreover, closely related species tend to make similar nests and place them in similar sites, so that the nest has some practical value for taxonomy; thus woodpeckers excavate holes in trees and make no nest inside, the anis *Crotophaga* spp. line their untidy nests with fresh green leaves and buzzards *Buteo* spp. and other raptors decorate theirs throughout occupation with some fresh material. However, though auks mostly nest on ledges or in crevices on cliffs near the sea, the Marbled Murrelet *Brachyramphus marmoratus* has recently been found to nest high in branches of tall conifers and Kittlitz's Murrelet *B. brevirostris* lays its egg on bare ground above the tree-line and far from the sea. Similar remarkable exceptions occur among parrots, which can be said to nest generally in holes of one sort or another; several pairs of Monk Parakeets *Myiopsitta monachus* build their nests of thorny twigs together at the ends of branches, finally forming large structures made up of separate nests, and the Australian Ground Parrots *Pezoporus wallicus* and Night Parrots *Geopsittacus occidentalis* construct nests of grasses in or under tussocks.

The greatest complexity and variation of construction occur among passerine birds. Non-passerines mostly build simple structures of sticks, reeds, etc., place their eggs on the ground or make holes for themselves, without adding material. In contrast, passerines that nest on the ground or in holes make more or less substantial nests. The earliest birds probably had the simplest nest-making habits, placing their eggs on the ground or in cavities without any material; later birds came to build simple structures or excavate holes. Presumably ground- and hole-nesting passerines adopted these habits secondarily.

Non-passerine birds. Though non-passerines mostly have rather crude nests, there are interesting contrasts and exceptions. Some hummingbirds build the smallest known nests, 2 cm across and 2–3 cm tall, whereas a long-established nest of the Osprey *Pandion haliaetus* or White-bellied Sea-Eagle *Haliaeetus leucogaster* may be a metre or more across and 2m tall. Also, the perfectly felted cups of plant-down and cobweb made by hummingbirds contrast extremely with the imperfect platforms of sticks made by some pigeons, though the frail nests of some doves (*Columbina* spp.) become consolidated and built up by the excreta of the young to form substantial structures.

Incubation mounds. The Australasian MEGAPODES have the remarkable habit of 'artificial' incubation. They make big mounds of sand, earth and leaves, in which the eggs are hatched by the heat of decaying vegetable matter, or lay the eggs in sand and crevices where they are incubated by the heat from the sun or from volcanic emanations. The Malleefowl *Leipoa ocellata*, and perhaps other species, carefully control the temperature in the mound during incubation.

Use of saliva. Swifts are interesting because many species use saliva for building and stick their nests in the shape of half cups on the sides of caves, in hollow trees or elsewhere. The Palm Swift *Cypsiurus parvus* of Africa sticks its nest to the underside of palm leaves. In the Far East species of *Aerodramus* nest in huge numbers in caves and provide edible nests, being the only birds of economic importance in this respect (see EDIBLE NESTS). The Cayenne Swift *Panyptila cayennensis* makes a remarkable cylinder, about 70 cm long, open at the bottom, of plant material and feathers felted together with saliva, the outside being left rough and plastering being done only from inside; about half-way up inside, a small shelf is made, where the eggs are laid; thus, like most other swifts, the bird nests in a hole, but it constructs its own hole.

Though swifts are well-known users of saliva in building, they are probably not the only group of birds to do so. The Australian scrub-birds *Atrichornis* spp. line their nests with masticated wet plant material, which dries out into a cardboard-like substance and in which saliva may play a part. Some cuckoo-shrikes (Campephagidae) probably use saliva to bind together plant material for nests or to make the nests adhere better to airy forks of branches where they are placed but this needs confirmation.

Aquatic nests. Grebes make pads of vegetation floating on water but attached to a plant; jacanas often make nests of rushes on the floating leaves of water-lilies or lotus; some rails and *Chlidonias* terns make simple nests of reeds and water-plants over water but usually in less open situations and not truly floating.

Ground-nesting. Other non-passerines may be roughly divided into ground-nesters, hole-nesters and builders of simple nests in trees. Simple ground-nesting without any material is characteristic of the Ostrich *Struthio camelus* (though other ratites may assemble some material in their nests), sand-plovers *Charadrius* spp., thickknees, sandgrouse and nightjars. Interestingly, the Egyptian Plover *Pluvianus aegyptius* (Glareolidae), the Kentish Plover *Charadrius alexandrinus* and at least some other species of *Charadrius* in Australasia bury their eggs in sand, though it is not entirely certain whether all do so by design rather than by accident, and cover them with sand when leaving the nest. Apart from auks (see above), most other Charadriiformes make some nest of plant material on the ground, often substantial as in the Black-winged Stilt *Himantopus himantopus*, and many gulls; yet the Green Sandpiper *Tringa ochropus* habitually uses the old nests of other species in trees. Albatrosses (Diomedeidae) build big mounds of soil and vegetation, and flamingos, mounds of mud. Other ground-nesters are some penguins (e.g. Adélie *Pygoscelis adeliae* and Chinstrap *P. antarctica*), making a scrape lined with pebbles; most ducks and geese (Anatidae), which are unique in using their own down as lining (though it is curious that lyrebirds *Menura* spp. add their own body-feathers to the lining of their nests during incubation); pheasants and their allies (Galliformes), which usually line their scrapes with leaves and grass; buttonquail, which make a partly domed nest of grasses; and cranes and rails (Gruiformes), which make substantial structures of plant material.

Hole-nesting. Non-passerines nesting in holes in the ground include shearwaters (Procellariidae), storm-petrels (Hydrobatidae), some kingfishers, motmots and bee-eaters, the last 3 making their own holes (often of considerable length) in banks or on flat ground, whereas the others are less liable to dig their own burrows. Groups that generally use existing holes in cliffs, trees or buildings are parrots, owls, trogons, rollers and hoopoes. Hornbills also do so, with the interesting modification that the entrance is usually restricted with plaster of some sort, the female helping to immure herself. Woodpeckers and barbers mostly make their own holes in trees but some do so in ants' or termites' nests and one woodpecker lays on the ground.

Simple structures. Pelecaniformes (cormorants, pelicans, frigatebirds), Ciconiiformes (herons, storks), birds of prey, Cuculiformes (cuckoos, turacos) and pigeons mostly make simple, if large, nests in trees but many, especially among birds of prey, use the old nests of other species, or nest on ledges or even on the ground. Among the Ciconiiformes, the Hamerkop *Scopus umbretta* of Africa is remarkable for making a big dome of sticks cemented with mud about a metre high and with the entrance at the side.

Passeriformes. In spite of great variety of form and building skill, most passerines make simple cup-shaped nests. The range of size and materials may be represented by crows *Corvus* spp. with big nests of sticks lined with finer plant material and wool, and by many small birds (e.g. fantails Rhipiduridae) with small neat cups of the finest plant material and cobweb. Nevertheless, small birds may make huge nests, the Firewood Gatherer *Anumbius annumbi* (Furnariidae) of Argentina being the classic example; it makes a nest about 70 cm deep and 30 cm across of big sticks with the entrance at the top and a crooked passage leading down to the nest cavity. On the other hand, some species make such flimsy nests that the contents are visible from below, e.g. the Ecuadorian Finch *Sporophila peruviana*, the Rufous Whistler *Pachycephala rufiventris* of Australia and even some honeyeaters (Meliphagidae). Most simple nests are supported in forks or on branches but open cups may be slung by the rims from supporting twigs, often at the inaccessible ends of branches; this habit seems more prevalent in the tropics and Australasia than in the Northern Hemisphere and is characteristic of some antbirds (Formicariidae), vireos (Vireonidae), crombecs (*Sylvietta* spp.) of Africa, orioles (Oriolidae) and many honeyeaters. Reed warblers *Acrocephalus* spp. customarily bind their nests to two or three upright supports.

Enclosed nests. Spherical nests of various sorts are common. Domed nests built of interlaced plant material with a large side entrance are characteristic of such low-nesting birds as warblers of the genus *Phylloscopus* (Sylviinae), pittas, lyrebirds, acanthizids of the genus *Sericornis*, fairy-wrens (Maluridae) and even some icterids, e.g. the Long-tailed Meadowlark *Sturnella loyca*. Others are neater, more felted structures of fine plant material and moss with small entrances at the side, as in some wrens (Troglodytidae), tyrant-flycatchers (*Camptostoma* spp.), becards (Tyrannidae), though these typically make flat tops to their nests, and acanthizids of the genera *Acanthiza* and *Gerygone*. The Yellow-rumped Thornbill *Acanthiza chrysorrhoa* has the extraordinary and unexplained habit of building an ordinary cup-shaped structure on top of, or near, its rather bulky and untidy domed nest, the entrance of which may be hard to find. Some warblers of the genus *Cisticola* achieve a similar result by binding in growing grass as a partial dome. Perfect ovoid nests with a small side entrance towards the top are built of moss and lichen by the Long-tailed Tit *Aegithalos caudatus* and even more perfect nests, felted out of fine plant down to the texture of surgical lint, are made by penduline tits *Anthoscopus* spp. of Africa and the Mistletoebird *Dicaeum hirundinaceum* of Australia. Untidy pendent structures, up to a metre or more long and often with a beard of material hanging down from the bottom and a projecting porch over the entrance, are made by some sunbirds. The African broadbills *Smithornis* spp. also make nests with a beard and the Common Tody-flycatcher *Todirostrum cinereum* constructs a long streamer of hanging material, in the centre of which it later works an aperture for the nest cavity. Ovoid, retort-shaped or bottle-shaped nests, occasionally on the ground, are made by estrildid finches of interlaced grasses, and individuals of some species (*Estrilda melpoda*, *E. troglodytes*, *E. atricapilla*) attach a semi-covered upper story or extension, apparently used for roosting. More striking are the large retort-shaped nests of spinetails *Synallaxis* spp. (Furnariidae), which make big spheres of thorny twigs measuring about 45 by 30 cm, enclosing a large nest chamber, with a long winding narrow tunnel as an entrance. Tailorbirds (*Orthotomus* spp., Sylviinae) in Asia and allied forms in Africa bind leaves together with cobweb or other material and build a nest in the pocket so formed.

Woven nests. Weavers (Ploceidae) of the Old World make various sorts of woven nests, from the globular structure of Village Weavers *Ploceus cucullatus*, which weave it rather carelessly out of strips of palm leaves, making an entrance near the top covered with a small porch, to the inverted sock of some species of *Malimbus*, neatly made from the fibres of palms with a tubular hanging entrance as much as 70 cm long and 10 cm wide. The culmination of this habit is shown by the Social Weaver *Philetairus socius* (Ploceipasserinae) of South-West Africa, which first constructs a roof of coarse straws in a large tree or on a telephone pole and then makes many nest chambers below, the whole forming a single huge mass. In contrast, the Icteridae (oropendolas, caciques and New World orioles) weave pendent bags with an entrance through a slit at or near the top. These bags may be a metre or so long in larger species and, because the birds usually nest colonially, a nesting tree may seem to be laden with monstrous fruit; however, some icterids (e.g. *Icterus mesomelas* and *I. graceannae*) make small, more conventional woven cups, pendent from their rims.

Mud nests. Perhaps the most remarkable mud-nest among passerine birds is that of the ovenbird *Furnarius leucopus* of South America, which makes a thick-walled domed structure on branches with an entrance at the side leading by a corridor into the nest chamber. The rock-fowl *Picathartes* spp. of West Africa make mud structures plastered on rockfaces. Simple, though large and heavy, mud cups are made by the White-winged Chough *Corcorax melanorhamphos* and Apostle-bird *Struthidea cinerea* (Corcoracidae) and magpie-larks (Grallinidae) of Australasia. Some thrushes (e.g. Song Thrush *Turdus philomelos* and Blackbird *T. merula*) and some corvids (e.g. Magpie *Pica pica*) use mud as a lining or foundation in more conventional nests as do phoebes *Sayornis*. Many swallows also use mud either for simple half-cups plastered to some support or for more complex flask-shaped nests.

Hole- and ground-nesting. The passerines with these nesting habits need no special mention, because the peculiarities of their nests are more often those of site rather than structure. However, it is interesting that pardalotes (Dicaeidae) make domed nests within the cavities where they nest. Also nuthatches *Sitta* spp. tend to restrict the entrance to their nests with mud. The Sand Martin (or Bank Swallow) *Riparia riparia* is notable for burrowing tunnels up to a metre in length. S.M.

NESTBOX: see NEST SITES, MAN-MADE.

NEST BUILDING: behaviour concerned with the excavation or construction of nests. Most species of birds lay their eggs in a previously constructed nest, which may be anything from a mere scrape in the ground to a highly elaborate structure, the building of which involves complex patterns of behaviour and the use of many different materials (see NEST). Construction is usually by the female, but the male often helps and in some polygamous species he may do nearly all the work (see POLYGYNY).

Nest building may involve the selection of a site (see NEST SITE SELECTION), its preparation, the collection of material, the carrying of that material to the site, and the actual construction of the nest. Preparation of the site is usually unnecessary in species which build open cup-nests, but in hole-nesters it may involve excavation or the cleaning out of a pre-existing cavity. Many ground-nesting birds first make a depression in the earth or sand.

In most simple nests, and in some complex ones, only one type of material is employed; but usually there are a number, some being used for the outside and some for the lining. Thus the Long-tailed Tit *Aegithalos caudatus* uses mainly moss, spiders' silk, lichen, and feathers. If more than one type of material is used, which type is brought to the nest may be dictated either by the internal state of the female or by stimuli from the partially completed nest. In domesticated Canaries *Serinus canaria* the change-over from collecting grass for the cup to feathers for the lining depends in part on stimuli from the partially constructed nest, and in part on an internal, possibly hormonal, change in the female (Hinde 1958). A variety of relatively stereotyped patterns of behaviour may be used in collecting the material and preparing it for use. Thus weavers (Ploceidae) tear up grass leaves longitudinally (Crook 1960) and Canaries sometimes mandibulate material in water. Nest building by the Wren *Troglodytes troglodytes* is stimulated by rain, the function of this apparently lying in the increased flexibility of the material (Armstrong 1955).

The material is usually carried in the bill; in some cases special movements make it more easily transportable (e.g. *Parus* spp.). Some love-birds *Agapornis* spp. carry material in the rump feathers (Moreau 1948).

Nest construction involves the integration of a number of stereotyped movements characteristic of the species. Closely similar movements are often characteristic of a wide range of related species. Amongst passerines, common movements are 'pulling and weaving', in which loose strands projecting from the rim arc pulled towards the breast and pushed down into the cup; 'scrabbling', in which the female presses down into the cup and pushes back hard with each leg alternately; and 'turning', in which she turns round while sitting in the nest and thus shapes the cup. Sometimes quite complex movement patterns appear; thus some weavers knot strands round twigs with half-hitches.

Redpoll *Carduelis flammea* collecting thistledown as nest material. (*Photo: K.J. Carlson*).

The appearance of each activity involved in nest building depends both on a certain internal state and on external stimuli. Thus all the nest-building activities of Canaries are increased by injections of oestrogen: the behavioural effectiveness of oestrogen is augmented by longer daylengths and by male song (Hinde and Steel 1966, 1978). In addition each nest-building activity is elicited by a particular stimulus situation (e.g. collecting by stimuli from the material, scrabbling by stimuli from the nest cup).

For the construction of a nest, these various patterns of behaviour may be integrated into functional sequences. The principal processes involved are:

(i) The various behaviour patterns of nest building share common causal factors, e.g. certain hormonal states.

(ii) Nevertheless, the various activities may appear at different threshold levels of these factors: thus as a female passerine comes into reproductive condition, she first shows gathering, then carrying, and then the stereotyped movements of nest construction.

(iii) Often each activity brings the bird into the stimulus situation where the next one is evoked; thus, gathering leads to carrying, carrying to placing material in the nest, and so on.

(iv) The performance of each activity is associated with a decreased tendency to continue or repeat that activity; thus the change-over from gathering to carrying, or from sitting building in the nest-cup to gathering again, depends not only on the stimuli presented as a consequence of the first activity, but also on a decreased internal tendency to continue it.

(v) Stimuli from the partially constructed nest may influence subsequent behaviour; thus a decrease in the size of the nest-cup may cause Canaries to bring a high proportion of lining material, and to bring material less often. In this way stimuli from the near-completed nest are instrumental in causing building to cease.

(vi) Although, in all species so far studied, the various constituent activities appear in individuals reared away from their parents and even away from the species-characteristic nest, learning may play an important role in nest construction. Thus the location of suitable sources of material must be learnt: Canaries kept without material learn to pull out their own feathers.

(vii) W.H. Thorpe has suggested that learning plays an essential role in the fine integration of the activities of nest building. Thus he suggests that, while building, the bird is responsive to stimuli similar to those

Crombec *Sylvietta brachyura* building nest. (*Photo: K. Carlson*).

which would be provided by a perfect nest; actions which make the existing structure approximate more closely to a finished nest are reinforced and thus repeated.

Existing evidence shows (*a*) that the performance of the constituent activities of nest building has some reinforcing value (e.g. the Canaries deprived of material, cited above, whose abnormal behaviour involved the movements of nest building but never led to the construction of a nest); (*b*) since the abnormal patterns seen in Canaries deprived of material do not appear in undeprived birds, it seems that the construction of the species-characteristic nest is learnt in preference to the mere performance of constituent activities which do not lead to a completed nest; (*c*) stimuli characteristic of the finished nest produce a decrease in building behaviour. All these points are in harmony with Thorpe's view, but experimental evidence in support of it is still lacking.

The hormonal basis of nest building probably differs between species. Oestrogens are primarily responsible in Canaries, but in some species androgens may be important (Noble and Wurm 1940). The behavioural effectiveness of a given hormone level may vary with external factors (Hinde and Steel). In many species there is a close link between nest building and courtship, and the peaks of nest building and copulation may coincide.

The nest is of obvious functional significance: the differences even between the nests of closely related species may be adaptive. Thus the nest form amongst West African weavers is more closely related to habitat than to systematic relationships, and each nest type has special protective functions in its environment (Crook). Some species decorate their nests; thus tits place fragments of torn leaves round the nest cup, and Starlings *Sturnus vulgaris* gather flowers; the significance of this is not understood.

Little is known of the evolution of nest building. It has been suggested that some of the shaping movements are derived from copulatory movements, and the collection of material from aggressive movements redirected on to grass stems, but there is no evidence to support these views. See also BEHAVIOUR, DEVELOPMENT OF. See photo ECTOPARASITE.

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NEST, COCK: term sometimes applied (also 'cock's nest') to extra nests or nest-like structures, not used for laying eggs, although the birds may roost in them. The male Wren *Troglodytes troglodytes* is well known to build as many as 8 of these unlined but otherwise substantial nests in a season. The female may choose one or more for lining and laying eggs in, sometimes in a subsequent year.

NEST FUNCTION: the common statement that a bird's nest is built to hold eggs does less than justice to its other functions. Among the thousands of species of birds there are many different types of nest: Collias (1964) and Goodfellow (1977) give good descriptive accounts of the range of nests built by birds. In the following discussion the word 'function' has been given a broader meaning than that adopted by some authorities, who would allow no functions for a bird's nest other than those of holding the eggs and chicks.

Protecting the eggs. Nests act to protect birds' eggs, both from environmental conditions and from predators. The temperature inside the nest of the Sociable Weaver *Philetairus socius* (see SPARROW-WEAVER AND SCALY-WEAVER) is as much as 23°C above the external temperature in winter in the Kalahari. Village Weavers *Ploceus cucullatus* spend less time incubating the eggs at high ambient temperatures than at low ones. Furthermore, the attentive periods of Village Weavers incubating in well-insulated nests are shorter than those of the same species incubating in less well-insulated nests. The Malleefowl *Leipoa ocellata* (see MEGAPODE) builds a nest that is also an incubator, a mound that not only passively protects the eggs from fluctuations in ambient temperatures, but one that is modified by the birds' behaviour to ensure that the two fluctuating heat sources, rotting vegetation and solar radiation, do not overheat the mound and that the heat lost to the environment does not cool it too much. The bird works daily to achieve a balance between these heating and cooling factors so that the temperature of that part of the mound where the eggs lie remains between 32° and 35°C throughout the 6 months when the eggs are in the nest.

Collias documents studies which indicate that some aspects of nesting behaviour and of the construction of birds' nests function to protect the nests, eggs and chicks from predation.

Stimulating the female. Experimental work has indicated an important stimulatory consequence of birds' nests, in addition to other, better documented, functions. Hinde (1967) and Hinde and Steel (1978) showed that, as the time of egg-laying approached in the domestic Canary *Serinus canaria*, the female's abdomen became increasingly sensitive to tactile stimuli (see NEST BUILDING). Further, they were able to show that ovulation could be induced by providing the birds with a nest of such shape that it fitted the female's body neatly and therefore stimulated her increasingly sensitive abdomen as much as possible. They concluded that the nest acted as an integrator of reproductive behaviour, especially as egg-laying approached, and that its structure was important in providing stimulation to the female which led to the secretion of secondary reproductive hormones, the development of the oviduct and ovulation itself.

Working in America with another species, the Ring (or Barbary) Dove *Streptopelia risoria*, Lehrman *et al* (1961) were able to show that egg-laying occurred faster in females given mates and nesting material than in those given mates but no nesting material. The significance of these experimental results may provide the key to understanding the bewildering variety of types of nests and at the same time offer an explanation of the frequency with which false nests are built before egg-laying, the considerable time spent by females of some species sitting in nests for some days before an egg is laid, the very small size of some nests compared with the size of the brood they eventually need to protect, and the structural differences between nests built before laying and those built or reconstructed at laying.

Hinde and Steel reported that male Canaries were less likely to sing when the female was engaged in nest-building than when she was not. Davies (1974) in a study of the Ring Dove concluded that much of the male's display and calling led to seating the female in a nest or potential nest site, and that once she was sitting on the nest, calling and display ceased. Unless it was crucial for the male to draw the female to the nest, it seems puzzling to risk directing the attention of predators to the nest even before the lengthy incubation period started. Davies suggested that the male had made a major contribution to the success of the breeding attempt if he got the female to sit in a nest, and thereby to receive tactile stimulation on her abdomen that would lead to rapid ovulation.

Skutch (1961) has reviewed the use made by birds of nests as roosting sites. He lists 79 species in which he found evidence of this behaviour, and it is now possible to add many more.

In Skutch's study of roosting, the nests of some species were specially built to serve as roosts and in others the birds used old breeding nests, but in some species the birds used the nest for roosting only during the period shortly before the eggs were laid in it, and then, especially those in which only the female roosted, the nest may have been acting to stimulate her to ovulate as well as acting as a roosting site.

Although this interpretation ought not to be generalized uncritically to apply to all species, nests have been reported to be regularly used as the focus of courtship by 43 species from 26 families, indicating that their nests may have an important function in the pre-egg-laying phase of the breeding cycle as well as in the protection of eggs and young. In a number of species one of the ritual displays given before egg-laying directs the attention of the female to a nest or potential nest site, and it is interesting to note that males of 349 species from 66 families have been observed to assist with nest-building, even if they take little other part in the parental care of their offspring.

The use of the nest in courtship and the male's assistance with nest-building are more conspicuous in some avian families than in others. In the Anhingidae, Ardeidae, Ciconiidae, Columbidae, Diomedeidae, Fregatidae, Pelecanidae, Procellariidae, Scolopacidae, Spheniscidae, Sulidae and Threskiornithidae the use of the nest as a focus of courtship is probably widespread, although it has been documented in only one or two species of each.

In most of these families, as well as the Accipitridae, Gaviidae and Picidae, the male is the principal nest-builder, especially in the early part of the breeding cycle. The use of the nest in courtship is probably less common in the passerines but is widespread in the Paridae, Ploceidae and Tyrannidae. On the other hand in 156 species from 24 families of passerines the male has been recorded assisting the nest-building, sometimes taking a major role, as in the Corvidae, Emberizidae, Icteridae, Parulidae, Troglodytidae and Tyrannidae, so that his interest in the nest during the courtship period is manifest. The involvement of the male in nest-building among the passerines has recently been reviewed by Verner and Wilson (1969) who conclude that males of most North American species assist with nest-building.

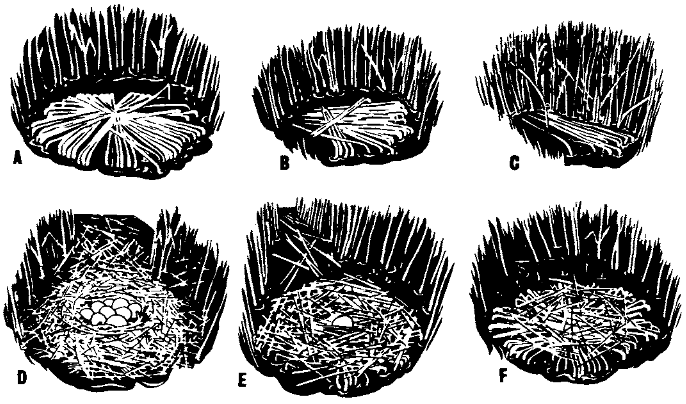

Fig. 1. Various nests of Magpie Geese *Anseranas semipalmata*, showing **A–C** roosting and courting forms, and **D–F** after egg laying.

Magpie Geese *Anseranas semipalmata* (see DUCK) illustrate the multiple role of birds' nests well. They build many, increasingly complex nests before egg-laying (Fig. 1) (Davies 1962). The convex types are used for roosting and courting. When the first egg is laid on one of these, uprooted vegetation is dragged onto it and it is converted into a concave cup which contains the eggs securely. Males undertake twice as much of the nest-building as the females in this species.

Many species are known to build and sit on false nests before egg-laying occurs, but the behaviour is well documented in the Magpie Goose. Brockway (1969) has described the behaviour of captive Budgerigars *Melopsittacus undulatus* in detail. She has shown that females enter the nestbox in response to a male giving the soft warble call and interprets this to mean that the call itself stimulates the female to ovulate. But if the sojourn of the female in the nestbox stimulates her to ovulate, the sequence of behaviour is then analogous to that of the male and female Barbary Dove described above.

Bowerbirds. If the nest is such an important part of the male's contribution to the breeding success, then the BOWERBIRDS present a particularly interesting case. The males build and attend a bower, a nest (in the widest sense of the word) which is never used as an egg nest at all. The bower can be viewed as a supranormal nest built by the male to stimulate the female to ovulate and accept copulation. The bower itself, of the avenue builders at least, is nest-like in structure, and careful study of the nests of the Satin *Ptilonorhynchus violaceus* and Spotted *Chlamydera maculata* Bowerbirds shows them to have flimsy bower-like walls. Many of the objects collected by the birds to decorate the bowers match the colours of the species' eggs and may therefore add to the effect of the bower as a supranormal nest.

Summary. The nests of birds hold the eggs and shelter them from some environmental hazards; they protect eggs, young and parents from predators; they serve as roosts and they act to co-ordinate the behaviour and physiology of the birds before egg-laying. The structure which is the characteristic nest of each species will represent a compromise that best serves each of these functions without damaging its usefulness in fulfilling the others. S.J.J.F.D.

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NESTING ASSOCIATIONS: the term includes all instances of one bird species often or habitually placing its nests singly or in colonies near those of other species or near habitations or structures of other living organisms. In many cases, these associations may be regarded as true symbioses. Excluded here are instances of organisms, usually insect larvae, which often are found in birds' nests.

The following types of associations have been described.

With other birds. A. Monospecific aggregations, or mixed species colonies of two or more often related species, e.g. gulls and terns, herons, icterids (see ORIOLE (2)), weaverbirds (Ploceidae).

B. One species nesting, singly or in scattered pairs, among pure or mixed colonies of other birds, e.g. Long-tailed Duck or Oldsquaw *Clangula hyemalis* and Sabine's Gull *Xema sabini* in colonies of the aggressive Arctic Tern *Sterna paradisaea*; the Turnstone *Arenaria interpres* among gulls and terns, and the Black-necked Grebe *Podiceps nigricollis* moving its nests with the yearly movements of Black-headed Gulls *Larus ridibundus*.

C. Groups of non-aggressive species near nest site of an aggressive, usually raptorial species, e.g. Starlings *Sturnus vulgaris* and House Sparrows *Passer domesticus* breeding on the fringes of the nest of an Imperial Eagle, *Aquila heliaca*, many African weavers building near a Black Kite *Milvus migrans* or a Marabou Stork *Leptoptilus crumeniferus* nest; species of tundra-breeding birds like geese (Anatidae) and waders (Scolopacidae) nesting with Snowy Owls *Nyctea scandiaca* and auks with Peregrines *Falco peregrinus*.

D. Single pairs of different species, e.g. Redshanks *Tringa totanus* near the alarm-giving Lapwing *Vanellus vanellus*; Yellow Warbler *Dendroica petechia* near aggressive Red-winged Blackbirds *Agelaius phoeniceus* or the Grey Catbird *Dumetella carolinensis*, both of which repel the brood-parasite, the Brown-headed Cowbird *Molothrus ater*.

E. Two bird species in the same nest, as in BROOD-PARASITISM, which is normally considered disadvantageous to the host species; but at least one species association, that of the Giant Cowbird *Scaphidura oryzivora*, a parasitic icterid and its icterid hosts, results under certain conditions in a peculiar symbiosis in which nests having one host chick and one cowbird have better host fledging success than nests having one or two host chicks but no cowbirds.

Only 13% of all birds are colonial nesters, but 93% of all marine birds nest in colonies, often mixed. Monospecific coloniality usually, but not always, evolves when a species exploits a food resource which is not defensible. This permits the evolution of nest aggregations. But the apparent converse does not always follow, i.e. even if food is defensible within a nest territory, coloniality may on occasion evolve, as in the marsh-dwelling blackbirds (Icteridae) of the New World.

The selective forces producing multispecies associations appear to be (1) nest site availability, (2) food availability and exploitation, and (3) predator pressure. In most associations, all three are involved to varying degrees. Aside from the aggressivity of the species involved, large numbers of birds simply nesting together can result in a swamping effect on predators. The earlier idea that some species are innately sociable is no longer tenable.

With insects. A. Nest cavity in structure made by insects, particularly both ground and arboreal termitaria. The habit is widespread, particularly in the tropics in trogons, puffbirds, kingfishers, jacamars; apparently habitual in the Buff-spotted Woodpecker *Campethera nivosa* of Africa and in the parrot genera *Aratinga* and *Brotogeris* in South America. In the cases involving some trogons, puffbirds, and parrots, the birds co-habit with the termites. The Neotropical White-tailed Trogon *Trogon viridis* habitually nests inside large nests of polybiine wasps. The wasps usually, but not always, desert their invaded nest. The woodpecker *Micropternus brachyurus* regularly nests in the spherical papier-maché-like nests of certain ants (*Crematogaster*) in South America.

B. Nesting near structures of stinging or biting social hymenoptera (wasps, bees, and ants), is widespread, particularly in the tropics in many passerine families e.g. Tyrannidae, Troglodytidae, Nectariniidae, Icteridae, Ploceidae, Fringillidae. Some raptors and storks also place their nests near aggressive ants or wasps.

With vertebrates. Birds have not formed strongly developed associations with many vertebrates other than that with man; some exceptions are:

A. The Water Thickknee *Burhinus vermiculatus* is said to place its nest near crocodile nests which are usually guarded by the female reptile, presumably against predators. Other associations consist of the use either by the bird or its associates of one or the other's burrows in the earth, e.g. the Tuatara lizard *Sphenodon punctatus* in the burrows of the New Zealand shearwaters, *Puffinus carneipes* and *P. bulleri*, the furnariid *Geositta cunicularia* nesting in the burrows of the Chinchillid rodent *Lagostomus maximus* in the Argentine pampas, and the Blue-and-White Swallow *Notiochelidon cyanoleuca* which in turn uses the abandoned nestholes of *Geositta*.

B. With man, commensalism is marked in several groups such as swallows (Hirundinidae) which use buildings as nest sites, storks (Ciconiidae), pigeons *Columba livia*, Jackdaws *Corvus monedula*, Rooks *Corvus frugilegus*, and various sparrows and weavers, especially *Passer* and *Ploceus*.

That one or more of the partners in most mixed associations is aggressive or offers efficient predator alarm argues that the antipredator function is a very strong selective component. That these associations are not more widespread also suggests that there are disadvantages as well. This has been documented in certain oropendolas and caciques (colonial-nesting Neotropical icterids), some species of which almost always nest in association with stinging wasps (*Protopolybia*, *Stelepolybia*, etc.) or stingless but biting bees (*Trigona*). Some species have colonies which traditionally associate with such insects and colonies which do not. A chief source of death in their chicks results from ectoparasitism by botflies (*Philornis* spp.). But colonies associated with wasps or bees suffer significantly less from botflies than do those without. The hymenoptera repel the flies in a manner which is not yet clear. Removal of the wasps and bees results in an almost immediate high incidence of botfly attacks. Similarly, colonies with wasps or bees suffer less from predation by opossums, toucans, and snakes (*Spilotes*, *Pseustes*) than do colonies which lack the hymenoptera. But because of apparent seasonal vicissitudes affecting the insects, colonies associating with wasps or bees have a short breeding season and but one chance per year to reproduce while those not associating have a relatively longer breeding period and may have two or three chances per year. An additional disadvantage is that branch breakage is common because of the weight of the bird nests surrounding the insect's nest. Oropendola and cacique nests in colonies lacking bees or wasps have a high incidence of brood-parasitism by the Giant Cowbird, with its advantages and disadvantages. The cowbird chick is fed by the host female and in turn eats ectoparasitic botfly larvae from the host's chick which results in lower mortality of the host chicks (see above). The oropendola chicks do not reciprocate. The advantage conferred by a single cowbird to its host sib is apparently lost in nests having 2 or more cowbird chicks because food competition between cowbird siblings is then involved. While the evolutionary advantages to this association may be clear, the proximate mechanisms are not. Oropendolas and caciques, or any bird that habitually associates with bees, ants, or wasps, are attacked, especially at the initiation of the association, but the Hymenoptera quickly habituate to them. Both visual and olfactory components may be involved. Many birds which habitually associate with stinging or biting Hymenoptera have a rather strong musty body odour, apparently lacking in close relatives which do not form such associations. The nature of this odour is unknown; naked chicks lack it and feathered adults possess it even after death. It is apparently not the same odour in different species—it is significant that almost all species in such associations build covered nests, presumably to cover the chicks from wasp or bee attacks. A current hypothesis is that the odour is not a repellent, but is rather a recognition signal promoting habituation in the aggressive insects. It must be emphasized that it is the birds which join the aggressive insects, not the reverse. However, docile wasps and bees often join the association after its initiation for much the same reasons as did birds. Lack of knowledge of the chronology and behaviour of these subsequent joiners has confused the issue of the evolutionary significance of the association. This is not to say that the aggressive insects do not receive an advantage. The birds often vigorously defend their colony site against anteaters (*Tamandua* spp.) which are enemies of stingless bees and against the caracaras *Daptrius ater* and *D. americanus* (Falconidae) which are enemies of both wasps and bees. The nesting associations here described do not confer equal advantages to all the partners nor complete protection to any. But that they do so more often than not, on the average, is the reason for their existence. (S.M.) N.G.S.

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NESTING BASKET: see NEST SITES, MAN-MADE.

NESTLING: see under YOUNG BIRD.

NESTORINAE: see PARROT.

NEST PARASITISM: see BROOD-PARASITISM.

NEST RECORDING: the central collection of avian breeding information by voluntary contributors using standardized recording cards. The accumulation of sufficient cards allows the analysis of particular aspects of breeding in different years, habitats and geographical regions.

History. The idea of a central collection of cards containing breeding data came from Sir Julian Huxley after his analysis of the detailed nest histories of the birds using nestboxes erected at Whipsnade Zoological Park, Bedfordshire, England in 1936. With J. Fisher, Huxley designed recording cards for the Hatching and Fledging Inquiry, as it was then called, and these were distributed to members of the British Trust for Ornithology in 1939. Observers were asked to concentrate on certain common species and the principal object of the Inquiry was to collect data on incubation and fledging periods, as well as clutch sizes of British birds.

In the first year some 600 cards were returned and this total doubled in 1948 when the present name Nest Records Scheme was adopted and a new recording card design used. During the 10 years 1970–1980 the annual intake rose to between 22,000 and 30,000 cards. The first full time organizer of the BTO Nest Records Scheme was appointed in March 1960 following the award of a grant from the Nature Conservancy.

A number of countries have started nest record schemes based on the original BTO format. Among the earliest were the USA and Canada, Germany, Switzerland and Finland by 1948, South Africa by 1951 and New Zealand by 1959. Many European countries now have schemes operating, including Belgium, Czechoslovakia, Denmark, Hungary, Iceland, the Netherlands, Italy, Spain and Sweden, while further afield schemes have been started in Australia, Zambia and Zimbabwe.

Objects. The objects of nest recording are to collect as complete a picture of the nesting cycle of the bird as possible by utilizing the often incomplete nest histories recorded by amateur birdwatchers, so amassing breeding information impossible to collect in any other way except at immense cost. Each card on its own tells very little but when several thousand are available for analysis the sample containing useful information becomes meaningful.

The card is designed so that one half contains boxes which give information on the species, observer, year, geographical locality, altitude, habitat, nest site and height of nest above ground. The other half of the card enables the observer to complete one line for each visit made to the nest, giving the date, time, number of eggs and/or young and a brief note on the observation if necessary: for example, whether eggs are warm or cold, female or male sitting and age of young. There is also a space for evidence of the success or failure of the nest. In the case of colonial species, special colony sheets may be provided.

The value of nest record cards is that they provide, in the case of common species, large annual samples coming from a wide geographical area and selection of habitats. Many birdwatchers are naturally interested in looking for nests and a lot of potentially useful information would be lost in individual notebooks if no standardized recording scheme existed.

The most important information which the observers record is the date on which the first egg was laid, clutch size, number of eggs hatched and number of young reaching an advanced stage such that there is a good likelihood of their leaving the nest successfully. To record these it is unnecessary and undesirable to visit the nest every day and observers are encouraged to plan their visits to collect the maximum amount of information with the minimum of disturbance.

Uses of the data. The nest record cards provide data on the basic breeding biology of each species. The main parameters that can be extracted are those for laying dates, clutch size and breeding success. If sufficient records are available, the effects of weather, habitat, latitude and altitude can be determined. Some nest record schemes now use computer facilities for the input of annual samples of cards for selected species so that any marked effect on breeding performance caused by environmental changes, such as the introduction of new agricultural chemicals, can be detected.

Certain types of bias are inherent in the nest record data and the analyst needs to be aware of them. Observers tend to search more vigorously early in the breeding season (in Britain) when the vegetation cover is least dense and nests are easier to find. The recording of nesting success has two main types of bias. Firstly, it is much easier to record a failure than a success and, secondly, nests found at later stages of the nesting cycle are biased towards success. Therefore various methods of analysing the data have been devised to eliminate as much of these biases as possible. R.A.M.

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NEST SANITATION: see PARENTAL CARE.

NEST SCRAPE: a small hollow excavated by a bird in soil, sand or shingle and which it may line with pieces of grass or similar material.

NEST SITE SELECTION: an aspect of behaviour the study of which involves such considerations as the season when birds select their nest sites, the interval between nest site selection and the start of building, the share of the sexes, and the factors that may influence birds in selecting nest sites. For the variety of sites used see NEST. In some species the availability of nest sites may be a critical factor in habitat selection (see HABITAT and TERRITORY).

The selection procedure

Time. Although the nest site is generally selected shortly before breeding, birds may also show interest in such sites in the preceeding autumn (as some birds of prey) or even several years before breeding (as the Fulmar *Fulmarus glacialis*). Mild spells in late winter can initiate song, courtship, and even nest site selection, in species that will not begin to build until several weeks later. There is thus often an appreciable interval between selection and building, from several weeks or months down to a day or less. A bird that has lost an early nest, or is proceeding to a second brood, may condense its nest site selection and building time in the urgency to breed. The pre-laying period is also short at high latitudes where the spring and summer seasons are short. In Norway the spring arrival time of the Brambling *Fringilla montifringilla* is about 3 weeks after the Chaffinch *F. coelebs*, but the onset of nest building is only separated by a few days in areas in which the two species breed sympatrically. Perhaps species with a more southern distribution, like the Chaffinch, have a long pre-building period in order to obtain an optimal territory in the more crowded southern areas, and also in order to locate suitable and well-hidden nest sites. Nest predation is more severe at low latitudes.

Shares of sexes. A survey of some 170 representative British breeding species (C. and D. Nethersole-Thompson 1943, 1944) included none in which the male and about 30 in which the female normally takes sole charge in nest site selection; in the remaining species both sexes participate, with males taking the initiative rather less often than females. This pattern is repeated in most orders of birds, although in the Anatidae and Galliformes the males evidently take little or no active part.

In some species (as in the *Sylvia* warblers) the male arrives before the female and builds several uncompleted nests, so that the female later on can choose which of them she prefers. The male Pied Flycatcher *Ficedula hypoleuca* also arrives before the female and defends a nest hole which the

Galahs *Cacatua roseicapilla* looking out of nest hole. (*Photo: J. Warham*).

female, in turn, may accept. The suggestion, based on observations at other stages in the breeding cycle, that in species in which the males take the initiative they are more brightly plumaged than the females, seems not to hold for males taking an active part in nest site selection, e.g. it holds for the Pied Flycatcher but not for the *Sylvia* warblers.

Titmice. In general, the bird's routine tends to be elaborate in species with special requirements, as in tits. They mostly nest in holes and may frequently be seen inspecting the holes from September to April, most actively just before nest building in spring, but also exhibiting a lesser peak of activity in October and November. Since tits also roost in holes in winter, their activity in autumn could equally be roost site selection; but as winter roosts are often used later for breeding, this distinction may be unimportant (see ROOSTING). In spring, hole inspection is most frequent in the morning and tails off markedly in mid-afternoon. Tits commonly deposit nest material in several holes before eventually lining and laying in one of them. In a typical hole inspection by the Great Tit *Parus major*, the male flies to the hole, leaving the female near by, and peers inside, turning his head sideways to display the white cheeks; he may also tap at the entrance. If the female responds by approaching the hole, she shivers her wings, increasingly the nearer she comes, and then normally enters the hole, sometimes preceded by the male; she may remain inside for a few minutes. If the female does not respond, the male usually returns to her and repeats the performance at the same or another hole. Thus he suggests a number of sites to the female, one of which she is likely to accept.

Fairy Tern *Gygis alba* egg in site on branch. (*Photo: N. van Swelm*).

Gulls and waders. Contrasting with the elaborate routine of many hole-nesting species is the nest site selection of gulls and waders (Charadrii). The male and female Herring Gull *Larus argentatus* indulge in frequent preliminaries to nest building, moving from one possible site to another. The final selection and beginning of an actual nest at one or other of the sites seems quite haphazard. In the Red-necked Phalarope *Phalaropus lobatus* both sexes together spend several days making scrapes in the soil more or less at random. Then, about an hour before laying, the female revisits many of the scrapes and apparently lays in whichever scrape she happens to be at when the egg appears. There are exceptions, of course, to this seemingly casual pattern, such as in the Greenshank *Tringa nebularia*, which prefers to nest close to some small landmark such as a log or large stone in the otherwise rather featureless landscape (C. and D. Nethersole-Thompson).

Nuthatch *Sitta europaea* at nest hole, reduced by mud plaster. (*Photo: E.J. Hosking*).

Open-nesting song-birds. Nest site selection by the majority of these comes somewhere between the elaborate procedure of the hole-nesters and the casual choice of most gulls and waders. In Scottish Crossbills *Loxia scotica*, for example, the nest site is usually chosen in a distinctive tour by both sexes, during which the female broods in various crotches; this is accompanied by frequent snatches of such irrelevant behaviour as bill-wiping, 'false feeding', and preening (see DISPLACEMENT ACTIVITY). The final choice of site is the female's.

Survival value.

Nest predation. Birds prefer to nest in sites which are not easily accessible to predators, e.g. holes, on cliffs, and on small islands. Certain tropical birds nest in close association with wasps' nests; and Bramblings often nest in colonies of Fieldfares *Turdus pilaris*, which are especially active in defence of their nesting area, and Tufted Ducks *Aythya fuligula* in mixed colonies of terns and gulls (see NESTING ASSOCIATION). The Redwing *Turdus iliacus* builds its nest higher up in trees and bushes early in the season before the vegetation develops than later on, probably in order to reduce nest predation.

Cover. Birds select sites which provide shelter against rain, wind, and sunshine. The White-crowned Sparrow *Zonotrichia leucophrys* builds its nest above the ground in those years when there is a lot of snow.

Competition. Competition for nest sites is generally keenest among birds with specialized requirements; in the Swift *Apus apus*, for example, exceptionally prolonged struggles for the possession of nestboxes have been described. Competition between members of the same species may be, to some extent, avoided by the territorial systems of some birds. Competition for nesting space is especially marked in densely colonial species, e.g. among seabirds, each species demanding a special type of ledge or other support for its nest, the presence of which may govern the birds' local distribution in the breeding season.

Building effort. Purple Martins *Progne subis* prefer apartments which have not been cleaned out after a previous occupancy. In open-nesting species the same nest may sometimes be used for subsequent nestings, within the same season (as in the Blackbird *Turdus merula*) and in successive years (as in the Fieldfare). This habit is rather unusual among song-birds, but is the rule among many birds-of-prey. Eyries of the Golden Eagle *Aquila chrysaetos* may be occupied (by succeeding generations) for centuries, although the birds often ring the changes on two or more alternative sites. By using an old nest as a basis, less energy is needed in building. An old nest may also be an indication of a safe site: the nest is not likely to fall down. For such species the breeding population size may occasionally be increased by providing artificial nest sites (as for the Osprey *Pandion haliaetus*). The Green Sandpiper *Tringa ochropus* is remarkable among waders for laying in old nests, mostly of the Song Thrush *Turdus philomelos*. Some birds appropriate freshly completed or occupied nests of other species; thus the House Sparrow *Passer domesticus* habitually evicts the House Martin *Delichon urbica*; and a pair of the American Parasitic Flycatcher *Legatus leucophalus* sometimes causes the rightful owners of several occupied nests to desert before settling on one of them. Nest appropriation has evolved independently in a number of different groups of birds throughout the world; it has perhaps reached its most refined form in wholly parasitic species such as the Cuckoo *Cuculus canorus* (see BROOD-PARASITISM).

Food. Nests are placed at convenient sites according to the food resources. For example, Great Tits collect food closer to the ground than Blue Tits *Parus caeruleus*, and also prefer lower nest sites. Species which defend a feeding range often build the nest at the centre of the territory.

See photo COLONIALITY. (J.A.G.) T.S.

Jackson, J.A. & Tate, J. Jr. 1974. An analysis of nest box use by purple martins, house sparrows and starlings in eastern North America. Wilson Bull. 86: 435–439.

Nethersole-Thompson, C. & D. 1943–44. Nest-site selection by birds. Brit. Birds 37: 88–94, 108–113.

NEST SITES, MAN-MADE: a wide range of types of artificial structures designed to attract and provide safe nesting places for birds. Most are nest 'boxes' suitable for species normally breeding in holes and cavities; others include ledges, excavated holes, artificial islands, floating platforms and the rearrangement of natural vegetation. The nestbox derives originally from the clay flasks first recorded in the late Middle Ages in Holland—they can be seen in F. van Valkenborch's Kirchmessfest (1597)—and from wooden cistulae (flasks) used in Silesia. Both were utilitarian: the first broods of sparrows *Passer* spp. and Starlings *Sturnus vulgaris* hatched in them were taken for food; so were the eggs of the Goldeneye *Bucephala clangula* 'farmed' in Lapland, at first by means of improved natural sites and later in boxes. (In recent years colonization of Scotland by this species has been largely effected by the provision of nestboxes.) In 1782 Gilbert White recorded that his brother had nailed up several large scallop shells under the eaves of his house in South Lambeth, London, and that they were immediately occupied by House Martins *Delichon urbica*, but Charles Waterton, the early 19th century Yorkshire squire, is believed to have been the first naturalist to put up numbers of boxes simply to encourage birds, and their use for this purpose developed during the century; by 1897 J.R.B. Masefield knew of 20 species that had occupied boxes or artificial platforms in Britain. Nestboxes were first applied on a large scale to attract and increase the numbers of 'beneficial' insectivorous birds in forests by Baron von Berlepsch in Germany; by about 1905 all the 300 boxes in his park, and 90% of some 2,000 boxes in his woods, were occupied by birds of 14 different species. Soon afterwards it was realized that whole populations of certain species could be induced to use nestboxes if enough were provided, and could thus be studied in many aspects of their population structure. Pioneer studies were those of S.P. Baldwin and W.W. Bowen on the House Wren *Troglodytes aedon* in the USA, begun in 1915, and of K. Wolda and his associates on the Great Tit *Parus major* in Holland, begun in 1920. But the species most suited to nestbox studies is probably the Pied Flycatcher *Ficedula hypoleuca*; since L. von Haartman began work on it in Finland in 1941, populations have been 'emboxed' in all the European countries where it breeds commonly, and tens of thousands of birds have been ringed.

The 19th century nestbox was made of wood, with a round entrance hole and a fixed lid, and was designed primarily to attract tits, Nuthatches *Sitta europaea*, redstarts *Phoenicurus* spp. and Pied Flycatchers. Von Berlepsch favoured a hollowed-out section of log, resembling as closely as possible the nest-hole of the Great Spotted Woodpecker *Dendrocopos major* which these small birds were accustomed to use under natural conditions. It has since been found, however, that the shape and external appearance of the box matter very little and that those made of planed boards are quite as effective as 'rustic' boxes with bark-covered sides. Certain rules nevertheless govern the correct construction and maintenance of safe and durable nestboxes and these have been described in a field guide published by the British Trust for Ornithology. For example, the entrance hole should be sufficiently high up the side or front panels of the box to make it hard for larger predators to reach the contents of the nest; the roof or lid should overlap the sides to keep off raindrops; and there should be no perches or ledges on which predators can get a grip.

Towards the middle of the 20th century nestboxes in materials other than wood were developed; plastics, cement and sawdust, cement bricks, hardboard, and tin all found advocates. Their advantage over wood lies in superior resistance to weather and to attacks by squirrels and Great Spotted Woodpeckers which became increasingly a nuisance in Britain in the 1950s. Their disadvantages include expense, brittleness, liability to overheating in exposed sites, excessive condensation, and in some instances weight. The Russians have experimented with bottle gourds as the cheapest form of artificial nest cavity; but it is apparently not possible to inspect the contents.

Nestboxes should normally be sited on the side of a tree or wall away from the hottest sun. H.N. Kluijver pointed out that on trees in western Europe this makes them vulnerable to the maximum flow of water after a rainstorm, but some compromise position can usually be found. In woods the main consideration is to site boxes away from twigs and branches which can be used by predators; an open approach for the nesting bird is also important. Provided that they are securely attached to a trunk or branch, nestboxes need not be rigid; in closed canopy woodland they can be fixed to branch snags by a wire loop and lifted down by the loop for inspection. In Britain, the Nature Conservancy Council conducted an experiment to find out the height preferred by small birds using nestboxes, but the results after 5 years were inconclusive; it seems probable that most species have little or no preference. However, boxes in most localities have to be sited at least 3 m above the ground to avoid human damage.

Ideally, a nestbox should have a fixed roof and open at the front for inspection; but where it is desired to catch the parent birds in the box for ringing and examination, a movable lid is preferable. Various devices have been developed for retaining adult birds in the box, from small external spring nets to internal treadles that release a shutter. In Britain, J.A. Gibb adapted the automatic swinging door used by racing pigeon owners in their lofts. This was followed by non-automatic shutters remotely operated by means of a fishing line passing under the lid and over the side of the box; J.H. Jenkins and P.A. Banks were responsible for ingenious variations of this idea. After capture in the box, the birds are most easily removed through a detachable version of the sleeve used in the catching boxes of Heligoland and other large traps (see TRAPPING).

The traditional design of nestbox has been adapted to attract various species: there have been boxes with narrow entrances and with entrances at the back, both intended for treecreepers *Certhia* spp.; multiple boxes for the Purple Martin *Progne subis*; boxes filled with wood chippings, sawdust, balsa wood or polystyrene blocks for birds like Chickadees *Parus atricapillus*, Willow Tit *P. montanus* and Great Spotted Woodpecker to excavate. D. Lack evolved elongated boxes with holes opening downward to embox a colony of Swifts *Apus apus*; others have taken this idea further to counterfeit the burrows of Sand Martins *Riparia riparia*, Wheatear *Oenanthe oenanthe* and Madeiran Petrels *Oceanodroma castro*; while artificial nests for Swallows *Hirundo rustica* and House Martin *Delichon urbica* have been successful in Switzerland and Britain. Removal of half the front panel converts the traditional nestbox into a covered tray or ledge suitable for Spotted Flycatchers *Muscicapa striata*, Robins *Erithacus rubecula*, and many other species. By increasing the size, owls, Kestrels *Falco tinnunculus*, Jackdaws *Corvus monedula*, Stock Doves *Columba oenas*, and ducks can be attracted. For the Tawny Owl *Strix aluco* a quite distinct chimney design was used most successfully by H.N. Southern, who slung it by wire bands under an upward sloping bough; an inspection mirror was fastened to the mouth of the chimney and a perforated floor allowed drainage. Similar but narrower boxes slung from horizontal boughs are attractive to Little Owls *Athene noctua*.

As well as nestboxes and their obvious derivatives, many other artificial means have been used to encourage nesting; the cart-wheels or platforms put up on houses in Holland and elsewhere for the White Stork *Ciconia ciconia* are one of the oldest devices and have been copied in the USA to attract Ospreys *Pandion haliaetus*. Woven baskets for Mallards *Anas platyrhynchos* are another Dutch idea, while in Iceland stone 'houses' are built for Eiders *Somateria mollissima*. Egg collectors used to 'farm' Greenshanks *Tringa nebularia* in Scotland by providing ideal nest sites for them, and other ground-nesting birds have been catered for in the same way. Von Berlepsch suggested tying twigs together to make better than natural forks for bush-nesting birds, 'nesting substrates' have been used by several species in America, and man-made stick nests taken by Long-eared Owls *Asio otus* in woods devoid of the old nest platforms of other large birds. The creation of bare ground patches or tunnels in dense ground vegetation have provided suitable nest sites for Nightjar *Caprimulgus europaeus* and Shelduck *Tadorna tadorna* respectively. More elaborately, artificial banks have been built up, in which Kingfishers *Alcedo atthis* were attracted to burrow.

The main development of the nestbox up to the middle of the 20th century took place in Europe and North America, although it was still not proved that large numbers of boxes did more than concentrate the birds using them. For example, in the Forest of Dean (Gloucestershire, England) as many as 189 out of 200 nestboxes spread over 24 ha were occupied in 1949; but no control data are available for the area before boxes were first put up there in 1942. In Russia, large-scale attempts to attract birds to forests involved over 10,000 nestboxes in 9 areas in 1953; they were occupied by nearly 4,000 pairs of 18 species. Partially successful attempts were also made to transfer both adults and nestlings to newly afforested areas. Foresters in India began putting up boxes in the 1950s, but the great variety of tropical species nesting in holes and cavities offer further opportunities for nestbox techniques. Water bodies such as reservoirs and gravel-pits which lack natural nesting places like graded banks, spits and small islands can be improved through the creation of rafts and raised islands providing nesting places for grebes, ducks and geese, waders, gulls, terns, rails, even passerines like the Reed Bunting *Emberiza schoeniclus*.

See photo CONSERVATION. B.C. and D.E.G.

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NETTING: see TRAPPING.

NEUTRAL CATEGORIES: in taxonomy, categories that can be used as terms without commitment to a view of the status of the subject matter, e.g. FORM; GROUP; COMPLEX.

NEW GUINEA SUBREGION: see AUSTRALASIAN REGION.

NEWTONIA: substantive name of the 4 species of *Newtonia*, a genus of flycatchers endemic to Madagascar (for family see FLYCATCHER (1)).

NEW ZEALAND SUBREGION: a division of the Australasian Region, but by some zoogeographers regarded as a separate minor region (see AUSTRALASIAN REGION; DISTRIBUTION, GEOGRAPHICAL).

NICATOR: substantive name of the 2 species of *Nicator*, an African genus formerly placed in the shrike family but now considered to be closer to the BULBULS.

NICHE: a term, often used loosely, referring to the ecological role that a species plays within a community; or, more rigorously, to the full range of environmental conditions within which it can survive. See ECOLOGY.

NICHE EXPANSION: an increase in the places where a population will breed or feed, or an increase in the kinds of food members of the population will eat. Niche expansion is most often discussed in the context of a change in the feeding ecology of a population of one species in the absence of one or more species with which it normally competes. The population may then be able to exploit a food resource or a feeding site previously used by the competitor. DENSITY COMPENSATION is a likely consequence of niche expansion.

Niche expansion may also happen in the absence of any change in the competitive environment, when a population learns to exploit a new food resource or nesting site.

NICTITATING MEMBRANE: a transparent fold of skin, present in birds, which can be drawn across the eye to form a third eyelid (see VISION).

NIDICOLOUS: young birds that remain in the nest after hatching. See YOUNG BIRD.

NIDIFUGOUS: young birds that leave the nest immediately or soon after hatching. See YOUNG BIRD.

NIGHTHAWK: substantive name of various New World species of Caprimulgidae; in the plural, general term for the subfamily Chordeilinae (see NIGHTJAR).

NIGHTINGALE: substantive name of some *Luscinia* spp.; used without qualification, in Britain, for *L. megarhynchos* (see under THRUSH). See photo VOCALIZATION.

NIGHTJAR: substantive name of the Old World species of Caprimulgidae (Caprimulgiformes, suborder Caprimulgi); in the plural, a general term for the family, but American usage prefers 'goatsuckers and nighthawks'; some species have special names derived from the calls.

About 70 species are known, generally grouped in 18 genera. On the basis of anatomical differences the family can be divided into 2 subfamilies, the Chordeilinae (nighthawks) and the Caprimulginae (goatsuckers).

Characterstics. Nightjars are mainly 16–41 cm long, up to 78 cm in a few species with greatly elongated tail feathers. The plumage is soft and is buffish, rufous, greyish, or nearly black. The upper parts are in general strongly mottled and vermiculated; the under parts are mostly barred or spotted and often with white patches on chin and throat, on the wings and on the tips of the tail feathers. In some species both a grey and a more rufous phase occur (see POLYMORPHISM). The sexes are normally somewhat different in colour. The tail is rather long; the wings are long and pointed; and the flight is silent and easy. The skull is flattened, with the bill short and weak. The gape, which is extremely wide, and in most species provided with strong bristles, enables the bird to catch insects (the main food) during flight. The eyes are large. The feet are commonly very short, with a feathered tarsus in some species; the toes are small, the middle toe possessing a pectinated claw.

Most species are crepuscular or nocturnal in habit. During the day the birds lie up closely and are difficult to detect owing to their cryptic coloration. Normally the birds perch on the ground or lengthwise on a branch.

Habitat. Some species frequent desert areas, others are inhabitants of open spaces in wooded districts, and some of forests.

Distribution and movements. This homogeneous family has a nearly world-wide distribution, but it is not represented in the most northern parts of America and Eurasia, in southern South America, or in New Zealand and many oceanic islands. The North Temperate Zone species migrate southwards for the winter.

Food. Insects are the main food of all nightjars.

Breeding. Generally no nest is made, the eggs being laid on the bare ground. These number 1 or 2, rarely 3. They are white to pinkish buff, beautifully marbled or blotched with black, brown or violet. Both parents incubate and care for the young, which are nidicolous and covered with protective (buff or greyish) down.

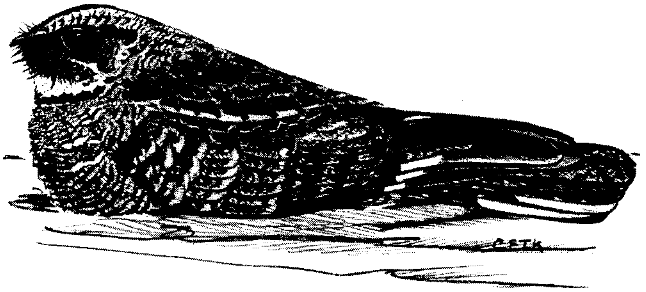
Chordeilinae. The nighthawks are restricted to the New World; the species lack rictal bristles. In North America the Common Nighthawk *Chordeiles minor* and the very similar Lesser Nighthawk *C. acutipennis* are well-known representatives. The first frequents open country or forest borders and is also found in the Greater Antilles; the latter, which is somewhat smaller and darker, ranges also over the greater part of tropical South America and is an inhabitant of desert areas or open sandy savannas. In both species the males are slightly larger than the females, and they have a white wing-patch and a subterminal tail-bar that are absent or smaller in the other sex. Both species are known to breed sometimes on the flat roofs of houses. The Lesser Nighthawk prefers to roost on the horizontal branches of low bushes.

Other species are the white-bellied Sand-coloured Nighthawk *C. rupestris* and the small Least Nighthawk *C. pusillus*. Both are distributed in the northern part of South America. The remaining 3 genera, which are monotypic, are likewise found in South America. The Nacunda Nighthawk *Podager nacunda* has a white belly and throat-patch, rather long unfeathered tarsi, and a melancholy voice; it is an inhabitant of the savannas and is known to migrate northwards.

Caprimulginae. More than half of the known species in the whole family belong to the typical genus *Caprimulgus*, of which many species are rather alike in plumage. The European Nightjar *Caprimulgus europaeus* is found from Great Britain and northern Africa far into Asia, and in winter migrants reach South Africa; the 'churring' or jarring note is the origin of the name. In eastern Asia the related Jungle Nightjar *C. indicus* occurs, and it is also distributed over India, in winter reaching the Greater Sunda Islands; the males differ from the European Nightjar in having subterminal white spots on the outer 4 pairs of tail feathers instead of on the outer 3 only. In the same area, from India and southern China through Indonesia to northern Australia, the Large-tailed Nightjar *C. macrurus* is widely distributed; it is distinguished from *C. europaeus* by the fact that the 4, instead of the 3 outer primaries show a white spot. In southern Europe and the western parts of North Africa, the Red-necked Nightjar *C. ruficollis*, with a yellow-rufous collar, is found. The paler and sandier coloured Egyptian Nightjar *C. aegyptius* inhabits the desert areas of south-western Asia and northern Africa. Different species occur in Africa, but the habits of many are not yet very well known, although mostly these seem not to differ greatly from those of the other members of the family. Some perform regular intertropical migrations (see MIGRATION). Some species, such as the Fiery-necked Nightjar *C. fervidus*, inhabiting the southern part of Africa, hunt from a fixed perch during the night instead of hawking over longer distances as do most of the other species. Different types of churring sounds are made by various species, while others have whistling calls.

North American representatives include the Whip-poor-will *Caprimulgus vociferus*, ranging from northern North America to well into Middle America; the closely related *C. noctitherus* from Puerto Rico had long been regarded as extinct, but has recently been rediscovered. Another species named from the call is the Chuck-will's-widow *C. carolinensis*; it is a somewhat larger species frequenting wooded marshes and rocky hills in the western parts of the United States and wintering in the West Indies and Middle America. Other species inhabit South America, such as the beautiful Cayenne Nightjar *C. cayennensis* with throat white, and sides of face and abdomen and the lateral tail feathers mainly white; another is the Dark Nightjar *C. nigrescens*, also found in northern South America.

The species of the genus *Eurostopodus* are distributed from south-eastern Asia through the Philippine and Indonesian archipelagoes to Australia. They lack the rictal bristles and have ear-tufts. Most species are rather large and dark, showing much black and dark brown but with a white throat-patch.



Large-tailed Nightjar *Caprimulgus macrurus*. (*C.E.T.K.*).

The White-necked Nighthawk *Nyctidromus albicollis* is an inhabitant of Middle and South America; it breeds under the cover of bushes, and the eggs are deposited on a thick layer of dead leaves. The Common Poorwill *Phalaenoptilus nuttallii* is a rather small species with a relatively short tail, occurring in North America. In winter birds of this species hibernate in rock niches and may return to the same hole every winter. During this winter dormancy the birds remain in a state of torpidity with an exceedingly low body temperature, 18°–19°C (64°–66°F) as against 40°–41°C (104°–106°F) normally (see TORPIDITY).

In some species the males show a remarkable elongation of certain feathers of wings or tail. In middle Africa the Standard-winged Nightjar *Macrodipteryx longipennis* is found; it is a rather dark species, in which the males have, during the breeding season, the shaft of the second primary (numbered from inside) greatly elongated, with the terminal portion vaned. In courtship the male flies very slowly, with wings stiffly bowed and vibrating, low over or around the female, with its standards held straight up above the wing and the shaft and terminal vane vibrating with the wing. In the southern part of Africa occurs the rather large Pennant-winged Nightjar *Semeiophorus vexillarius*; its second primaries are extraordinarily prolonged and ribbon-like. In the small Long-tailed Nightjar *Scotornis climacurus*, inhabiting middle Africa, the central tail feathers are greatly elongated. The males of the South American genera *Uropsalis* and *Macropsalis* are distinguished by a forked tail with much elongated lateral feathers. In *Hydropsalis*, from South America, the outermost as well as the central tail feathers are prolonged.

G.C.A.J. (J.M.)

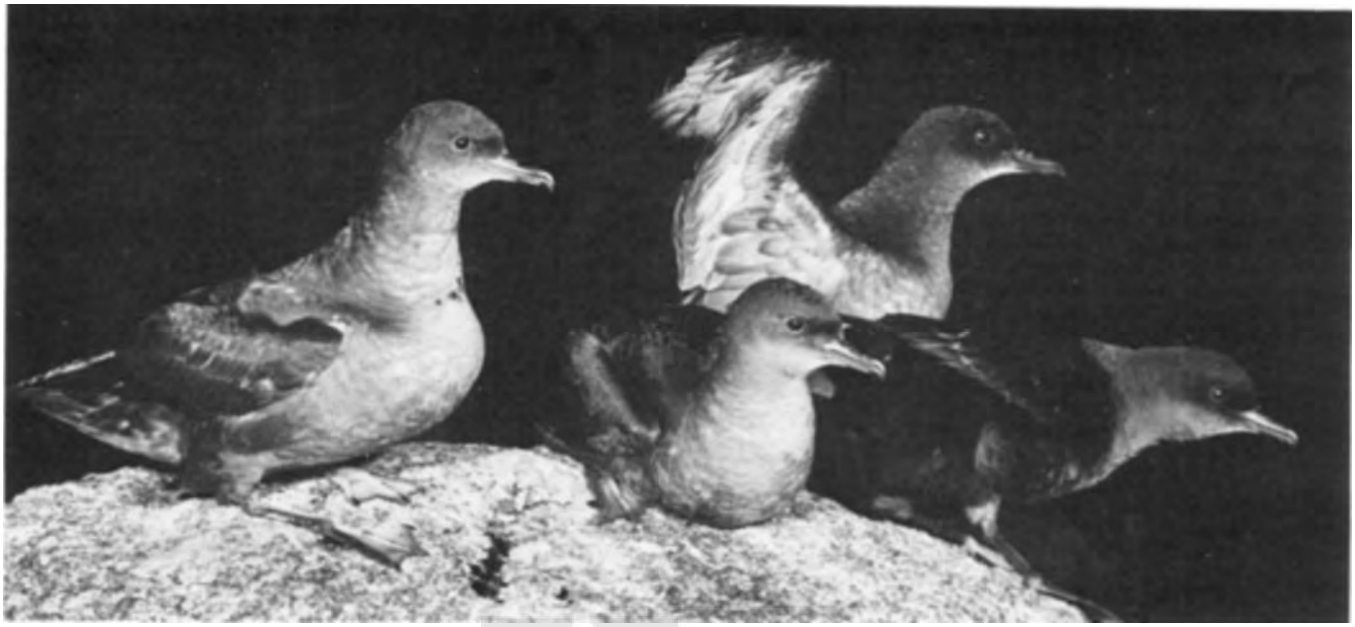
NIGHTJAR, OWLET: see OWLET-FROGMOUTH.

NIGHTJAR, TREE: see POTOO.

NILTAVA: substantive name of species of *Niltava*, a large mainly south-eastern Asian genus of flycatchers (for family see FLYCATCHER (1)).

NITROGEN METABOLISM: see EXCRETORY SYSTEM; METABOLISM.

NOCTURNAL HABITS: characteristic of a minority of bird species, the great majority being entirely diurnal. Outstanding examples of special adaptations to activity in minimal light intensities are found in the Strigiformes, Steatornithidae, and the Apterygidae (see, respectively, OWL; OILBIRD; KIWI); but some of the owls—although all show the main adaptations to nocturnal habits—are in fact diurnal, or largely so. Other birds, notably the Caprimulgidae (see NIGHTJAR), are crepuscular in habits, being active in the dim light of dusk and dawn rather than in full night or day; the Bat-hawk *Machaerhamphus alcinus* is a special case (see HAWK). Others again are nocturnal in their nesting activities but to a large extent diurnal in their search for food; examples are many of the petrels (Procellariiformes), e.g. Manx Shearwater *Puffinus puffinus*, and a few penguins (Spheniscidae), e.g. Little Penguin *Eudyptula minor* (see PETREL; PENGUIN). Further, many aquatic and wading birds (e.g. Anatidae and Charadrii), in particular, are partly nocturnal as well as mainly diurnal, showing considerable activity on nights that are not too dark on the water or open ground. Even among birds that are as a rule strictly diurnal, many migrate by night, e.g. numerous small species of the Passeriformes (see MIGRATION). This may be largely or wholly an adaptation to the need for using the day for feeding.



Short-tailed Shearwaters *Puffinus tenuirostris* waiting to take off from a vantage point, ascended before dawn. (*Photo: J. Warham*).

As the counterpart of nocturnal activity, quiescence during the day calls for concealment. This may be achieved in dense foliage or ground vegetation, or by virtue of cryptic coloration in more open situations. In many instances, however, the birds spend the day in holes or burrows used for nesting, and sometimes also for roosting outside the breeding season. This is true of various owls. Petrels that nest in burrows tend to have their comings and goings during the hours of darkness, and in the daytime are either underground or out at sea. The Little Penguin, mentioned above, is similarly nocturnal to a large extent when ashore at its breeding places. The Oilbird *Steatornis caripensis* nests, and has its daytime roosts, in the utter darkness far inside great caves, where it finds its way by echolocation; similar nesting and navigational habits are found in certain SWIFTLETS, but these birds are otherwise diurnal.

Nocturnal habits constitute a form of concealment, and like other forms may be either defensive or aggressive. The flightless kiwis feed at night; and the oceanic petrels safeguard their unavoidable visits to land, for breeding, by resort there to nocturnal habits. On the other hand, owls use darkness—and their silent flight—for hunting; at the same time they exploit a particular source of food in animals that are themselves nocturnal. Likewise, the crepuscular nightjars feed on insects that fly in the twilight; and the case of the Bat-hawk is self-explanatory. In contrast, the Oilbird is frugivorous—the only nocturnal bird that is. The activities of shore birds are often governed more by the state of the tide than by the alternation of night and day.

Tawny Frogmouth *Podargus strigoides* at night. Note the large eyes, placed for binocular vision, as in owls. (*Photo: J. Warham*).

Swallow-tailed Gull *Creagrus furcatus*; the large eyes indicate the habits of the only nocturnal gull. (*Photo: E.J. Hosking*).

For sensory adaptations to nocturnal activity see ECHOLOCATION; VISION.

A.L.T.

NODDY: substantive name (plural 'noddies') of *Anous* spp. (see TERN).

NOMADISM: term used to describe movements of species that do not normally revisit either breeding site or non-breeding areas (see MIGRATION).

NOMEN: with adjectives conservandum, dubium, novum, nudum, oblitum, and triviale (see below).

NOMENCLATURE: the scientific naming of species and subspecies, and of the genera, families, and other categories in which species may be classified (see TAXON). Scientific names are necessary because there must be names that are internationally understood, and also because vernacular names, where such indeed exist in common speech, are governed by popular usage and are thus liable to be inexact in their application or to change in meaning with the passage of time (see NAME, various entries). In practice, scientific nomenclature has fallen short of the ideal, for reasons partly inevitable and partly arising from human wilfulness and negligence. The only hope of uniformity lies in the subordination of individual views or prejudices to the generally accepted code and authority; to regard nomenclature as more than a means to an end is pedantry, and to take a minority course in a matter of convention is merely a nuisance.

International code. So far as the Animal Kingdom is concerned, the practice of scientific naming is governed by the International Code of Zoological Nomenclature, and no other code has validity in any branch of zoology. The International Code is a system of rules and recommendations originally authorized by the International Congresses of Zoology. The current (third) edition of the Code (formerly 'Rules') is that provisionally approved by the Division of Zoology of IUBS (the International Union of Biological Sciences) at Helsinki (1979) and published in 1984. 'The object of the Code is to promote stability and universality in the scientific names of animals, and to ensure that the name of each taxon is unique and distinct. All its provisions and recommendations are subservient to these ends, and none restricts the freedom of taxonomic thought or action.'

Two points in the earlier history of international rules are of particular ornithological interest. The first set of rules to be generally accepted was that adopted by the V International Congress of Zoology in 1901; the British representative on the small drafting committee was an ornithologist, P.L. Sclater. Among earlier codes was that prepared, with special reference to birds, by the American Ornithologists' Union in 1885. Notable predecessors were the Strickland Code adopted by the British Association for the Advancement of Science in 1842, and the Dall Code published by an American zoologist in 1877.

Binominal system. The Code embodies in legislative form the methods used by Linnaeus (Linné) and first consistently applied in the Tenth Edition of his *Systema Naturae.* These constitute the Binominal System (sometimes 'binomial' or 'binary'); and this has as its temporal starting point 1 January 1758, the year in which the edition was published. The essence is that every species is placed in a genus, and that the name of a species is a binominal combination, or 'binomen' (plural, 'binomina'), consisting of the name of the genus and a second word denoting the particular member of it; the first term of the binomen is the 'generic name', the second the 'specific name' (formerly 'specific trivial name'—the nomen triviale of Linnaeus himself). The name of a genus is used alone to designate that taxon as such. The specific name of a species has no meaning in isolation.

Trinominal system. This is a more recent extension (Schlegel 1844) of the Binominal System and is covered by the same rules. Where a species is divisible into subspecies (sometimes called 'races'), the binomen constituting the name of the species is for each of them extended by a third term, the 'subspecific name'; the 'trinomen' thus formed is the name of the subspecies. The species as a whole is nevertheless still referred to by its binomen. The subspecies that contains the name-bearing type of its species is the 'nominotypical subspecies', and the third term of its name is a repetition of the second.

The International Code expressly does not provide for the nomenclature of infrasubspecific forms, e.g. 'varieties'; nor does it extend to the naming of HYBRIDS. Further, when a number of geographical populations described as separate subspecies are found to intergrade, more or less continuously, the CLINE (although of great importance in reality) is not itself a nomenclatural entity.

Groups of taxa. The Code in its most recent form recognizes three basic taxa—the species, the genus, and the family. On these it founds what it calls (for purely nomenclatural purposes) the 'species group' of taxa, comprising species and subspecies; the 'genus group' of taxa, comprising genus and subgenus; and the 'family group' of taxa, comprising superfamily, family, subfamily, tribe, 'and any supplementary categories required'. The names used for taxa within each group are 'co-ordinate', and are subject to the same particular rules (additional to the general rules applicable to all names). The names of taxa in the genus group and family group are single words. (For the other meaning of the term see SPECIES GROUP (1)).

The Code expressly excludes provision for the nomenclature of taxa above the rank of superfamily. This is 'because the practice of zoologists in regard to them is not sufficiently uniform to permit the formulation of rules covering them at this time'. The taxa most commonly used at this level are class, subclass, superorder, order, and suborder; of these, class and order may be regarded as basic (see TAXON).

Availability of names. The first requirement of a name is that it should be made 'available' for the purposes of nomenclature. This is done by proposing it, for a particular use, in a publication. The form of the name, the information about its proposed use, the circumstances of proposal, and the method of publication must be in accordance with the conditions laid down in the Code. These conditions have been made progressively more stringent in respect of names proposed after certain dates—1930, 1950, 1960; the conditions applied to names proposed earlier (from 1758 onwards) are necessarily in more general terms. A name once duly made available, even if it is or becomes invalid for reasons mentioned later, retains a permanent status in nomenclature; generally speaking, it can be used (at the same group level) only for its original purpose—except that the availability of a specific or subspecific name in one genus does not affect the use of an identical name in another. A name proposed in a manner or circumstances that do not make it 'available' acquires no such status and is not thereby barred for the future; such a name is called a nomen nudum or (if it failed in respect of uncertain application) nomen dubium.

Priority; validity of names. 'Priority is the basic principle of zoological nomenclature. Its application may be moderated however, under conditions specified in the Code, to preserve a long-accepted name in its accustomed meaning.' Accordingly, the valid name of a taxon is the oldest available name applied to it, provided (i) that it is not invalidated by any provision of the International Code, e.g. those relating to homonymy (next section); (ii) that it has not been suppressed by the International Commission (mentioned later); (iii) that it has not become a forgotten name (defined below); and (iv) that it has not been superseded by the Commission's express grant of precedence to some other name (which thereby becomes what is sometimes called a nomen conservandum). The exceptional use of what are known as 'plenary powers' by the Commission, in the suppression and validation of names, is no new thing. Such a 'forgotten name' is one that 'has remained unused as a senior synonym of a name in general current use for more than 50 years', and it cannot be brought into use except by direction of the Commission. This provision should discourage the kind of antiquarian research that has too often led to instability of nomenclature by reviving names of overlooked priority discovered in old works, sometimes of indifferent merit.

Preoccupation; Homonyms. A name that has been made available is automatically invalidated if found to be preoccupied by an earlier use, either in the identical form (for species-group names) or in some very close approximation to it (as defined in the Code). The rule is that a name of supraspecific rank must be unique in the Animal Kingdom; a name of specific or subspecific rank must be unique in the particular genus. Identical names for different taxa are 'homonyms' of each other; a difference of a single letter, except where dependent on a variable spelling of the original word, is sufficient distinction (i.e. '*Apus*' and '*Apis*' are not homonyms). The name in its oldest use is the 'senior homonym', in any other use a 'junior homonym'. The 'law of priority' operates here also; the 'senior homonym' is valid, if other conditions are satisfied, while junior homonyms are invalid. They must be replaced, by a junior synonym, if one exists, or by a 'new replacement name' (nomen novum) if there is none—the term does not apply to a name for a new species.

'Primary homonyms' are those that were in fact homonymous from the outset, although possibly not detected as such until later. 'Secondary homonyms' are those that have become so as the result of taxonomic change—identical specific names may properly exist in related genera, but if these genera are later merged the two specific names become homonyms and one is invalidated; similarly, the splitting of a genus may validate a name that had hitherto been a junior homonym.

Synonyms. Whereas 'homonyms' are identical names proposed for different purposes, 'synonyms' are different names proposed for the same purpose. The operation of the 'law of priority' in respect of synonyms has already been noted, but some points of terminology remain to be mentioned. The oldest of a set of synonyms is the 'senior synonym', and is the valid name if other conditions are satisfied; the remainder are 'junior synonyms' and are invalid, except that the next in order of priority will be promoted if for any reason the existing senior synonym is invalidated (e.g. through being or becoming a junior homonym).

Synonyms are 'objective' (sometimes 'absolute' or 'nomenclatural') when they expressly refer to the same 'type' (see later), so that there can be no doubt about the identity of their meaning; they are 'subjective' (sometimes 'conditional' or 'zoological') when the identity of meaning is a matter of opinion and could thus be disputed. Loosely, 'synonym' without qualification is often applied to any junior synonym, as distinct from the valid name. A list of the names given by various authors to a particular taxon is known as the latter's 'synonymy'; this includes authors' names and publication dates, sometimes with full bibliographical references. The term may also be used for the relationship between different names for the same taxon.

The type concept. It has become a fundamental principle of nomenclature that a name is firmly attached to a 'type'. However the subjective limits of a nominal taxon may be altered, the name stays with the objective type, i.e. with the part of the original taxon that includes it. 'The name-bearing type provides the objective standard of reference by which the application of the name it bears is determined, no matter how the boundaries of the taxon may change.'

The type of a species-group taxon is a 'type specimen', originating from a 'type locality' (see TYPE SPECIMEN; and TYPE LOCALITY). The type of a genus-group taxon is a 'type species'. The type of a family-group taxon is a 'type genus'. Within a group the type of any taxon is also the type of its nominotypical subordinate taxon, if any.

A type species must nowadays be expressly designated by the author of the name of a genus-group taxon; for older nominal taxa there are various methods of selecting a type for a genus if no designation was originally made (see TYPE SPECIES). A type genus is that on which the name of a family-group taxon is based—the names of such taxa are purely derivative, not invented ad hoc. The type genus is not necessarily the one with the oldest name; and there are provisions to obviate changes in the names of the family-group taxa with changes in generic names.

Form of names. Scientific names must be either Latin or so formed that they can be deemed to be Latin; they are often derived from classical Greek, or formed from modern personal and geographical names or the like—and may even be arbitrary fabrications (thus, e.g. '*Dacelo*' is an anagram of '*Alcedo*' (see NAME, SCIENTIFIC)). They must be single words—two single words in a binomen, three in a trinomen; if a compound word is used, the parts must be united without a hyphen (subject to one rare exception probably not occurring in ornithology). Names must be written entirely in Latin or neo-Latin letters; and no figure, diacritic mark, apostrophe, or diaeresis may be used. The printing of linked vowels as diphthongs is now deprecated.

Pre-existing names that do not conform with the requirements are to be treated as incorrect original spellings and (like inadvertent errors) corrected; the corrected form keeps the date and authorship of the original. If the name consisted of two parts, these are to be united and any hyphen or apostrophe eliminated; if one part was in contracted form, the implication is that this should be written in full to make union possible. Diacritic marks are simply omitted, except that when the German umlaut sign is deleted the letter 'e' is to be inserted after the vowel that was modified. To give examples: *novae hollandiae, clot-bey, l'herminieri, st. thomae*, and *rüppellii* respectively become *novaehollandiae, clotbey, lherminieri, sanctithomae*, and *rueppellii*; to some extent usage had been tending in this direction before the 1961 Code made the changes mandatory. Certain recommendations concerning the formation of new names are appended to the Code.

Species-group names. A specific or subspecific name ('species-group' name in this sense—see SPECIES GROUP (1)) must be an adjective in the nominative singular agreeing in gender with the generic name, and changing in this respect if necessary; or a noun in the nominative singular standing in apposition to the generic name; or a noun (or, in some circumstances, an adjective used as a noun) in the genitive case. The genders and proper declension of non-classical names may often be difficult to determine, but the Code gives detailed guidance. A specific or subspecific name is always spelt with a small (lower case) initial letter.

Genus-group names. A generic or subgeneric name must be a noun in the nominative singular or be treated as such. It is always spelt with a capital initial letter. A subgeneric name does not form part of the binomen or trinomen, and except in taxonomic works it need not usually be shown at all; when required, however, the subgeneric name is given in parenthesis between the generic name and the specific name. (This practice must not be confused with that of showing a familiar but discarded generic name in parenthesis or brackets after the generic name actually used; such a name should be distinguished, within its parenthesis, by some such expression as '. . . formerly known as *X-us*'.)

Use of italics. Generic, subgeneric, specific, and subspecific names are preferably printed in a typeface different from that of the text, usually in italics. This does not apply to the names of higher taxa.

Family-group names. The names of family-group taxa are nouns in the nominative plural, and are always spelt with initial capital letters. They are formed from the name of the type genus, with the termination '-idae' (the 'i' is short) in the case of families and '-inae' in the case of subfamilies; the terminations '-oidea' and '-ini' are recommended in the case of superfamilies and tribes respectively.

Names of higher taxa. As already mentioned, the names of taxa above the level of superfamilies are not governed by the International Code, and even within the ornithological field there is variation of practice. One convention (followed in the present work) is to derive the name of an order or suborder from that of an included family, adding the termination '-iformes' in an ordinal name, and using a normal Latin plural for a subordinal name; when this is not done, there may be confusing identity between an ordinal name of one author and a subordinal name of another (see ORDER). In a different convention, ordinal names may be independent fabrications, e.g. 'Tubinares'. The type concept does not, in any event, apply at these higher levels.

Emendations. A scientific name, once established, cannot be rejected or altered simply because it is found to be inappropriate or even misleading. The stability of the conventional labels of which the system consists is more important than the accuracy of the meanings that prompted their adoption, e.g. than whether *maximus* is indeed the largest, or *sinensis* is characteristically Chinese. Further, a specific name cannot be rejected because it is a tautonym of the generic name, at one time thought by some to be objectionable.

It is, however, permissible to correct a lapsus calami or a copyist's or printer's error in a name as originally proposed (and mandatory to remedy defects in form such as the intrusion of a hyphen or apostrophe). Otherwise, the original spelling must be retained even if it is demonstrably erroneous in some respect. Subsequent misspellings of an original name—as distinct from deliberate 'emendations' within the permitted limits—have no nomenclatural significance.

Authorship. When the name of a genus (or subgenus) is mentioned by itself, the name of the author who first proposed it may be added; it is not usual to do this in respect of names of higher taxa. When the binomen constituting the name of a species is given, the name of the author who first proposed the specific name may be added; if he originally named the species in a different nominal genus, his own name is placed within parentheses to denote that he did not use the present combination in its entirety. A similar convention applies to the names of the authors of subspecific names, shown after trinominal combinations. The year of publication, or even the complete reference, may follow the author's name if the nature of the subject calls for this. Unless there is special reason to fear ambiguity in the use of a scientific name, however, authors' names are seldom necessary except in systematic publications.

International Commission. The International Commission on Zoological Nomenclature is a permanent body that originally derived its powers from the International Congresses of Zoology (now succeeded by IUBS). It makes recommendations to successive 'Congresses' for the clarification or modification of the Code. Between 'Congresses' it makes provisional amendments to the Code in the form of 'Declarations', and it gives 'Opinions' and 'Directions' on nomenclatural matters not involving changes in the Code. It exercises 'plenary powers' to suspend the application of provisions of the Code in particular cases where stability or universality seems likely to be disturbed; among other things, it can annul or conserve any name. On the basis of the Opinions rendered, it compiles 'Official Lists' of accepted, and 'Official Indices' of rejected, names and works. The International Trust for Zoological Nomenclature is an administrative body acting for the Commission in matters of property and publication. The Standing Committee on Ornithological Nomenclature, appointed by the International Ornithological Congresses, has no powers of decision but makes recommendations to the International Commission with regard to names in the Class Aves.

A.L.T.

Jeffrey, C. 1977. Biological Nomenclature (2nd edn.) London.
Mayr, E. 1969. Principles of Systematic Zoology. New York.

NOMINAL TAXON: the taxon, as objectively defined by its type, to which a given name applies (see NOMENCLATURE). A nominal taxon persists as a nomenclatural entity even if it has ceased to correspond with any taxon currently recognized for other purposes.

NOMINATE: obsolete equivalent of NOMINOTYPICAL.

NOMINOTYPICAL: adjective applied to a subordinate taxon, denoting that it contains the type of a subdivided higher taxon and bears the same name as that taxon (amended in suffix in family-group names, according to rank). Thus, every subdivided species has a nominotypical subspecies, in the trinomen of which the second and third terms are identical; every genus subdivided into subgenera has a subgenus with the same name as itself; and (for example) every family divided into subfamilies has a subfamily with the same name as itself (apart from ending in '-inae' instead of '-idae'). On the other hand, the definition (by its reference to types) excludes a species of which the specific name *happens* to be a tautonym of the generic name, and a genus with a name providing the stem of family-group names. It should be noted that the concept is purely nomenclatural; a nominotypical subspecies has no inherent pre-eminence over its fellows, and the term 'typical subspecies' is ambiguous as an equivalent. See NOMENCLATURE; TAUTONYMY; TYPE.

NON-BREEDER: an individual which does not nest in a particular breeding season.

NONPAREIL: cage-bird dealers' name for the Painted Bunting *Passerina ciris* (see BUNTING).

NONSENSE ORIENTATION: see NAVIGATION.

NON-VOCAL SOUNDS: see MECHANICAL SOUNDS.

NOSTRIL: see NARIS.

NOTOGAEA: see under ARCTOGAEA; DISTRIBUTION, GEOGRAPHICAL.

NUCHAL: pertaining to the nape (see TOPOGRAPHY).

NUCLEUS: see CELL.

NUKTA: name used in India for the Comb Duck *Sarkidiornis melanotos* (see DUCK).

NUKUPUU: *Hemignathus lucidus* (for family see HAWAIIAN HONEYCREEPER).

NULL HYPOTHESIS: see BIOSTATISTICS.

NUMBERS: the number of different kinds of birds in the world, and their distribution by zoogeographical regions; the numbers of individuals of any one kind in some stated area; the total of birds of all kinds in a given area; the grand total (so far as even an intelligent guess is practicable) of birds of all kinds in the whole world; also the number of individual birds constituting spectacular assemblies or taking part in great migratory movements. See also CENSUS; CLUTCH-SIZE; COUNT; DISTRIBUTION GEOGRAPHICAL; ECOLOGY; QUELEA CONTROL.

Number of species. Mayr (1963) estimated the number of living bird species at about 8,600. More recently a somewhat larger number is generally accepted, as there has been a tendency for some widespread polytypic forms to be subdivided and a number of new species have been discovered; a recent authoritative list (Morony *et al* 1975) recognizes 9,016 species. The new species discovered in successive recent decades are listed and discussed in a series of papers by Mayr and others (most recently, Mayr and Vuilleumier 1983). The number of new species found in the Peruvian Andes, including some very distinct birds of uncertain taxonomic affinities, has been especially striking.

Geographical incidence. No uniformly comparable estimates are available of the numbers of species in different zoogeographical regions. Obviously there is considerable overlap from region to region, and there is also the question of reckoning the sea birds, more readily grouped by ocean than by landmass. With such reservations in mind, general indications can be given: the number of breeding species in the Palearctic Region is about 950, in the Nearctic Region about 750. The Afrotropical Region may have over 1,500 species, Australasia (including New Guinea) about 1,100, seasonal migrants apart. The richest avifauna of all is found in the Neotropical Region—South America has been called the 'bird continent'—which is credited with some 2,500 breeding species.

Size of species populations. Accurate estimates of population size are usually extremely difficult to obtain. Large, spectacular birds which are easily identifiable and have a very limited range (like the California Condor *Gymnogyps californianus*) are relatively easy, as are those species restricted to just one or two islands; next come colonial seabirds with a limited number of colonies and a definite breeding season, so that expeditions may count occupied nests at each colony; thereafter the problems, and the errors in estimates, inevitably increase. A further hazard is that bird populations are dynamic in time, space and numbers: distributions may change and numbers may increase or diminish startlingly (in human terms) as part of a natural series of fluctuations. Nevertheless, such estimates as are available are of interest.

Small populations. Fisher (1960) listed nearly 100 species in danger of extinction or with populations of less than 2,000 birds. The IUCN *Red Data Book* documents many of these which must be on the verge of extinction. There were just 12 Japanese Crested Ibis *Nipponia nippon* in 1965, 22 in 1984; and the California Condor population, estimated at below 50 birds in 1975, had fallen to about 20 in 1983. The case of the Hawaiian Goose or Nene *Branta sandvicensis* is hearteningly different. Fisher listed only 50 birds remaining in 1946, but an intensive and skilfully managed rearing programme centred on the Wildfowl Trust at Slimbridge, Gloucestershire, and later in collections elsewhere, has raised this number sufficiently for several hundreds of captive-reared young to be liberated on a reserve specially purchased for them on the Hawaiian island of Maui. The Whooping Crane *Grus americana* had a world population of 33 in 1959, 50 in 1968; by 1980, partly as a result of cross-fostering, the eggs being incubated and the chicks reared by other crane species, this had risen to 120. The wild population in 1984 was about 100.

Some larger populations. In 1939, Fisher and Vevers surveyed 19 out of 22 known Gannet *Sula bassana* colonies, and believed that there were then about 165,600 Gannets breeding in the world. Since then, such large increases have occurred that the 1939 world population was almost doubled by the 1969 British and Irish 'Operation Seafarer' census of 138,000 pairs (Cramp *et al* 1974). The most recent estimate, in 1976, puts the world Gannet population at about 213,000 site-holding pairs, plus about 70,000 non-breeding birds (Nelson 1978). On a more parochial scale, the Great Crested Grebe *Podiceps cristatus* can be taken as an example of the handful of species in Britain for which regular census figures are available. From less than 100 birds in the latter half of the 19th century, the 1931 census showed about 2,800 adult birds. A repeat in 1965 showed an increase to about 4,500, and a further repeat in 1975 showed the increase to have continued, with between 6,000 and 7,000 adult birds counted. Possibly this increase arises in part from bird protection legislation, but more likely it is based on the tremendous boom in sand and gravel extraction for building purposes and the consequent creation of new stretches of suitable water. Even so, the grebes have had to contend with increasing chemical pollution of the water and disturbance from various recreational activities.

Whilst the threat of extinction may be an effective stimulus to count scarce species, the financial threat posed by some birds to agricultural crops has provoked censuses of potentially damaging species. Thus the US Fish and Wildlife Service was able to document the results of state wide Red-winged Blackbird *Agelaius phoeniceus* roost surveys during the winter 1976/77 in Tennessee and Kentucky, which showed 25 roosts containing in excess of one million birds each and a total of 47 million birds for the two states.

Also in North America, maximum annual wildfowl bags are established each year on the basis of population estimates. Regular counts of the Greater Snow Goose *Anser caerulescens* have shown a dramatic change in status from rarity to pest during this century. In 1900, the autumn population lay between 2,000 and 3,000; in 1921 between 5,000 and 6,000; in 1941 at about 20,000 and in 1966 about 80,000. Then the real expansion began, following a series of summers with good weather and successful breeding. A peak of almost 230,000 was reached in 1975, and numbers have since fluctuated about 200,000.

The commonest bird in the world. Darwin suggested that the Fulmar *Fulmarus glacialis* was the commonest bird, pehaps basing his view on his encounters with Fulmars at sea in the North Atlantic. Fisher disagreed and proposed that another predominantly Arctic-breeding bird, the Little Auk *Alle alle*, might exceed the Fulmar in numbers. Difficult though such numbers are to estimate, or indeed comprehend in Britain where only a handful have been seen, there may be more than 100 million of the Antarctic-breeding Wilson's Petrel *Oceanites oceanicus*.

It is possible also to guess at the most numerous land-bird. It could be either the House Sparrow *Passer domesticus* or the Starling *Sturnus vulgaris*, both now world-wide in scope, partly because of introductions. One of the weaver birds, the Red-billed Dioch or Quelea *Quelea quelea*, widespread in tropical Africa, in which single flocks may be over 1,000,000 strong, is an even more powerful contender. *Quelea* causes serious damage to cereal crops, and it is recorded (Crook and Ward 1968) that in the Republic of South Africa devastation of crops continued even after the slaughter by aerial spraying of over 100 million *Quelea* in one year. Considering that this estimate is only of the proportion of dead birds from only a proportion of *Quelea*'s vast range, this is likely to be the world's most numerous bird.

Some local populations. At least three attempts have been made to estimate the summer land-bird breeding population of Britain. The first was by E.M. Nicholson, who in 1932 arrived at a figure of about 80 millions. J. Fisher calculated about 100 millions in 1939, revising this to about 120 millions in 1946. These estimates were based on randomly taken sample counts from various habitats at various times, but since 1961 most census work has been carried out by members of the British Trust for Ornithology, on a greatly expanded and properly organized basis in the Common Birds Census (CBC). Using figures available from the annual census returns, and Ministry of Agriculture land-usage statistics, Fisher and Flegg (1974) arrived at a figure of about 134 millions for 1972.

Bird population density varies widely with habitat: rough figures derived by Fisher and Flegg from the CBC indicate that with 17 birds/hectare, scrub is the richest habitat, closely followed by suburban and woodland areas, with a considerable gap to farmland at 6 birds/hectare, water areas 2.5 and most barren, moorland and hill grassland with about 1 bird/hectare.

Obviously, the numbers of the various species differ greatly. Of about 500 species on the British list, only about 100 contribute significantly in numbers, and the great bulk—about 75%—is made up by less than 50 species. Fisher (1940) calculated that the most numerous birds in England and Wales were the Chaffinch *Fringilla coelebs* and the Blackbird *Turdus merula* with about 10 million each, followed by the Starling and the Robin *Erithacus rubecula* with 7 million each and the House Sparrow with 3 millions. Fisher and Flegg (1974) produced new estimates, with the Blackbird at 15 million, a newcomer, the Wren *Troglodytes troglodytes* in second place at 10.5 million, the Robin at 10 million, Chaffinch and Dunnock *Prunella modularis* at 8 million, and the Willow Warbler *Phylloscopus trochilus*, the most numerous summer migrant, with 6 million. An interesting contrast comes from Merikallio (1958), who carried out a comprehensive study of the birds of Finland. Most numerous was the Willow Warbler, with about 11.4 million, followed by Chaffinch (10.6), Tree Pipit *Anthus trivialis* (3.3), Willow Tit *Parus montanus* (2.8) and Spotted Flycatcher *Muscicapa striata* (1.9).

Assemblies and movements. Some of the most spectacular manifestations of bird-life are to be seen at the breeding places of colonial nesters. Even the enormous gannetries of Grassholm, Bass Rock and St Kilda in Britain are dwarfed by the Antarctic rookeries of the Adélie Penguin *Pygoscelis adeliae* with over one million pairs or Sooty Tern *Sterna fuscata* colonies on oceanic islands estimated at 1–10 million pairs. Perhaps the most spectacular feeding concentration of all must be the million or more Lesser Flamingos *Phoeniconaias minor* gathering on Lake Nakuru in Kenya. Roosts, too, hold large numbers. City centres like Trafalgar Square in London attract huge Starling flocks, but reed-bed roosts of millions of Sand Martins *Riparia riparia* and in the USA of the Red-winged Blackbird *Agelaius phoeniceus* may contain birds at a density exceeding 2.5 million birds/hectare.

Birds on migration often travel in vast flocks, though as so many are night migrants, these tend to be more often observed by radar. Perhaps the most spectacular sights are at the short sea-crossings beloved by soaring birds, at the Bosphorus and the Straits of Gibraltar, where countless thousands of raptors and storks cross to Africa in spirals vanishing from sight into the sky. Looked at on a wider scale, the figures are even more impressive. Moreau (1961) gave his reasons for supposing that about 600 million European birds perform the Mediterranean-Saharan transmigration each autumn. This means that 150,000 birds per km of longitude enter North Africa, an average of 2,500 per km daily over 2 months. (A.L.T.) J.J.M.F.

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NUMBER SENSE: see COUNTING.

NUMERICAL TAXONOMY: see CLASSIFICATION.

NUMIDINAE: see GUINEAFOWL.

NUN: substantive name of some mannikins *Lonchura* spp. (see ESTRILDID FINCH).

NUNBIRD: substantive name of *Monasa* spp. (see PUFFBIRD).

NUNLET: substantive name of *Nonnula* spp. (see PUFFBIRD).

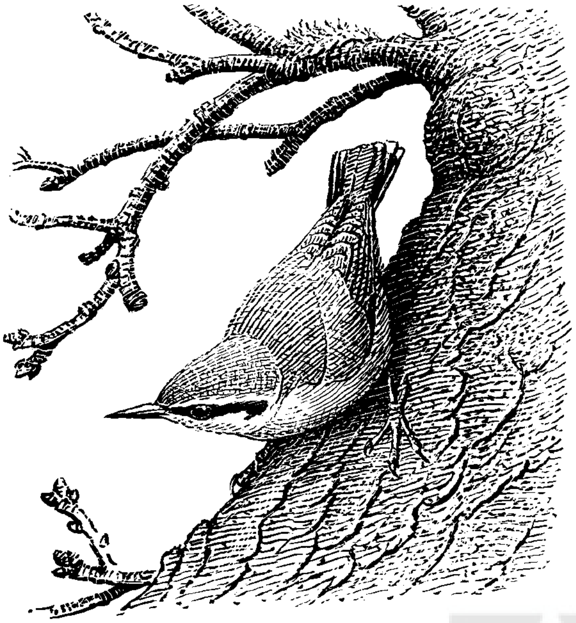
NUPTIAL: pertaining to the breeding season, a term applied especially to plumage and display.

NUTCRACKER: substantive name of the 2 species of *Nucifraga*; used without qualification, in Britain, for *N. caryocatactes* (see CROW (1)).
See photo FOOD STORING.

NUTHATCH: substantive name of the more typical species of Sittidae (Passeriformes, suborder Oscines); used in Britain without qualification for the common European species; in the plural, general term for the family. The family is widely distributed.

Characteristics. Nuthatches are small birds, mostly *c.* 14 cm long, but some up to 20 cm. They are all similar in form; a compact body with a short tail, very long sturdy toes and claws, and a long symmetrically tapered bill. In many species a black stripe runs through the eye, and some have a black cap. The upper parts are blue-grey in most of the typical species, blue-green in 3 found in southern Asia. The under parts are white, grey, reddish brown, or chestnut. Sexual dimorphism is already evident in the juvenile plumage of some species.

All members of the family are climbing birds that seek their food on trees, or in a few cases on rocks. Instead of using the tail for support when clinging to a tree trunk, like woodpeckers or treecreepers, they climb obliquely, with one foot high to hang from, and the other low for support. They can climb down a tree, head foremost, by the same method.



Nuthatch *Sitta europaea*. (*D.W.*).

Habitat. The great majority of the true nuthatches *Sitta* inhabit broadleaved, coniferous or mixed woodland, either lowland or montane, though the rock nuthatches *S. neumayer* and *S. tephronota* are found typically on rock faces or on buildings, as is the European *S. europaea* occasionally.

Distribution. The family is predominantly Holarctic, with 4 species in North America and the rest in Asia and Europe. The family is not represented in South America, Australia or New Zealand. So far as is known nuthatches are non-migratory, except for individuals of the Red-breasted Nuthatch *Sitta canadensis*. The most widely distributed species is *S. europaea*, of which the many races range through the whole of Europe and northern Asia to the limit of tree growth, with a small population in Africa across from Gibraltar. The recently discovered *S. ledanti* is restricted to one mountain in Algeria. *S. europaea* is particularly adaptable, not specialized but capable of utilizing most kinds of trees and of seeds, making caches of the latter in autumn. The Chestnut-bellied Nuthatch *S. castanea* of southern Asia is similar, but differs in voice and in showing marked sexual dimorphism. The Eastern Rock Nuthatch *S. tephronota*, specialized as regards habitat, is found in the warmer parts of Asia; in Persia it occurs along with Neumayer's Rock Nuthatch *S. neumayer*, which reaches its western limit at the Adriatic. The Giant Nuthatch *S. magna* is restricted to the mountains of central Burma, northern Thailand, and Yunnan; it is as large as a Great Spotted Woodpecker *Dendrocopos major* and flies like a member of that family (Picidae). Other species in eastern Asia are the White-tailed Nuthatch *S. himalayensis*, the Yunnan Nuthatch, *S. yunnanensis*, and the Chinese Nuthatch *S. villosa*. Very similar is the Corsican Nuthatch *S. whiteheadi*, once thought to be conspecific with the Red-breasted Nuthatch of North America. In the Near East is found the rather unusually coloured Krüper's Nuthatch *S. krueperi*. In the southern part of North America are found 2 closely related forms, the Pygmy Nuthatch *S. pygmaea* and the Brown-headed Nuthatch *S. pusilla*. In the mountain ranges of Afghanistan and Kashmir dwells the White-cheeked Nuthatch *S. leucopsis*; very similar but somewhat larger is the White-breasted Nuthatch *S. carolinensis* of North America. In southern Asia there are 3 brightly coloured species: the Velvet-fronted Nuthatch *S. frontalis* (coral-red bill in some races), the Azure Nuthatch *S. azurea* (confined to Indonesia) and the Beautiful Nuthatch *S. formosa* (Sikkim to eastern Assam).

Food. Insects, spiders, and other small invertebrate animals are eaten. The birds inhabiting northern or mountainous areas feed largely on seeds in winter, and some small species are specialized for eating the seeds of conifers. Seeds and all larger prey species are hammered into cracks and are there either broken into small pieces or opened up by strong pecks. The European species is able to open even hazel-nuts, hence the name 'nuthatch' (nut hack). Many species store food, especially seeds, by hiding them singly in cracks or under bark, if possible hiding them so that they are not visible.

Behaviour. Nuthatches are strongly territorial, and some defend a territory even in winter, when, however, some are social and form flocks.

Voice. There are various calls, but the song mostly consists of repeated single notes that often sound like a trill. The songs of several species can be imitated by whistling.

Breeding. Members of the genus *Sitta* mostly nest in natural hollows in trees, but some small species make holes for themselves in dead wood; 2 species nest in crevices in rocks. Several species reduce the size of the entrance with mud and fill up all cracks; one fills up cracks only. Two rock nuthatches wall up a semi-enclosed hollow and constructs an entrance tube.

The 6–10 eggs are white with reddish spots. Incubation takes 14–15 days. The young usually remain in the nest for 22–24 days and when fledged are fully capable of flying and climbing; in a further 8–12 days they are independent.

See photo NEST SITE SELECTION. H.L.

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NUTHATCH, CORAL-BILLED: see VANGA.

NUTRITION: the qualitative and quantitative aspects of diet. An adequate diet must supply a bird with (1) sufficient energy for activity and thermoregulation and (2) specific nutrients, such as amino acids, vitamins and minerals that are essential for body growth and maintenance. Energy requirements have been extensively studied in many domestic and wild species under a variety of environmental conditions (see ENERGETICS) but the detailed requirements for specific nutrients of most birds are still poorly known.

Energy. Energy-yielding compounds are usually required in daily amounts of several grams per kilogram body weight. For many bird species the major energy-rich component of the diet is carbohydrate in the form of starch and sugars derived from vegetable foods such as seeds, fruit and foliage, though some seeds and fruit are also rich in fats. Cellulose and lignin are not digested by most birds, though those with large gut caeca, e.g. the subfamily Tetraoninae, may do so (see ALIMENTARY SYSTEM). Animal prey provides fats and some carbohydrates as a direct energy source. Usually, however, the large proportion of protein in animal food must also provide energy by the deamination (removal of the nitrogen group) of its constituent amino acids. The resulting organic acids can then be metabolized in the same way as the breakdown products of fats and carbohydrates (see METABOLISM).

In the long term the energy expenditure of a bird is balanced by an equal intake of energy as food. If food intake is temporarily insufficient the remaining energy requirement is supplied by the consumption of body reserves, primarily fat, e.g. during overnight fasting, during incubation, or to sustain long-distance migration. If food intake exceeds the immediate energy requirement the surplus may be stored as fat, irrespective of the nature of the food.

Water. Water comprises about 70% of non-fat body tissue. Small birds lose water more rapidly than large ones so that the daily rate of water intake is inversely related to body size. However, the minimum water requirement to avoid dehydration is considerably less than the *ad lib* consumption. Some desert birds may not need to drink at all, maintaining their water balance by concentrating their urine and by efficient conservation of the free water in their food (even dry seed contains some free water), together with water produced chemically by oxidation of the food.

Specific nutrients. While an adequate energy balance may be maintained by the breakdown of a wide variety of fats, carbohydrates and proteins, other essential metabolic processes demand the inclusion in the diet of minimum quantities of specific nutrients.

Protein and amino acids. The maintenance of life requires a basal rate of nitrogen metabolism adequate for the continual renewal of body tissues. Additional nitrogen is required for processes such as growth, moult and reproduction. In the chicken on a nitrogen-free diet the basal rate of nitrogen excretion is about 2 mg per calorie basal energy expenditure but is double this amount when dietary nitrogen is freely available. In chickens and in the American Tree Sparrow *Spizella arborea* the latter rate of nitrogen excretion is obtained on a diet containing about 7% protein.

The form in which dietary protein is ingested is of great importance. The amino acids from which new protein is constructed cannot all be synthesized in the body from other nitrogen sources. Certain essential amino acids (arginine, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine) must therefore be present in the food, usually in daily amounts of about 0.1 g per kg of body weight or less. Not all are essential at all stages of the life cycle, e.g. histidine is not required for maintenance yet is essential during growth and reproduction, whereas glycine is necessary during growth only. The synthesis of large amounts of feather keratin during moult requires an abundant supply of the non-essential sulphur-containing amino acid cystine, which is not required in such quantities by other body tissues. Most birds, whose moult is prolonged over many weeks, can nonetheless meet this extra demand from the diet or by synthesis from other amino acids (Newton 1968).

The seasonal dietary changes observed in wild birds will frequently indicate changes in requirement for protein, or for particular amino acids. For example, while the seed food of granivorous birds may provide an adequate balance and quantity of amino acids for moult, it may be inadequate for egg production and chick growth. In particular seeds are deficient in lysine, so that the diet during breeding, particularly of laying females and growing chicks, is supplemented by insects that are rich in lysine. An interesting temporary dietary specialization is shown by parent Great Tits *Parus major*, which feed their nestlings between 5–8 days old with large numbers of spiders (Royama 1970). Presumably spiders, which are otherwise unprofitable food, contain a nutrient essential at that stage of growth, which is scarce in other food.

Minerals. As well as the main structural elements (calcium and phosphorus) and elements essential for maintaining homeostasis in body fluids (sodium, potassium, chlorine), other trace elements are required in much smaller amounts (magnesium, manganese, zinc, iron, copper, selenium and iodine). Compared with the organic constituents of the diet, minerals show a much higher degree of recycling within the body. Iron (for haemoglobin synthesis), iodine (for thyroid hormone synthesis) and calcium are all recycled to some extent, so that the daily maintenance requirements may be difficult to determine. Calcium is particularly important during growth for bone formation and during laying for eggshell production. The maintenance requirement for calcium in hens is about 100 mg per day. Some of the calcium for eggshell formation is stored prior to use in medullary bone but many species supplement this to a large extent from dietary calcium, often collected specially in the form of snail shell, bone fragments or calcareous grit on the days when the eggs are receiving their shells in the oviduct. Calcium has been thought to limit reproduction in vultures, which feed only on the soft portions of carcasses. Various diseases of poultry are known to result from deficiencies of trace elements such as zinc, copper, manganese and selenium.

Vitamins. Vitamins are required daily in the diet in only microgram quantities per kg of body weight but their absence can cause severe deficiency diseases. The water-soluble vitamins (e.g. the B vitamins thiamine, biotin, riboflavin and folic acid; vitamin C) function as coenzymes in specific metabolic reactions that occur widely in the body. Deficiencies of several B vitamins result in various leg disorders, at least in poultry, where they may develop rapidly despite the synthesis of all the B vitamins in the gut by microbial action. Many birds synthesize vitamin C in the kidney or liver or both, while others require a dietary source, e.g. the Red-vented Bulbul *Pycnonotus cafer*.

The fat-soluble vitamins (A, D, E and K) act only at restricted locations in the body. Vitamin A is essential in the formation of visual pigments in the retina. It may be obtained directly in the diet or by the ingestion of β-carotene from plant food, which is converted to vitamin A in the intestinal wall. Carotenoids are also important in the diet as precursors of many feather pigments, e.g. the yellow of orioles *Oriolus* spp. and the reds of bush-shrikes *Laniarius* spp. and the Scarlet Ibis *Eudocimus ruber*. An adequate dietary supply of vitamin D_3 is important to laying hens since this has to be stored in the egg to ensure proper bone mineralization in the chick. Vitamin K stimulates the normal clotting of blood and deficiency, to which poultry are particularly susceptible, leads to haemorrhaging. P.J.J.

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NYCTIBIIDAE: see under CAPRIMULGIFORMES; POTOO.

NYCTICORACINI: see HERON.

NYE: see ASSEMBLY, NOUN OF.

O

OBSERVATORY, BIRD: an establishment, usually on a coastal headland or off-shore island, maintained primarily for the study of bird migration by observation and ringing (see MARKING; TRAPPING). In Britain, the mainland observatories tend to operate throughout the year whilst most island observatories confine activities from early spring to late autumn. The opportunity of handling large numbers of birds caught for ringing is used for various associated studies. Some observatories have experienced full time wardens, whilst others rely entirely on voluntary manning. Visitors are accommodated at most observatories.

The prototype observatory was established on the North Sea Island of Heligoland in the mid-19th century when Heinrich Gätke commenced systematic recording of migrants. In addition to collecting specimens, which included many vagrants previously unknown in Western Europe, Gätke introduced a daily survey and estimation of numbers of migrant birds, which he continued until 1887. The daily census of birds present within a defined area is now standard practice at all British bird observatories and at many on the continent of Europe. The modern bird observatory at Heligoland was established by Weigold in 1909, when large scale trapping and ringing of migrants in specially designed wire-netting traps (still universally known as 'Heligoland traps') largely replaced the collection of specimens.

In the early years of the present century, pioneering work in the British Isles was carried out by W. Eagle Clarke who spent substantial periods at such vantage points as Fair Isle, St Kilda, the Kentish Knock Lightship and the Eddystone Lighthouse. The repeated visits by Misses E.V. Baxter and L.J. Rintoul to the Isle of May (Firth of Forth) and of C.J. Patten to various Irish lighthouses were in the same tradition. Regular observatories came later, and their development has been a marked feature of non-professional ornithological endeavour since 1945.

In Britain only two observatories were in operation before 1945: on the island of Skokholm (Dyfed) founded by R.M. Lockley, and on the Isle of May. Following the war disruption, both observatories reopened and others were started by local interests, often at locations where ornithologists of an earlier generation had found observation and collecting profitable. Observatories have always remained autonomous, but have enjoyed very close links with the British Trust for Ornithology which has co-ordinated their activities and regularly published their findings.

Most observatories have produced detailed annual or bi-annual reports, and considerable analyses have been carried out, using the voluminous logs containing daily counts. Published results have shown the timing and scale of visible migration and, in many cases, the different migratory patterns of birds originating from different geographical areas. Furthermore, the daily counts of migrants covering a period of past decades are being used as crude indicators of the fluctuations of bird populations.

The present English observatories are Dungeness and Sandwich Bay, both in Kent, Portland Bill in Dorset, Lundy Island off Devon, Walney Island in Cumbria, and on the east coast Holme in Norfolk, Gibraltar Point, Lincolnshire, and Spurn Point, Yorkshire. Bardsey Island, Gwynedd, is the main Welsh observatory following the termination of ringing at Skokholm in 1976. The Calf of Man is located just south of the Isle of Man.

In Scotland, Fair Isle, Shetland, is especially famous for rare vagrants and the Isle of May is situated in the Firth of Forth. Cape Clear in south-west Ireland is an outstanding observatory for recording seabird migration. An observatory is established on Copeland Island off the east coast of Northern Ireland.

Observatories elsewhere in Western Europe record visible migration and operate ringing stations, especially in the Baltic Countries. In 1903, ringing commenced at Rossitten—a location then German but now renamed Rybachi and still operating as an observatory under its Russian staff. In southern Sweden, vast migrations are continuously recorded at Ottenby and Falsterbo, the latter being a particularly famous location for the observation of Scandinavian raptor passage. Ringing stations, too numerous to name individually, are now operating observatory techniques in most Western European Countries.

In North America bird observatories are fewer than in Europe, but tend to be far larger establishments, each with permanent scientific staff. The Manomet Observatory in Plymouth, Massachusetts, and Point Reyes Observatory in California both research bird migration and are important ringing stations. These observatories are also concerned with wider ecological studies, especially on marine mammals.

In Canada, Long Point Observatory is located on the north shore of Lake Erie. The observatory provides accommodation for both amateur naturalists and professional biologists and additionally Long Point administers two local summer field stations where visitor accommodation is also available. R.F.D.

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OCCIPUT: the back of the head (adjective 'occipital')—see TOPOGRAPHY.

OCEANIC BIRDS: birds capable of supporting themselves by feeding at a distance from land. Species confined to inshore waters such as divers and ducks are not usually included among seabirds, and it seems logical to exclude from the oceanic category the diving petrels, cormorants, darters, pelicans, skimmers, and about two-thirds of the terns and gulls as well, which rarely or never feed as far as 20 km from land. Distributions of inshore feeders are based on the geography of the land, and oceans tend to be barriers to their spread, whereas the distributions of the most pelagic species (e.g. albatrosses Diomedeidae) are based on the geography of the oceans and correspond, e.g. with those of whales. This restriction leaves a total of about 175 oceanic species, belonging to 13 families in 4 orders: (1) Sphenisciformes—PENGUINS; (2) Procellariiformes—albatrosses, shearwaters, PETRELS, storm-petrels; (3) Pelecaniformes—boobies, GANNETS, FRIGATEBIRDS; (4) Charadriiformes—PHALAROPES, SKUAS, GULLS, TERNS and AUKS.

Feeding ecology. All sea-feeding birds have enlarged nasal glands, capable of excreting brine through the nostrils or mouth (see EXCRETION, EXTRARENAL) and thus ridding the body-fluids of excess salt. Oceanic birds have no need of fresh water; and none are dependent on plant foods. As on land, species frequenting the same feeding areas (habitats) tend to occupy different niches, separated by the nature of the foods they eat and/or their feeding methods (Ashmole 1971; Murphy 1936; and Fig. 1). Bird habitats at sea are defined by less familiar variables than those on land.

Primary production in the ocean depends on microscopic green plants which live within 50–100 m of the surface (the euphotic layer); at greater depths there is not enough light for photosynthesis. The limit to productivity is set by the amount of nutrients available (especially nitrates and phosphates) and the rate at which they circulate through the food chain. The plants are eaten by small herbivores, mostly crustacea, and these by one or more tiers of carnivores. The cycle is completed by microbes which decompose dead organic matter and return the nutrients to the water; but there is a tendency for some of it to fall out of the euphotic layer before decomposition is complete, and thus gradually remove the nutrients from the system.

Over the continental shelf productivity is generally high because, in comparatively shallow water, nutrients are fairly quickly restored to the surface by tidal and other water movements. This constitutes the *neritic province*, and in it living food of suitable size for birds is often abundant, not only at the surface but in midwater and on the bottom. One finds surface-feeders like gulls, and diving birds like cormorants, penguins, auks and ducks, some of which can go right to the bottom at 100 m or more. In high latitudes plant productivity falls low in winter when the days are short, and some parts of the sea are covered with pack-ice, but many of the animals (including fish) survive in undiminished numbers, in more or less quiescent states. Zooplankton is greatly reduced. Some of the birds migrate towards or even beyond the tropics, but many temperate neritic species are able to stay broadly in the same waters throughout the year.

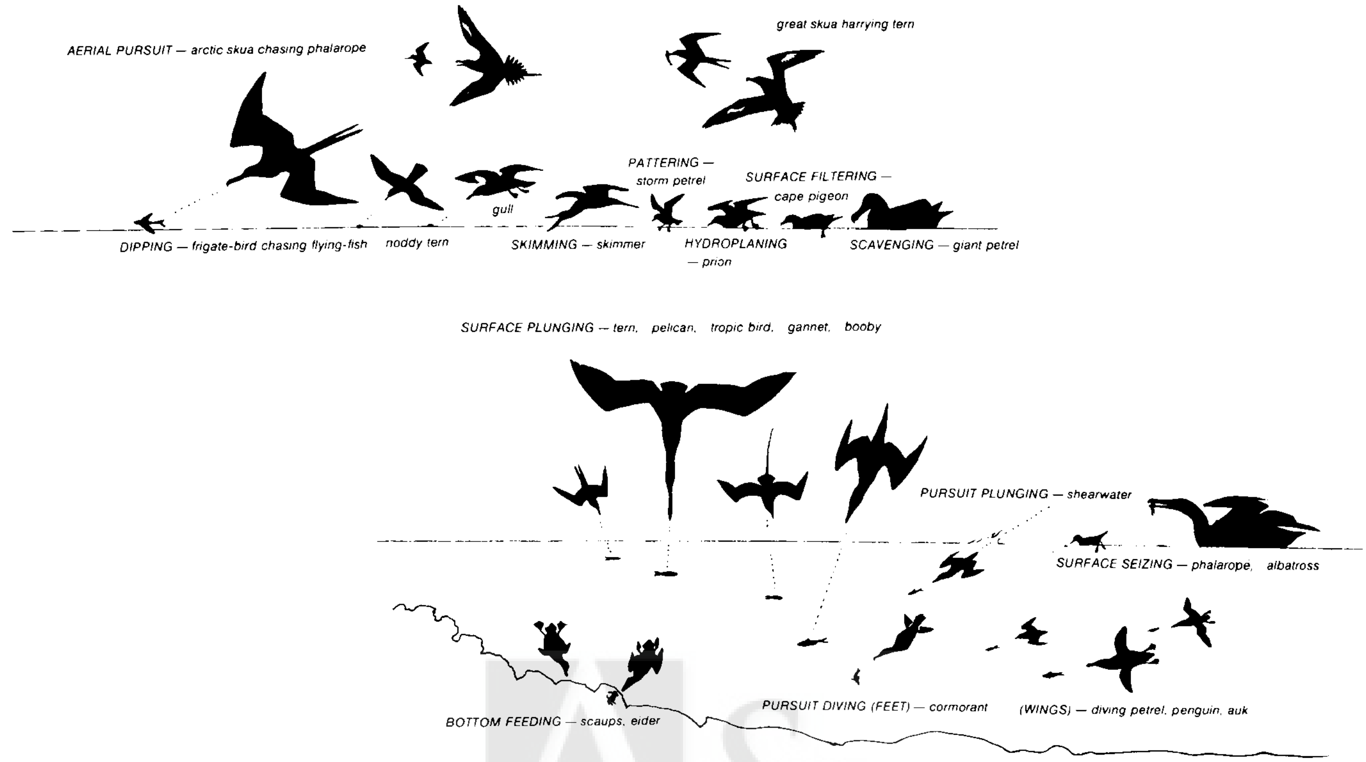

Fig. 1. Seabird feeding methods. (After Ashmole in Nelson 1978, The Gannet).

Outside the continental edge lies the deep-water *pelagic province*. At the higher latitudes the plankton is again seasonal, often with a major burst of plant cells in the spring. Much of the abundant dead matter falls straight into the depths below and its nutrients are lost, at least for the rest of the season; they are only restored to the surface mainly through water-mixing in winter storms. The annual productivity of bird foods—mainly fish, squids and shrimps—is only a half to a third what it is in neritic waters on the same parallel; but a dozen or so transequatorial migrants among the shearwaters and storm-petrels manage to enjoy summer feeding twice a year.

Seasonal changes are less marked in the subtropical and tropical waters. A very warm and therefore light and stable stratum, floating on top in the absence of strong winds, tends to prevent mixing. Productivity, although continuous, is therefore low, of the order of 1% of that in temperate neritic waters. The dearth of living organisms makes the water clear and blue, and deepens the euphotic layer; but what nutrient cycling there is, is efficient in the sense that little organic matter is lost into the abyss (Cushing 1975).

The squid and fish that support the birds are sparse and keep down out of reach by day. Nevertheless this is the habitat of many gadfly-petrels and storm-petrels, tropic- and frigate-birds, boobies and sooty terns, all remarkably adapted to search for scarce food. Most feed from the air by dipping or quick-plunging (swimming under water evidently does not pay; the water being so clear, taking prey by surprise may be impossible). Their opportunities come when they find and follow schools of dolphins or tunnies, which drive flying-fish and other prey to the surface; or in the dusk and darkness when the plankton migrates to the top; or in places where the productivity is higher.

High productivity in tropical waters is confined to local areas where nutrient-rich water has upwelled from below, as it does on a vast scale in the Canary and Benguela currents, and the California and Peru currents, which flow towards the Equator along the western coasts of Africa and the Americas. Trade-winds blowing offshore (and Coriolis force) roll the currents over to seaward, bringing up richer water on the landward side in which the plankton quickly starts to 'bloom'. Productivities can rise as high or higher than any found in temperate neritic seas, as off Peru with its once vast anchoveta fishery and its teeming guano birds. In some places the water drifts out to the westward in a tongue for hundreds of kilometres before the effect has completely waned, and so provides a large fertile enclave, isolated at a great distance from the nearest comparable habitat. As a result, while low-latitude pelagic birds tend to have wide if not pantropical ranges, the upwelling specialists typically include endemics. The Humboldt-Peru current has most, including the Peruvian Booby *Sula variegata*, but the Benguela quite closely resembles it in having an endemic penguin and two salt-water cormorants, all diving in the turbid waters.

Upwellings cause water to spread out on the surface, creating a 'divergence'. Winds can also drive two currents together, and force the denser water-mass to dive under the lighter, at a 'convergence'. The movements, though sometimes vast, are slow, so that anything carried on the surface stops when it reaches the sinking front and stays there. The front is soon marked by flotsam and a slick of oil (at least in part of biological origin) and immediately below the surface there is a similar pile-up of plankton buoyant or active enough to remain at the top and escape going under. This attracts fish and squids, and they attract birds sometimes in hundreds, hour after hour, at what may be the only place in a day's flight where they can feed to repletion and pick up a load for a far-away chick. Many such convergences (and divergences too) are local and transient, being produced by the swirls where currents meet. They occur in all seas, attracting terns, storm-petrels and phalaropes among other birds, but their importance diminishes in the higher latitudes where food is easier to find.

In the global patterns of ocean circulation, particular water masses tend to perpetuate their own special characteristics of temperature, salinity and productivity. Recent exploration, e.g. the International Indian Ocean Expedition in the 1960s, has served to emphasize how responsive oceanic birds can often be to small differences in these characteristics, and the extent to which the birds have exploited them to diversify the number of pelagic niches. Many pairs of related species can be listed which avoid the costs of interspecific competition by becoming specialized to live in subtly different ocean habitats and thus promoting their own mutual exclusion.

Wind drift. The wind must also play a part in differentiating habitats. Oceanic birds range from sparrow-sized storm-petrels to the great albatrosses weighing 7–12 kg. A wind strength of 100 km/h is enough to blow spume off the combers, and the smallest swimming birds risk hurtling with it, unable to hold on. Wrecks of Leach's Storm-petrels *Oceanodroma leucorhoa* are well known in Britain, when migrant individuals have been caught in autumn gales and driven exhausted ashore. Less commonly phalaropes are similarly overtaken, and also Dovekies or

Little Auks *Alle alle* although they, being able to dive, are less vulnerable. Normally the boreal storm-petrels and phalaropes complete their passage south before the gales, and they winter in calmer climes. Some terns make non-stop ocean flights but are not necessarily in danger when driven ashore.

The larger pelagic species can often use the wind to advantage, e.g. to increase their hunting range. Sooty Shearwaters *Puffinus griseus* breed in the southern hemisphere and winter in the temperate westerlies of the North Pacific and North Atlantic. The majority of them direct their northward flight to reach the windward side of either ocean, thereby providing for the maximum leeward travel before they eventually return south to breed, thus completing a wide loop. The Short-tailed Shearwater *P. tenuirostris* does the same, but only in the Pacific. Many ringing recoveries of young Giant Petrels *Macronectes giganteus* prove that the majority leave their birthplace downwind, and that some survivors are capable of circling the southern ocean in 12 months (J.W.H. Conroy); this may be a normal though perhaps not inevitable routine. Some Wandering Albatrosses *Diomedea exulans* evidently do the same (J.L. Mougin *et al*). A yearly circuit on the 50th parallel would require a mean leeward drift of 70 km/day, a trifling distance to these untiring travellers.

Oceanic birds show by their ability to get back, after long absences, to remote islands that are dots in the ocean, and to their nests, when experimentally removed and released at distances exceeding 1,000 km, that they have superb navigational powers. These resemble in their effectiveness those exercised by a mariner with his sextant, chronometer and almanac. They may also be the same in principle, because physics seems to offer no feasible alternative (see NAVIGATION).

Flight. Albatrosses and large shearwaters rival the vultures as economical fliers. They obtain free 'lift' from the combination of wind and waves. Waves tend to run with the wind but less fast, so that the overtaking air-stream flows up the back of each swell. Borne on its long stiff wings the bird alternately rises and falls, sweeping down into a wave-trough across the wind, turning steeply to windward to rise into the updraft above the on-coming wave, which carries it slanting up to a height of 10–15 m where the air-stream levels out. It then uses its height to glide off in the desired direction. The manoeuvre is endlessly repeated, 10–15 times a minute, the rate varying with the size of bird, wave and wind. P. Idrac found that albatrosses could glide indefinitely, given a surface wind of 18 km/h or more; a Fulmar needed at least 22–25 km/h. Calm weather tends to impose insupportable costs on an albatross and may force it to stay on the water. For this reason most species keep out of the tropical doldrums, though the Waved Albatross *D. irrorata* is endemic to Galapagos, which is on the Equator.

Most if not all oceanic birds habitually fly by night as well as day. More remarkably, frigatebirds are known to reach 1,000 km from land at times, and Sooty terns *Sterna fuscata* can turn up almost anywhere in the tropical oceans, without ever resting on the water at all. Neither of them have waterproof plumage. Sooty terns experimentally prevented from taking off became waterlogged in as little as 25 min and were unable to rise until they were dried. Frigatebirds take longer to soak but are equally averse to swimming; they are big birds but astonishingly light, patrolling from a height as they ride on thermals and eddies. The Sooties beat their buoyant wings like other terns, and are not known to alight except on land at their breeding places. Indisputable facts have finally eroded disbelief, and the conclusion first published by the pioneer behaviourist J.B. Watson in 1908, that they can remain airborne, feeding by dipping to the surface, for months at a time has finally won the day. It is not inconceivable that they could doze at times, holding their posture, altitude and course by subconscious perception and control.

Many oceanic birds will land unafraid on floating objects including bergs and sea-ice, though they will not alight on unfamiliar ground or, in the case of terns, on the water.

Population ecology. The southern hemisphere, with vaster oceans, supports far more species than the northern. The largest taxon, the Procellariiformes (see PETREL), comprises nearly 100 species of which well over half breed in the South Temperate and Antarctic zones, about a quarter in the tropics, and only the remaining sixth in the North Temperate and Arctic. Oceanic birds generally nest colonially. The pelagic foragers especially have frugal, protracted life-styles presumably evolved in response to low and irregular rates of food intake. Most lay only one egg or rear only one chick from c/2. Incubation and fledging periods are prolonged, the former for reasons unknown, the latter presumably because the requisite amount of food may often take long to provide, even for one chick. Although parents and chick are both inured to fasting, nestling losses are often high. Such slow reproduction must necessarily be matched by longevity; thus a Fulmar Petrel *Fulmarus glacialis* (the best attested example), if it survives to breed, will live on average to about 44 years of age, showing how remarkably the risks to survival can be avoided. Predators lurk in the water, not in the air, which may partly explain the value of perpetual flight, as an alternative to speed in the water.

Another common trait is long adolescence, often exceeding 5 and sometimes 10 years, which holds an unusually large segment of the population as non-breeders, permanently at sea or annually visiting the breeding colonies just to prospect. The reproductive rate is so low, even at best, that it needs only minor misfortune to put mortality ahead. The equilibrium would be unstable were it not for this great reserve of recruits, built up in good years, ready for the chance to fill gaps in the breeding establishment. Being colonial birds as well, the breeders must be prone to occasional wholesale destruction from local disasters. A standing reserve appears to be an essential stabilizing element in the long-life, slow-breeding strategy. An added benefit is that, except in emergencies, all new breeders will already have survived an arduous test of fitness (Wynne-Edwards 1962).

Efforts to study the oceanic distribution of seabirds and its seasonal changes, go back to about 1920. Bird densities are still measured and compared by counting the numbers seen per unit time, in strip-transects from moving ships or (rarely) from light aircraft. Because there are specific differences in bird size, conspicuousness, and behaviour towards ships, it is difficult to convert the data into absolute densities per unit area. A few estimates of biomass, food consumption and energy flow have, however, been attempted (see Sanger 1972 and Furness 1978 for further references). See photo AGE. V.C.W-E.

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OCELLA: eye-like pattern on plumage, e.g. in the train of a Peacock *Pavo* sp.

OCREATE: same as 'holothecal' (see BOOTED).

ODONTOGLOSSAE: former ordinal name of the Phoenicopteri (see under CICONIIFORMES; FLAMINGO).

ODONTOGNATHAE: a superorder of extinct birds (see under CLASS).

ODONTOPHORINAE: see PHEASANT.

ODONTOPTERYGES: see under FOSSIL BIRDS.

ODOUR: not noticeable in most birds, but some species give off a characteristic smell. The latter is often, for widely unrelated species, described as 'musky', but in the absence of any systematic study it cannot be assumed that the realities so named are similar. The male Musk Duck *Biziura lobata* in the breeding season is said to be inedible because of its musky odour. The mature Muscovy Duck *Cairina moschata* smells musky and so does the adult Magpie Goose *Anseranas semipalmata*. Among other birds in which a characteristic odour is commonly remarked are the Hoatzin *Opisthocomus hoazin*, Bald or Waldrapp Ibis *Geronticus eremita*, Puffin *Fratercula arctica*, Hoopoe *Upupa epops*, several Hawaiian honeycreepers (Drepanididae) and most, if not all, of the Procellariiformes. The comparatively odourless state of the intact body of most birds, as contrasted with mammals, can be related to the scarcity of cutaneous glands. Glands in the ear secrete a wax and others around the vent of some birds produce a mucus, but when an odour is present it is usually ascribed to the fatty acids of the uropygial or oil gland (see OIL GLAND; SKIN). Such compounds may enable colonial procellariiform birds to identify by smell their own burrows, chicks and mates. Grubb (1979) found that breeding Leach's Storm Petrels *Oceanodroma leucorhoa* walked upwind to their burrows after dark, and that plugging the nares or olfactory nerve prevented return. The functions of any scents from the uropygial glands of other birds have not been examined.

One species where the oil gland does not seem to be implicated in a noticeable odour is the Crested Auklet *Aethia cristatella* where the bill plates have been described as smelling like tangerine oranges.

Offensive odours may be emitted by ejecta from either end of the alimentary canal, both vomiting and defaecation being common reactions to threat of danger. In certain species these seem to have a repellent role. The wax esters in the stomach oil of Procellariiformes (see PETREL) have been shown to be dietary in origin and not the result of proventricular secretion as was thought. Regurgitation is more frequent and appears to be under greater control in the chicks of surface-nesters than of hole-nesters, suggesting that the squirting of stomach oil is a defence mechanism in the former. Many female ducks produce offensive excreta while incubating, and are apt to defaecate over their eggs when suddenly flushed. In the Eider *Somateria mollissima*, the faecal matter is particularly foul-smelling. Its unusual nature is probably due to the absence of food in the gut (incubating females sit for 26 days without eating) and the activity there of many anaerobic bacteria. The presence of the excreta with its foul odour has been shown to give the eggs protection against egg-eating mammals such as rats, and against Crows *Corvus corone*. Faeces from non-breeding Eiders do not have the same deterrent effect.

The nesting and roosting places of some species become highly odorous through the accumulation of droppings and food refuse. The nests of many sea birds, raptors, and coraciiform species are cases in point.

For the olfactory sense of birds, see SMELL; see also PALATABILITY OF BIRDS AND EGGS. (A.L.T.) J.K. (1)

Grubb, T.C. 1979. Olfactory guidance of Leach's Storm Petrel to the breeding island. Wilson Bull. 91: 141–143.

Imber, M. 1976. The origin of petrel stomach oils—a review. Condor 78: 366–369.

McDougall, P. & Milne, H. 1978. The anti-predator function of defaecation on their own eggs by female Eiders. Wildfowl 29: 55–59.

Quay, W.B. 1967. Comparative survey of the anal glands of birds. Auk 84: 379–389.

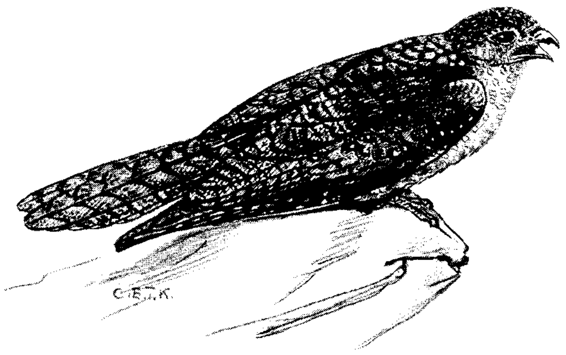
OESOPHAGUS: consisting of the gullet and, where present, the crop (see ALIMENTARY SYSTEM).

OESTROGEN: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

OFFSHORE HABITAT: see OCEANIC BIRDS.

OILBIRD: *Steatornis caripensis*, sole member of the Neotropical family Steatornithidae (Caprimulgiformes, suborder Steatornithes). It is known also as 'Guacharo' and, in Trinidad, 'Diablotin'. Although the Oilbird is generally placed in the order Caprimulgiformes, usually in a suborder of its own, its affinities are still not clear; in any event it occupies a very isolated position. Anatomically it is in general closest to the caprimulgiform birds, but in some characters it resembles the owls (Strigiformes) more closely. In its ecology and behaviour it differs strikingly from the other caprimulgiform birds, and indeed from all other birds. It is the only nocturnal fruit-eating bird.

The Oilbird (length *c.* 35 cm) is in appearance something between a large nightjar (Caprimulgidae sp.) and a hawk (Accipitridae sp.). It has a powerful hooked bill surrounded by long vibrissae, long wings with a span of just over 1 m, an ample tail, and short weak legs. The plumage is rich brown, barred with black and with a scattering of white spots that are especially conspicuous on the wing coverts. Oilbirds are gregarious, cave-living, nocturnal birds; they spend all the day crouched on ledges in the caves that they inhabit, flying out at night to feed on the fruit of various forest trees, chiefly palms and members of the Lauraceae. The fruit is plucked on the wing by means of the strong hooked bill; in intervals between feeding the birds have been reported to perch on bare branches, but so far very little is known about their behaviour outside the caves. Fruit is brought back whole to the caves, apparently in the stomach (as there is no crop), and digested there during the day. The seeds are regurgitated and fall on the lower ledges and floor of the caves, forming a deep rich humus in which etiolated seedlings sprout but soon wither through lack of light.



Oilbird *Steatornis caripensis*. (*C.E.T.K.*).

In addition to the clicking sounds which enable Oilbirds to navigate in pitch-dark caves (see ECHOLOCATION), they utter extremely loud screaming and snarling calls, which from a chorus of several hundred birds in a large cave become almost deafening. When flying at night outside the caves they utter occasional harsh cries, but not the echo-locating clicks. As their eyes are rather large and very sensitive to light, it seems probable that it is by sight that they orientate themselves outside the caves.

It is probable that scent plays an important part in the locating of food trees. Many of them are notably spicy or aromatic, and the Oilbird's olfactory apparatus is very well developed.

The nest is a bulky structure with a shallow saucer-shaped depression, placed on a ledge usually high up on the cave wall. It is made predominantly of regurgitated fruit of paste-like consistency applied directly from the side of the bill, but disgorged seeds and to a lesser extent the bird's own excreta also contribute to the structure. Nests are used year after year and grow in height as more material accumulates. The tempo of breeding is extremely slow. The eggs, usually 2–4 in a clutch, are laid at intervals of several days; incubation lasts about 33 days; and the young remain in the nest for up to 120 days. Both parents incubate the eggs. The young are hatched with a little sparse down, grow a second coat of down after about 3 weeks, and then the adult plumage. They become very fat, reaching a weight half as great again as the adult's by about the 70th day and then gradually losing the excess weight as the feathers grow. Because of the great amount of fat, which when boiled down yields an odourless and durable oil, young Oilbirds used to be, and to some extent still are, collected by the natives of the regions where they occur—hence their name. In Trinidad, eggs may be found at any time; but most clutches are laid in the early months of the year.

Oilbirds occur from western Guyana through Venezuela and Colombia, to Ecuador and Peru, and in Trinidad. They are everywhere very local, depending on the presence of suitable caves. Most of these are in mountainous country, but in Trinidad there are some colonies in sea-caves along the rocky north coast. D.W.S.(1)

Snow, D.W. 1961–62. The natural history of the Oilbird, *Steatornis caripensis*, in Trinidad, W.I. Zoologica (N.Y.) 46: 27–48; 47: 199–221.

OILED BIRDS: see OIL POLLUTION.

OIL GLAND (alternatively 'uropygial gland'): an externally secreting organ located at the rump in the dorsal caudal tract at the bottom of the tail feathers. The uropygial gland (other synonyms: preen gland, glans uropygialis) is a symmetrical bilobed organ, the halves of which are separated by an interlobular septum which ends in a muscular isthmus in the papilla. Each lobe possesses a large number of tubules in which fat cells are produced. The decay of these cells (holocrine type of secretion) forms the greasy gland secretion which then enters into a cavity whence it leaves the gland through two or more orifices. The exterior of the gland, although concealed by overlapping plumage, may be bare but surrounded by a circlet of small feathers or covered by down.

The gland may be more or less well developed in different groups of birds; swimming and diving species, however, generally possess large glands (e.g. penguins, grebes, petrels, gulls, ducks). It is also very large in the Osprey *Pandion haliaetus*. But even passeriform birds have comparatively large preen glands. The relatively heaviest glands (in percentage of body weight) were found in the Little Grebe *Tachybaptus ruficollis* (0.61%) and the Wren *Troglodytes troglodytes* (0.58%); the lightest (0.02%) in the fruit-doves (*Ducula, Ptilinopus*). Small or very small glands are found in pigeons, nightjars, parrots and herons. It seems that originally all birds possessed an uropygial gland, but some species lost it during evolution. Actually, a gland can be recognized in the embryonic stages of birds which lack a gland in the adult form (bustards, rheas, emus). Except for some small glands in the external ear passages, the uropygial gland is the only entirely developed skin gland in birds in contrast to the numerous sebaceous glands in mammals. Nevertheless, there exist numerous fat-producing loci in the integument of birds.

The uropygial gland secretion predominantly consists of monoester waxes composed of more or less highly branched fatty acids and alcohols. The qualitative patterns vary significantly at the ordinal, or in some cases even at the family level. Thus relationships among birds can be studied by comparing these patterns (Chemotaxonomy); e.g. penguins and petrels exhibit very similar patterns and the wax profiles are consistent within the Anseriformes.

Although early speculations on the function of the uropygial gland secretion agreed that it serves as a water repellent and preserves the bird against wetting, recent investigations make other functions more likely. Besides making the feathers flexible, the secretion seems to play an important role in plumage hygiene, since some of its constituents possess bacteriostatic and fungistatic properties; in the female Mallard *Anas platyrhynchos* fungistatic fatty acids are produced exclusively during the pre-incubation period and disappear thereafter.

Regarding the often strong smell of preen gland secretions (especially in petrels) which is supposed to originate from the free wax constituents after lipolysis (the waxes themselves are odourless), it has been claimed that they are involved in chemical communication (pheromonal activity). Recent findings support this at least for geese.

Experimental evidence has been presented that in some birds (e.g. the domestic chicken) the secretion applied to the plumage may have an antirachitic function enabling vitamin D to be synthesized under the influence of sunlight. These findings, however, could not be reconfirmed with pullets or pigeons, and it is thus very doubtful that the uropygial gland generally provides birds with vitamin D.

Gland-ectomizing experiments have been performed with various species. No adverse effects were observed after the removal of the gland in pigeons, sparrows and chicken. Experiments on ducks, however, mostly agree in the observation that the plumage condition degenerated after gland removal, feathers becoming rough, dry and disordered. (A.L.T.) J.J.

OILING: see COMFORT BEHAVIOUR; OIL GLAND.

OIL POLLUTION: the discharge of petroleum oils at sea became a serious problem when ships were converted from burning coal to oil during the second decade of the 20th century. Adverse publicity followed by legislation in the industrialized countries led to some improvement between the wars, but the problem recurred in a new form after the second world war when oil was no longer refined on the fields and tankers carrying it to users started to wash the waxy residues out of their tanks at sea afterwards. This has now been controlled to a large extent by the provision of reception facilities for waste oil at tanker ports, but they are still lacking in some ports used by cargo vessels while 'flag of convenience' fleets in particular are still notoriously careless. The great increase in size of tankers in recent years has also led to some spectacular wrecks, starting with the *Torrey Canyon* off Cornwall in March 1967, while during 1979 an oil-well began to leak off the east coast of Mexico.

Oil floats on water and presents a special hazard to social aquatic birds which are accustomed to react to hazards by diving rather than flying, such as penguins, auks, divers, grebes, cormorants and sea duck. It varies in composition and has a variety of actions. Initially it may contain toxic compounds which may be inhaled by birds or get on their exposed parts and be ingested while preening, and these may cause local inflammation, pneumonia, enteritis and systemic poisoning, notably damage to the liver and kidneys, though it is not clear to what extent this is also due to stress, exposure, hypothermia, dehydration and electrolyte disturbances. These toxic compounds may be lost from the oil by evaporation and solution and it then becomes inert and causes its worst damage through contamination of the plumage and destroying its buoyant and insulating properties. The birds are no longer able to fly or feed, exhaust themselves swimming and keeping warm and die of exposure. Quite a small amount of oil may be sufficient to kill them or contaminate eggs.

In recent years there has been a growing number of investigations of oil pollution. Light crude oils soon evaporate, while heavy ones are reduced to solid inert tar-balls, and the worst damage is caused by refined residual fuel oils which remain liquid longer and may contain toxic substances. The movement of the oil is most markedly influenced by the wind, and travels at about 3.3% of its speed; bird bodies drifting after the oil at about 2.2% of the wind's speed, so the extent to which spilt oil and bird bodies come ashore depends on the wind. The amount of damage caused to bird populations depends mainly on whether the oil happens to drift into areas such as feeding grounds, the waters off breeding colonies, or estuaries frequented by large concentrations of social swimming species. The damage tends to be very much worse in hard weather during the winter in high latitudes, probably because the oil remains fluid longer at low temperatures and large numbers of birds then tend to accumulate in vulnerable places. Investigations have shown that the mortality which is usually under one dead bird per km of beach surveyed may then reach tens or hundreds of birds per km.

Disasters involving thousands of birds are not infrequent and they may at times involve tens of thousands, but while mortalities running into hundreds of thousands have been claimed they have still to be proved. It is also still debatable whether oil pollution causes permanent harm to bird populations. It has been claimed that oil is responsible for a decline of auks along the southern periphery of their range all round the Northern Hemisphere, but in western Europe at least the decline began in the eastern English Channel before the onset of serious oil pollution. While massive oil pollution certainly caused a temporary decline of auks and especially Puffins *Fratercula arctica* on the most important French colony on the Sept Iles off Brittany, it remains to be seen whether the damage is permanent. Similarly, while it has been reported that oil pollution has caused a decline of sea-duck, especially Long-tailed Duck or Oldsquaws *Clangula hyemalis* wintering in the Baltic, the reliability of the figures is questionable.

While the permanence of the damage caused by oil to bird populations is questionable, there is no doubt whatsoever that oil pollution presents a humanitarian problem. Oiled birds are very conspicuous along the shore and attract vast public sympathy. Continual attempts are made to rescue them, often with little success. Recent research indicates that the main problems are that they often cannot be secured until they are moribund, and that people then have difficulty in feeding and cleaning them adequately. To achieve the best results the fittest birds must be selected and they then need to be fed and if necessary tube- or force-fed appropriate foods, usually small fresh fish (except for ducks), until they have at least regained their natural weight; they do better if they exceed it. When fit they need to be washed very thoroughly with a mild detergent or soap and rinsed continually until their plumage spontaneously regains its normal fluffy quality, after which they must be kept clean. The Royal Society for the Prevention of Cruelty to Animals is now obtaining a ⅓ success rate with auks in Britain, and the South African National Committee for the Care of Coastal Birds (SANCCOB) a ⅔ success rate with penguins. The procedure is hardly economic, but could be sufficient to save small threatened bird populations.

It is better to avoid pollution. Ornithologists were largely responsible for securing the first legislation by the United Kingdom in 1922 prohibiting the discharge of waste oil in territorial waters. Other countries took similar action, but it was soon recognized as an international problem. An international conference was held in Washington in 1926 when it was debated whether to prohibit discharges entirely, or restrict them to specified zones; a convention to observe zones was never ratified though some shipping companies observed it. An Advisory Committee on Oil Pollution of the Sea was set up on the initiative of the British Section of the International Council for Bird Preservation to bring together all the interests in the countries affected in 1952. This committee organized another international conference the following year; the UK convened an inter-governmental conference in 1954 which agreed on a new convention. Among other things it provided for extensive zones where pollution was prohibited, for the installation of separators to remove oil from discharged ballast-water, and for reception facilities for the oil in ports. After it had been accepted by 10 nations this Convention came into force for tankers in 1958 and dry-cargo ships in 1961, by which time 15 nations supported it. It was the precursor of many further measures.

In recent years the aim has been to prevent pollution entirely by increased care, enforced by severer sanctions and the development of a growing series of procedures for cleaning ship's tanks and then purifying any water that is discharged, and ultimately to keep ballast water in separate tanks away from contaminants. There has also been growing research into means of clearing up spilt oil, though these remain extremely inefficient and expensive. A growing number of nations is now also taking measures to regulate the condition and movements of shipping. It has become clear that the easiest way to control this persistent problem is through strict supervision of oil-handling procedures to prevent leaks, though regrettably it seems unlikely that they will ever be eliminated entirely. The results of individual incidents appear to be purely temporary, and despite a great deal of discussion and some research no remote consequences of pollution by the commoner petroleum compounds have yet been proved though persistently repeated pollution certainly leads to a local deterioration of the environment. (P.B.-S.) W.R.P.B.

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OIL, STOMACH: see PETREL.

OLDSQUAW: American name (spelt as one word in AOU list) for the Long-tailed Duck *Clangula hyemalis* (see DUCK).

OLD WORLD WARBLER: see WARBLER (1).

OLFACTION: see SMELL.

OLFACTORY BULBS: parts of the forebrain (see NERVOUS SYSTEM; SMELL).

OLIGOTROPHIC: see EUTROPHIC.

OLIVE-BACK: alternative substantive name of some waxbills *Estrilda* spp. (see ESTRILDID FINCH).

OMAO: or Hawaiian Thrush *Phaeornis obscurus* (for subfamily see THRUSH).

OMENS, BIRDS AS: the use of birds in augury (ornithomancy) or, more loosely, as omens individually (see FOLKLORE, BIRDS IN). This can be traced back into many parts of the Ancient World, where, for instance, birds were among the sacrificial creatures in whose entrails portents were 'read'. Indeed, the very word 'augury' refers to divination by means of birds, the first syllable, *au-*, deriving from Latin *avis*; similarly *auspex*, whence our 'auspicious', denoted a man who watched birds (for divinatory purposes). In recent times organized omenist systems have survived in vigorous form only in south-eastern Asia, where in some places they constitute a full-scale 'animist pagan' system of ethics. This system is strongest among the inland peoples of Borneo, all of whom have versions of belief by which actions of a few selected species of mammals, reptiles and especially birds are taken to indicate metaphysical conditions favourable or otherwise to current or intended enterprises. Birds generally form between half and three-quarters of the animist code. Identification between birds and man is easy enough, in a pre-Darwinian context where man seldom feels superior and often regards other life around him, e.g. the munias (Estrildidae) which threaten his rice crops each year, as nearly co-equal.

The position of the bird in relation to the observer, and its movements or calls in flight, are the principal factors in interpreting the augury. A bird crossing one's path from left to right may be dangerous, from right to left very encouraging. Variants are innumerable, methods of propitiation numerous. In extreme conditions of persistent bad omens a group may even abandon their whole longhouse village; among the remote Sabans and Muruts of central north Borneo, to abandon a rice-field painfully cleaned from virgin jungle is not at all uncommon.

Elaborate bird usages have lately disappeared from all but the remotest areas. Bird beliefs remain deeply engrained, however, associated with the part omen and other birds play in folklore, notably as ancestral demigods and mighty warriors. Bird augury was based largely on fertility and associated beliefs linked to head-hunting and war, and augurs were deliberately consulted before any such operations could be undertaken. The cessation of head-hunting in this century invalidated some of the basic premises. Yet the greatest ceremony over a large part of Borneo today is still 'Gawai Burong', the Feast of the Birds, now in effect a peaceful secular continuation of a once blood-marked rite of rejuvenation and continuity, symbolized in the great birds.

A feature of bird augury is the variability of the birds selected. Thus the Sea Dayaks of south Borneo use one of the medium-sized woodpeckers and a tiny one *Sasia abnormis*, a rare jungle kingfisher *Lacedo pulchella*, the noisy Crested Jay *Platylophus galericulatus*, two rather uncommon and quiet trogons (Trogonidae), and a beautifully voiced shama *Copsychus* sp. The Land Dayak, Maloh, Kenyah, and Kayan peoples, however, put dominant emphasis on noisy, small, very common spider-hunters *Arachnothera* spp. and determine much of their daily and nightly lives thereby—whereas the Sea Dayaks ignore these.

The Sea Dayak omen birds are all regarded as interchangeable bird-man deputies for their ancestor hero, Sengalang Burong (Hornbill-Kite), and his brave sons-in-law. Related ideas were held in ancient Greece, northern India, and modern Africa; Sir James Frazer wrote in *The Golden Bough*: 'When the Nandi men are away on a foray, nobody at home may pronounce the names of the absent warriors; they must be referred to as birds'.

All the Borneo omen birds are resident species; but it does not follow that all were originally so in the lands whence these peoples came in protohistorical times. Certainly, there is another important sequence of thought—notably in China and Borneo—centred on migratory birds. It is not difficult to see how this could lead directly to an omenist system. In China such beliefs persist even under Communism. The 'Red Bird of the South' ('teng huang'), a frequent phoenix-like form in Chinese art for over 2,000 years, is a symbolic bisexual conglomerate of several birds—the quail, coming to north China from the south as a portent of summer all along the mighty Yellow River, the peafowl, pheasant, junglefowl, eagle, and flying dragon. At the other end of the scale, in the remotest hinterland of central Borneo, the Kelabits determine their crucial rice-planting cycle by the arrival of a series of migrating birds reaching the Equator from the far north, indicating to man the sequence of clearing and planting, bedding, weeding, protecting, and harvesting the vital rice padi. These birds, which give their names to the months, are an eastern race of the Yellow Wagtail *Motacilla flava*, Brown Shrike *Lanius cristatus*, Japanese Lesser Sparrowhawk *Accipiter gularis*, and Siberian Pale Thrush *Turdus pallidus*; all 'winter' above 900 m in the Bornean uplands and return north during March-April, after the rice crop has been gathered in. (T.H.) G.E.S.T.

OMNIVOROUS: having a varied and unspecialized diet.

ONTOGENY: the developmental history of the individual (see DEVELOPMENT, EMBRYONIC; GROWTH; also BEHAVIOUR, DEVELOPMENT OF). This is contrasted with the evolutionary history of the species (or other taxon)—see PHYLOGENY.

O-O: see HAWAIIAN HONEYCREEPER.

OOCYTE: a cell in the sequence leading to the formation of an ovum (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

OOLOGY: the scientific study of the eggs of birds, with particular reference to external characters such as shape and size, texture and coloration of shell, and number in clutch (see EGGS). Extension beyond this overlaps the more general field of reproductive physiology and behaviour (see, for example, BREEDING SEASON; CLUTCH-SIZE; IN-

CUBATION; LAYING; BROOD-PARASITISM). The study of the contents of the egg, and of the developing chick within it is covered by DEVELOPMENT, EMBRYONIC.

The main descriptive phase of oology as a form of systematic work has been completed for most parts of Europe and North America; but in some parts of the world there is still very much to be learnt, the eggs of many species being as yet either wholly unknown or the subject of only meagre information. Regrettably, scientific oology is obscured by controversy over egg-collecting, now illegal in many countries except under licence, but still rife in Britain. B.C.

OPENBILL: also 'Open-billed Stork' *Anastomus* spp. (see STORK).

OPEN SEASON: period when certain birds may legally be shot for sport.

OPERCULUM: a covering flap, as over the anterior nares or the external auditory meatus in some birds (see BILL; NARIS; OWL).

OPISTHOCOMI; OPISTHOCOMIDAE: see under GALLIFORMES; HOATZIN.

OPTIC LOBES: parts of the brain (see NERVOUS SYSTEM).

OPTIC NERVE: see VISION; NERVOUS SYSTEM.

OPTIMAL FORAGING THEORY: the application of OPTIMALITY THEORY to the study of how animals search for and exploit food. In this approach it is hypothesized that foraging behaviour can be described by mathematical models which assume that the animal is designed (by natural selection) to maximize some aspect of foraging success such as energy intake, protein intake or balance of nutrients. Such models can be tested, thus revealing whether the particular design criteria and constraints embodied in the model are correct.

OPTIMALITY THEORY: a body of mathematical theory concerned with the analysis of the 'best way' to allocate 'scarce resources' among various alternatives. Although originally developed in the context of engineering and economics, optimality models have been applied to biology in an attempt to understand how organisms have been designed by natural selection. For example, many features of living organisms, from the biochemical to the behavioural level of organization, can be accounted for by the hypothesis that the maximal energetic efficiency is a design criterion.

It is sometimes mistakenly thought that optimality models are used to test the idea that organisms are optimal. This is not so. They allow one to test whether the design criteria and constraints embodied within the models are realistic. Optimality models are used as an analytical tool because of the conviction that natural selection favours good design.

ORANGEQUIT: *Euneornis campestris*, a small Jamaican passerine bird of uncertain affinities, tentatively placed in the subfamily Thraupinae (see TANAGER). It has a sharply pointed, decurved bill and feeds largely on nectar.

ORANGETHROAT: *Luscinia pectardens* (for subfamily see THRUSH).

ORBIT: see SKULL.

ORBITAL: applied to a distinctive area, in some plumage patterns, round the eye.

ORBITOSPHENOID: a paired bone of the SKULL.

ORDER: a primary taxonomic category, a sub-division of a class, and a grouping of families; other categories may be interpolated between these primary ones to build up a more elaborate hierarchical system, especially subclass and superorder on the one hand, suborder and superfamily on the other (see CLASSIFICATION; TAXON). In accordance with the International Code of Zoological Nomenclature every ordinal name ends in '-iformes'; earlier use favoured '-morphae'.

Whereas the family is the most convenient group for most general purposes, the aim of ordinal grouping is to express a supposed phylogenetic relationship between families. At this level, however, the suppositions tend to become very uncertain and highly speculative; the content of orders has therefore not only changed greatly with advancing knowledge but is also the subject of differing views. Authorities who are sceptical about evidence of relationships naturally tend to preserve a greater number of separate orders of limited content; those who are bolder place more families together and thus reduce the number of orders. Authors who adhere to cladistic systematics must by necessity use either a relatively large number of orders or an almost infinite number of taxonomic subdivisions or do both.

Nevertheless, many orders are not in serious dispute. Some of these comprise only a single family, and the ordinal rank merely expresses the view that the family does not appear to have any known near relationships; others comprise a few families that are generally accepted as being more related to each other than to other families. The greatest difference of opinion concerns the large assemblages of families regarded by some as gruiform and coraciiform respectively. Even the Order Passeriformes, generally accepted as having ordinal characteristics clearly separating it from all the other groups, has been treated in a cladistic system as two orders of supposedly independent phylogenetic origin: Tyranniformes and Passeriformes *sensu stricto* (Feduccia 1975, 1977).

In listing orders it is customary to begin with those that are believed to be the most primitive and to proceed towards the most highly developed, the Passeriformes. The placing of the orders is obviously speculative in high degree; any list must be arbitrary in that no linear arrangement could adequately express four-dimensional relationships grown in space and in time. The classification of orders followed here is that proposed by Voous and represents in some way a combination of the well-known systems of Wetmore and Stresemann. It can be found in the Table of Classification in the preliminary pages.

Suborder. The suborder is a secondary taxonomic category, a subdivision of an order and a grouping of superfamilies (if any) and families. Not all orders are divided into suborders, the category being used only when required; its necessity depends on the philosophy of the classification system followed and is greatest in cladistic systematics. Other systems may tend to give independent ordinal rank to what are considered suborders elsewhere. Names of suborders end in ordinary Latin plural forms ('-i, '-ae', '-es'). As some authors end their ordinal names in the same way, these can be identical with the subordinal names of others. The International Code of Zoological Nomenclature does not apply at this level.

For superorder see under CLASS; for superfamily see under FAMILY.
K.H.V.

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ORGANO-CHLORINE: see TOXIC CHEMICALS.

ORIENTAL REGION: one of the main zoogeographical divisions of the Earth (see DISTRIBUTION, GEOGRAPHICAL); also known as the Indian Region, although that adjective is better retained for the subregion covering the greater part of continental and peninsular India, with Sri Lanka.

Boundaries. The Oriental Region lies mainly between 68° and 135°E and between 10°S and 32°N, therefore largely within the tropics. Its northern boundary, dividing it from the Palearctic Region, runs from the Hindu Kush Mountains in the west along the entire length of the Himalaya, and farther east to include Yunnan and Szechuan. It continues roughly south of the basin of the Yangtze Kiang to form an indeterminate frontier with the Manchurian Subregion of the Palearctic till it reaches the East China Sea in the neighbourhood of Ning-po in *c.* 30°N. From its western extremity the boundary trends south-west, excluding Afghanistan and Baluchistan, and may conveniently be taken as the valley of the

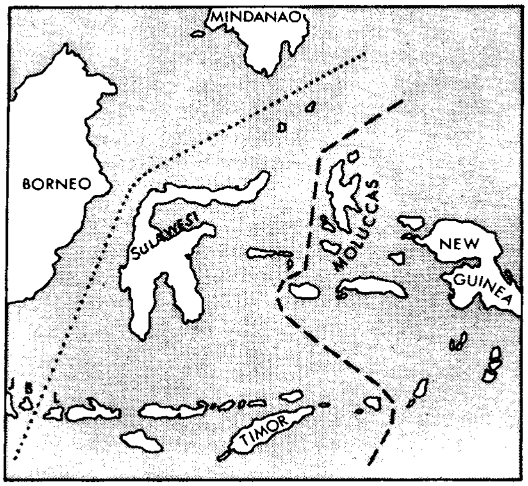

Fig. 1. Transitional zone at boundary with the Australasian Region. The classical Wallace's Line (dots) approximates to the western limit of this zone—J = Java (part), B = Bali, L = Lombok; Weber's Line (dashes) represents its median, where the two faunas are more nearly balanced. The islands between Wallace's Line and New Guinea are sometimes collectively termed 'Wallacea'.

Indus down to its mouth near Karachi in Pakistan.

South of the Asian mainland, the Oriental Region includes the continental islands of Taiwan and Hainan as well as the greater part of the Indonesian Archipelago, the Philippines, Borneo, Sulawesi, and the Greater and Lesser Sunda Islands east to Timor. There are curious clear-cut divisions as well as close intermingling between the characteristic Oriental and Australian faunas on many of the islands in this area, and the line of demarcation from the Australasian Region is not easy. In the last century, since Wallace first postulated the boundary between the islands with a mainly Indo-Malayan fauna and those with the Australo-Papuan type, a succession of investigators (including many ornithologists) have conducted intensive faunal studies on the islands to determine their correct biogeographical status. The demarcation originally proposed by Wallace—'Wallace's Line' as Huxley named it—on the basis of the presence or absence of certain typical bird and other animal groups of the Oriental and Australasian Regions at first enjoyed a wide measure of acceptance from zoologists on account of the truly remarkable examples of clear-cut divergence which it showed, e.g. as between the islands of Bali and Lombok, separated by a deep and narrow strait (only 25–30 km wide), and as between Borneo and Sulawesi. Many dominant Oriental bird groups, e.g. the barbets (Capitonidae), range as far east as Bali and then suddenly break off, being completely absent from Lombok and beyond. Woodpeckers (Picidae), abundant in the Oriental Region as far east as Borneo, Java, and Bali, are very poorly represented (by only 4 or 5 species) in Lombok, Sulawesi, and eastward up to the Moluccas, being absent over the rest of the Australasian Region. On the other hand, many typically Australian groups, e.g. honeyeaters (Meliphagidae) and cockatoos (Cacatuinae), reach westward as far as Lombok, but there end abruptly. The faunal differences on the opposite sides of the Strait of Macassar, between Borneo and Sulawesi, are superficially even more striking; they are not confined to birds but extend to mammals and other animal groups.

The line, as postulated by Wallace, passed between Bali and Lombok in a north-easterly direction, through the Macassar Strait separating Sulawesi from Borneo, and then on ENE between Mindanao and Sangi Islands, passing west of the Marianas or Ladrones group. Huxley's proposed modification, by drawing it north from the Macassar Strait to pass between Palawan and Mindoro Islands, excluded the Philippines from the Indo-Malayan Subregion.

On statistical analyses of the extensive data accumulated by investigators since Wallace's time, on a percentage basis of typically Oriental and typically Australasian faunal elements present or absent on the various islands, it was realized that a more rational boundary between the two regions would be one that showed a faunal balance, i.e. with the Oriental and Australasian elements in more or less equal proportions. A line of this nature can of course be only arbitrary, since the 50:50 balance does not hold good for all taxonomic groups. Such a line of faunal balance between the Oriental and Australasian faunas was first demonstrated by Weber, in 1902, to exist much farther east than Wallace's Line. As modified by subsequent investigations, Weber's Line runs roughly along the Molucca Passage between Sulawesi and the northern Moluccas, southward between Sula Islands in the west and Obi Islands in the east, swings west of Buru, and, leaving Timorlaut Islands on its east, curves WSW along the edge of the Sahul Shelf to include Timor in the Indo-Malayan Subregion. Thus, on consensus of current views, all the islands in the intermediate zone between Wallace's Line and its eastern counterpart—the 'Wallacea' of some zoologists—belong to the Indo-Malayan Subregion.

Characteristic groups. One bird family is peculiar to the Oriental Region, the leafbirds (Irenidae), and is in fact confined chiefly to the Indo-Chinese Subregion. The Oriental Region shares with the Afrotropical Region, either exclusively or overwhelmingly, the passerine families Eurylaimidae, Pycnonotidae, Nectariniidae, and Ploceidae. The typical Ethiopian family of the honeyguides (Indicatoridae) is represented here (but in no other region) by the common genus *Indicator*. Many genera, e.g. *Harpactes* (Trogonidae), *Nyctiornis* (Meropidae), *Psittacula* and *Loriculus* (Psittacidae), *Acridotheres* and *Gracula* (Sturnidae), and *Pericrocotus* (Campephagidae), are confined to it and do not occur at all outside its limits. The family Phasianidae is particularly well developed in the Oriental Region, the spectacular genera *Pavo, Gallus, Lophura, Pucrasia, Catreus, Argusianus, Polyplectron*, and *Rollulus* being peculiar to it.

Subregions. The region is readily divisible into the following three main subregions upon the general spectrum of their avifauna and other animal groups:

1. The Indo-Chinese Subregion (= 'Himalo-Chinese' of H.J. Elwes and H.F. Blanford)
2. The Indo-Malayan or Malaysian Subregion (= 'Malayan' of above authors)
3. The Indian Subregion

The first two are essentially very similar in regard to their physiography, being covered largely with tropical and subtropical vegetation, the result of heavy monsoon rainfall and high humidity. Nevertheless, they each exhibit marked peculiarities in many of their plant and animal manifestations, the first subregion showing an affinity with the Palearctic in its temperate zone forms, e.g. the Fringillidae, while the second possesses elements with distinctly Australo-Papuan affiliations.

The Indo-Chinese Subregion. This includes the southern aspect of the entire Himalayan Range (up to the tree-line—3,000 to 4,000 m elevation), particularly the section that lies east of the Arun-Kosi River in eastern Nepal. Beyond, its boundary extends into north-western and eastern China, marching with the Palearctic Region. Many typically eastern genera, e.g. *Paradoxornis*, terminate in Sikkim and Nepal, but the avifauna of the Himalaya westward of the division indicated retains its overall Indo-Chinese character in diminishing degree. This tendency is well illustrated by many other timaliine genera, e.g. *Garrulax*, abundantly represented in Yunnan and the eastern Himalaya, but sparsely in the western.

Besides the Himalaya, this subregion includes Assam, Burma, Thailand, and Indo-China (Vietnam), i.e. the entire portion of the Oriental Region lying on the Asian mainland east of the Ganges delta, with the exception of the Malay Peninsula. It also includes the islands of the Andamans group, as well as Taiwan and Hainan.

The Indo-Malayan or Malaysian Subregion. This lies for the most part within a tropical belt 10° on either side of the Equator and includes the Malay Peninsula south of the Isthmus of Kra, together with all the islands of the Archipelago west of Weber's Line. The Nicobar Islands, off the western tip of Sumatra, show closer avifaunal affinities with this subregion than with the Andamans, which are spatially nearer to Burma. This subregion is more exclusively tropical and forested than either of the others. Its avifauna lacks all traces of Ethiopian affinities, so noticeable in the Indian Subregion. It also lacks temperate zone forms of the Himalaya with Palearctic affiliations, such as the rose finches (Fringillidae).

The Indian Subregion. This stretches southward from the foot of the Himalaya to include the entire peninsula and Sri Lanka. Its western boundary is that of the Oriental Region—the Indus Valley—while on the east the deltas of the Ganges and Brahmaputra rivers demarcate it from the Indo-Chinese Subregion. Two clear-cut 'provinces' are recognizable which, for convenience, may be termed (*a*) The Peninsular Province, covering all India and Sri Lanka except the portions under (*b*);

(*b*) The South-western Province, the tropical humid, heavy-rainfall zone commencing at the northern extremity of the Western Ghats in Khandesh and the Surat Dangs, but more properly south from about Goa (c. 15° 30′ N) including western Karnataka, the Nilgiri and Palni Hills, and Kerala, together with its virtual extension in south-western Sri Lanka—the so-called 'Low-country Wet' and 'Central Hill' zones.

The avifaunal character of the Peninsular Province is largely Palearctic and Ethiopian. A typical example of the latter is the cursoriid genus *Rhinoptilus* (currently merged in *Cursorius*) with several species in Africa but only a single one, *C. bitorquatus*, in peninsular India. There is an almost complete absence of characteristic east-oriental genera of birds in this province, as there also is in the Afrotropical Region.

The South-western Province, although much smaller, is one of the most interesting areas, from the biogeographical point of view, by virtue of the very striking similarities and parallelisms its fauna and flora exhibit with those of the far-flung Indo-Chinese and Malaysian subregions. It constitutes the western terminal of what is known as the 'Indo-Malayan Arc' or 'Horseshoe' of animal distribution: Malaya–Burman-eastern Himalaya–Sri Lanka. Several typical sedentary birds inhabiting its two extremities (e.g. *Chrysocolaptes lucidus, Buceros bicornis*) are morphologically inseparable, even at subspecific level. These remarkable 'relict populations' of south-western India, now cut off from their nearest neighbours in the Himalaya by up to 2,500 km, have received special attention from zoologists in recent years. Much interest has been aroused by the very attractive 'Satpura hypothesis' of the Indian zoologist, S.L. Hora, which seeks to explain the history, route, and mechanics by which freshwater hill-stream fishes, and other specialized hygrophilous fauna of the Indo-Chinese Subregion, reached Kerala and Sri Lanka. This hypothesis postulates a once continuous mountain trend from the eastern Himalaya and Garo Hills, across peninsular India over the Rajmahal Hills and the Satpura Mountains, and then southward over the Sahyadris or Western Ghats to Kerala and Sri Lanka. Sri Lanka, which was alternately joined to and separated from peninsular India during various geological epochs, bears evidence of having received distributional faunal waves from the mainland. Under periods of prolonged isolation, many endemic races (or species, as some ornithologists consider them) have developed on the island.

The avifauna of the humid South-western Province contains one monotypical muscicapine genus, *Ochromela* (now *Muscicapa*), peculiar to its mainland section. Numerous examples can be cited of birds not occurring in the adjoining Peninsular Province, but having close affinity, or even identity, with forms living in the eastern Himalaya and in the Indo-Chinese and Indo-Malayan Subregions generally. Prominent among such are laughing thrushes *Garrulax* spp., Fairy-bluebird *Irena puella*, woodpeckers of the genera *Dinopium, Hemicircus, Dryocopus*, and *Picumnus*, Great Hornbill *Buceros bicornis*, spinetail swifts *Chaetura* spp., Broadbilled Roller *Eurystomus orientalis*, Malabar Trogon *Harpactes fasciatus*, Frogmouth *Batrachostomus moniliger*, and the falconid genus *Aviceda*. Some of these birds, e.g. *Dryocopus, Hemicircus, Picumnus, Buceros*, curiously enough, are not found in Sri Lanka: the complete absence of vultures *Gyps* spp., so common and abundant on the Indian mainland, is another anomaly not easily explained considering the powerful flight and far-ranging capabilities of these birds. S.A.

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ORIENTATION: see NAVIGATION.

ORIGIN OF BIRDS: see EARLY EVOLUTION OF BIRDS.

ORIOLE (1): substantive name of most species of Oriolidae (Passeriformes, suborder Oscines); in the plural, and in an Old World context, general term for the family Oriolidae. This is a homogeneous group of about 28 species placed in 2 genera, 24 species in *Oriolus* and the remainder in *Sphecotheres*. Tentatively classified with the orioles is the little known Kinkimavo *Tylas eduardi* of Madagascar, and it has recently been suggested that the 2 FAIRY-BLUEBIRDS, *Irena cyanogaster* and *I. puella* of the Oriental region may be aberrant orioles.

The family name is from the Old French *oriol*, which in turn was probably derived from the Latin *aureolus*, meaning golden or yellow, and applied originally to the Golden Oriole *Oriolus oriolus*.

Characteristics. The orioles differ from the New World orioles (Icteridae) by having 10 primary feathers (see ORIOLE (2)). Old World orioles are robust birds ranging in size from about 20–30 cm in length, and have decurved bills. The wings are long and pointed; the tail has 12 feathers.

Habitat, distribution and movements. The family Oriolidae occurs in forests and woodlands throughout Africa south of the Sahara, across Asia, the Philippines, Malaysia to New Guinea and Australia (though not in New Zealand) with one species, the well-known Golden Oriole *O. oriolus* ranging right across the southern Palearctic region as well as into India, but wintering exclusively south of the Sahara. Other non-forest inhabiting species are to some extent migratory. Speciation has been most active in the eastern quarter of the family's range, where there are so many islands. Most species of Oriolidae occur in the tropics or sub-tropics.

Distribution and characteristics. The Golden Oriole, 5 closely related African species, and some of the Oriental species have the male plumage patterned brilliant yellow and black, with black usually on the head, primary and secondary wing feathers and on the upper tail coverts. One species, *O. chlorocephalus*, limited to a few montane forests in eastern Africa, has the combination of clear yellow and rich olive-green. The 2 Australian species are much duller, greenish and streaky. Several Oriental species are predominantly black, with patches of rich crimson; e.g. the Maroon Oriole *O. traillii*; while the Black Oriole *O. hosii* is almost wholly black except for chestnut under tail coverts. As a rule, those orioles that have yellow pigment in the plumage have bills coloured a dull red or pink, while those with crimson in the plumage have the bills horn-coloured or bluish. The 4 species of figbird placed in the genus *Sphecotheres* occur in the forests and open woodlands of the Timor-New

Black-naped Oriole *Oriolus chinensis*. (*D.A.T.*).

Guinea-Australia area. They are distinguished by bare skin around the eye and an exceptionally short bill. Figbirds are duller in plumage than other orioles, and have dull yellow, green, brown, grey and white in their plumages. Bills are black and legs are red in males; females have both bills and legs reddish-brown. In at least one species, *S. vieilloti*, the red colour of the bare skin of the adult male apparently fades after the eggs have hatched. Throughout the family the females are, with very few exceptions, duller or more streaked—or both—than the males. Juveniles resemble females.

The orioles provide some typical examples of evolution on small islands. *O. crassirostris* of São Tomé in the Gulf of Guinea has lost most of the brilliant yellow so prominent in the African species from which it was probably derived, and it has an abnormally short and rounded wing. In the Moluccas, *O. bouroensis* and its relatives have lost both black and lipochrome to such an extent that they have become dull brownish birds (see MIMICRY).

Food. All the species are exclusively arboreal, feeding on insects and fruit. In the *Sphecotheres* spp., commonly known as figbirds, fruit is the major component of the diet. The African Blackheaded Oriole *O. larvatus* also takes nectar by probing into flowers.

Voice. Certain features of the voice are widespread in the family, namely the sweet, fluting and liquid songs and calls, and also a harsh growling or bleating note. The figbirds have a chattering call and appear to be more noisy than *Oriolus* spp., particularly when feeding.

Breeding. The typical nest of *Oriolus* spp. is a deep cup, closely woven of beard lichens or grass, and slung in a horizontal fork on a lateral branch high above ground. Nests of *Sphecotheres* spp. are not woven and are small untidy cups placed in horizontal forks in foliage and may be up to 20 m above ground. The eggs of *Oriolus* spp. have rich dark blotches or spots on a white, buff or pink ground. Eggs of the figbirds are greenish, from a pale apple-green to a dull olive-green, with dark markings. The nests and eggs of several species of Oriolidae remain to be described.

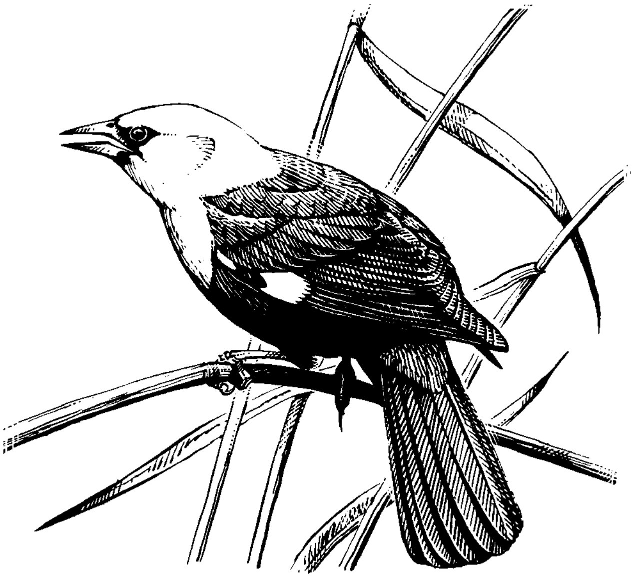
In the European Golden Oriole care of the eggs and young is shared by both adults of the pair (incubation and fledging periods each *c.* 14–15 days), but very few detailed studies of any of the other species have been made. (R.E.M.) W.R.J.D.

Greenway, J.C. Jr 1962. Family Oriolidae. *In* Mayr, E. & Greenway, J.C. Jr (eds.). Checklist of Birds of the World, vol. 15. Cambridge, Mass.

ORIOLE (2): substantive name of *Icterus* spp.; in the plural form 'American orioles', general term for the family Icteridae (Passeriformes, suborder Oscines). This strictly New World assemblage of 9-primaried song birds is derived from emberizine stock and forms a remarkably heterogeneous family of medium-sized birds that includes such diverse natural groups as the oropendolas, caciques, grackles, American blackbirds, American orioles or troupials, cowbirds and meadowlarks.

Characteristics. The approximately 90 species in this family range in size from 15–53 cm in length. All have unnotched conical bills that are usually pointed and not longer than the head; rictal bristles are lacking or obsolescent. In some of the larger species, especially oropendolas and caciques, the culmen is expanded or swollen basally, especially among males, to form a conspicuous frontal shield or casque. The predominant body colour in the family is black, but some species lack black entirely, and in most the basic colour is conspicuously patterned with red, orange, yellow or brown. Iridescent gloss is characteristic of the black of many species. Many species, particularly those with non-monogamous mating systems, are strongly sexually dimorphic in size and behaviour. Plumage dimorphism is also common, especially at high latitudes, but most of the tropical forest species are monochromatic. In many species with pronounced sexual dichromatism there is a first-year male plumage, typically intermediate between that of the female and the adult male, which may be highly variable. Streaked plumage is present in both sexes of grassland species such as meadowlarks (*Sturnella, Leistes*) and among females of many marsh (some *Agelaius*) and wet grassland (Bobolink *Dolichonyx oryzivorus*) species. In most species the non-breeding plumage is identical with the breeding plumage, but males of some black species acquire brown tips to their feathers during the post-breeding moult, the full black plumage being acquired gradually through wearing of the feather tips. The male Bobolink undergoes a striking change of plumage during the winter, acquiring the drab, streaked plumage of the female.

Distribution. American orioles are best represented in the lowland tropics, but there are common species at temperate latitudes and in tropical montane habitats. One species, the Rusty Blackbird *Euphagus carolinus*, breeds north of the Arctic Circle, while the Austral Blackbird *Curaeus curaeus* breeds to the southern limits of land in Tierra del Fuego. Icterids are found in virtually every type of vegetation in the New World except tundra. The largest number of species is found in tropical forests, especially disturbed areas, but these birds are among the dominant species in savannas, grasslands and marshes. In the western Amazon basin, up to 12 species can be found in a single habitat.



Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. (*D.A.T.*).

Populations. Because many icterids are found in disturbed habitats, they have often benefited from human-induced environmental changes. Many species have readily adapted to croplands and grazed pastures. The Red-winged Blackbird *Agelaius phoeniceus* is one of the most abundant breeding birds in North America. The Brown-headed Cowbird *Molothrus ater* has undergone enormous expansion in both range and population size in North America during the past half century. Its southern counterpart, the Shiny Cowbird *M. bonariensis*, is also rapidly expanding its range northward through the West Indies. Some species, such as Red-winged Blackbirds, cowbirds and grackles *Quiscalus*, have become crop pests. None of the species, except for a few on the West Indian islands, appear to be declining in abundance or in danger of extinction.

Movements. Most tropical species of icterids are sedentary or undergo only limited seasonal movements in response to changing patterns in availability of fruit and insects or vegetation disturbance. There is one interhemispheric migrant, the Bobolink, which breeds in southern Canada and northern United States and winters primarily in the pampas of Argentina. Most of the North Temperate breeding species migrate south for the winter, but few penetrate farther than Central America, and many winter as far north as snow-free ground is usually available. In South America, where there is so little temperate land mass and climates are maritime, there is relatively little northward movement for the winter. Some species, such as the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*, which depend on large populations of emerging aquatic insects for breeding, change breeding locations substantially between years, whereas others are highly sedentary and show great local variations in plumage and voice.

Food. The key to the evolution of the icterids lies in their ability to open their bills forceably against considerable pressure. Most species in the family use such gaping movements extensively during feeding and this behaviour reveals food not available to species that must find it on the surface. Gaping is used to extract food from epiphytes on trees, especially bromeliads (oropendolas, caciques, orioles and the endemic Jamaican blackbird *Nesopsar*), flowers (many genera), dead branches and crevices in bark (caciques), the bases of clumps of grasses (meadowlarks), pine needles (orioles), the ground (meadowlarks), under rocks and cowpats (many blackbirds, cowbirds) and fruit (orioles, caciques and oropendolas). Some, such as grackles, also have powerful muscles for closing the bill and are able to crush large seeds. The nestlings of most species are fed primarily on arthropods, but many species are partially frugivorous (tropical species) or granivorous (most temperate species) during the non-breeding season. Many icterids are highly adapted for foraging on the ground and progress by walking. Marsh-nesting species are able to forage efficiently in the dense vertical growth of those habitats, often by straddling between stems with their legs extending laterally from their bodies. Many are adept at holding prey in their feet while subduing and dissecting it with the bill. Ground-foraging species are also able to expose hidden food by scratching, usually using both feet in a rapid backward movement, one foot being moved slightly after the other. A common pattern of movement employed by flocking species feeding in open grassland and cropland is one in which birds at the rear of the flock fly over their flockmates to the front and feed in a fixed spot until they are at the rear, when they repeat the movement again. When viewed from a distance such a flock appears to 'roll' across the field.

Behaviour. Diversity of social organization is one of the most notable characteristics of the American orioles. Some species are monogamous and defend large, exclusive territories during the breeding season (meadowlarks, *Dives*, most orioles, some caciques), others are monogamous but colonial (*Quiscalus, Euphagus, Curaeus*), some are territorial but polygynous (some *Agelaius, Xanthocephalus, Dolichonyx*), some are colonial and polygynous (oropendolas, some caciques, some grackles, especially *Cassidix*). An unusual form of breeding is found in the cowbirds, most of which do not build their own nests but lay their eggs in the nests of other species. Only the Bay-winged Cowbird *Molothrus badius* of temperate South America incubates its own eggs and feeds its own young. Some of the cowbirds are highly host-specific, usually within the family Icteridae. For example the Screaming Cowbird *M. rufoaxillaris* apparently parasitizes only the Bay-winged Cowbird, while the Giant Cowbird *Scaphidura oryzivora* parasitizes only oropendolas and caciques. Even the more catholic species, such as Brown-headed and Shiny Cowbirds, heavily parasitize other members of the family. Occasional bigamous matings have been reported in normally monogamous species, presumably the result of local imbalances in sex ratios, but the well-developed non-monogamous mating systems are not due to sex ratio imbalances. Sex ratios of nestlings at the time of fledging are close to 1:1 in those few species that have been studied intensively. There are substantial populations of non-breeding males, usually younger birds, in the polygynous species. These non-breeders may obtain territories when numbers of older birds are low, and can be induced to take over territories by the removal of established adults.

Voice. Icterids produce a wide variety of notes ranging from harsh and guttural to very musical. In general the monogamous, territorial species are excellent songsters and some species, such as the Melodious Blackbird *Dives dives*, the Shiny Cowbird and the Chopi Blackbird *Gnorimopsar chopi*, are highly prized as cage birds in Latin America. Among tropical species that remain permanently paired on territories, it is common for both sexes to sing, probably because individuals of both sexes must seek replacement mates with approximately equal frequency. In a few species, most notably the Melodious Blackbird, this has been developed into a complex and precisely timed duetting in which each member of the pair sings a different part of the complex song. Song is restricted to males in most migratory monogamous species. Among monogamous species song rates drop strikingly as soon as pairing takes place, but song rates of polygynous males remain high through much of the breeding season. Males of many species sing regularly in autumn and winter flocks, often in loud choruses, but the function of that singing is obscure. In general, species with colonial breeding systems have more vocalizations than territorial species and, among polygynous species, males have many more vocalizations than females. In some polygynous species, females defend space within the territories of the males and may use specific vocalizations and displays to exclude other females.

Breeding. The nests of icterids are among the most varied of any avian family. Terrestrial species build well-concealed but simple (Bobolink) or domed (meadowlarks) nests on the ground. The marsh-breeding species build most of their nests in the emergent aquatic vegetation while savanna and scrubland nesting species build their nests in bushes and trees. Orioles suspend their woven, sack-like nests from the tips of the branches of trees where they are inaccessible to most mammalian and reptilian predators. The colonial oropendolas and caciques nest in large, usually isolated trees, and build their remarkable hanging nests, that may measure up to 1½ m in length, in large groups. In most species, nests are built entirely by the females, who also perform incubation unaided by their mates for 11–14 days. Clutches of 2–3 are characteristic of tropical species while 4–6 eggs are usual for the higher latitude species. Nestling periods range from about 10 days in the smallest to about 5 weeks in the largest species. In the monogamous species both sexes share in the feeding of the young, but in some polygynous ones only the female brings food. In these species the males continue to defend territories and attempt to attract additional females. The evolution of these differences appears to be related to the value to the males of differing patterns of investments. In the Yellow-headed Blackbird, for example, where breeding is highly synchronous, most males do feed nestlings, preferentially at the first nest to hatch on their territories. In the Red-winged Blackbird, however, where new females are attracted over a much longer period of time, most males do not feed nestlings, but many feed fledglings later in the season when the probability of attracting additional females is low. Many species are single-brooded, but double broods are raised by at least part of the population in a few species. In most species, renesting occurs if the first nest is destroyed. Helpers at the nest are known in several species (Bay-winged Cowbird, Austral Blackbird, Brown-and-yellow Marshbird *Pseudoleistes virescens*), but the genetic relationships between nest owners and helpers are unknown. However, helping does occur in species that do not remain as family units on territories during the non-breeding season. (E.R.B.) G.H.O.

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ORIOLIDAE: a family of the PASSERIFORMES, suborder Oscines; ORIOLE (1).

ORNAMENTATION, BIRDS IN HUMAN: Gilbert's lines in *The Gondoliers*, 'I wonder whether she'd wear a feather—I rather think she should!' reflected the fashion of the age. They appeared in 1889, the very year that saw the foundation of the [Royal] Society for the Protection of Birds to combat the plumage trade. Appalling numbers of egret (e.g. *Egretta*) plumes (commercially misnamed 'ospreys'), as well as hummingbird (Trochilidae) and bird-of-paradise (Paradisaeidae) corpses, were being imported for the ornamentation of fashionable ladies, and it was not until the 1920s that legislation and the vagaries of *la mode* put a virtual end to the slaughter. Today in Britain some men's hats are still sold with a small gamebird feather in the band, but about 1950 hatters ceased to stock the sprays or 'mounts' of feathers that could be transferred from one hat to another. In the western world the wearing of feathers is nowadays restricted mainly to those who fulfil certain conditions. Ostrich *Struthio camelus* feathers adorn some official cocked hats, the bonnets of bagpipers, and until recently the coiffures of debutantes. Raptor plumes are thought proper to the bonnets of certain Highland chiefs, and the Black Watch wear the Red Hackle of feathers dyed to match the blood spilt by the regiment at Fontenoy. Here the aesthetic appeal of the feather is complemented by its function as a signal of rank, privilege, or group membership. The same is true in much of the 'primitive' world. To peoples without chemical dyes feathers offer a source of bright colour equalled only by flowers, and much less fragile; but some birds too have qualities that a man would wish to share, such as keen sight or skill in taking prey, and which he may acquire by donning their plumage. Dissociation of the purely decorative from the symbolic or the sacred in this field is difficult and will not be attempted here. For whatever motive, Man's use of feathers goes far back into prehistory and is, on varying levels of frequency, world-wide, attaining its most noteworthy development in the Americas and Oceania.

In North America eagle feathers were highly valued, especially the white, dark-tipped tails of the immature Golden Eagle *Aquila chrysaetos*. A few tribes kept caged eagles, but among some Plains Indians the birds were hand-caught by men concealed under carrion-baited screens of foliage and released minus tail. The feathers were hung from weapons, pipes and bridles, and especially worn in the hair of warriors to indicate, by a precise code of notches, painting and angle, the wearer's deeds. Originally only Plains men of outstanding valour might aspire to the now familiar eagle-plume 'war bonnet', which in its earlier forms was much less stylized both in shape and in the feathers employed. Various species contributed to the simpler crowns and circlets worn in the eastern and southern Woodlands, where the Wild Turkey *Meleagris gallopavo* was favoured. Among other uses, turkey feathers were tied into fibre netting to produce mantles both warm and decorative. Nineteenth century traders found an avid market for turkey feathers among the Upper Missouri tribes, outside the bird's normal range. The sedentary Pueblo Indians of Arizona and New Mexico used feathers mainly as altar decorations and aspergilla, and for *pahos*, the wooden pegs with a single pendant downy feather embodying a prayer and used somewhat in the manner of votive candles. Certain Pueblo ceremonies, however, called for topknots of scarlet parrot feathers, obtained from live birds traded north from Mexico.

The most imaginative North American featherwork developed in California, in the form of ceremonial kilts and elaborate head-dresses of brilliant passerine feathers, sometimes dominated by long black plumes from the Condor *Gymnogyps californianus*. The Pomo made exquisite coiled baskets studded with crests of quail (*Lophortyx* sp.), scalps of woodpeckers and flickers (Picidae), and hummingbird feathers. Red feathers from the Pileated Woodpecker *Dryocopus pileatus* served both for ornamentation and as currency. Birds were important to the Indians of the North Pacific Coast but their heraldic carvings of eagle, raven and hawk belong most properly to art. Feathers were little used here, but at the numerous formal feasts the bark head-rings of the participants must be filled with loose white down; and puffin beaks (*Fratercula corniculata* or *F. cirrhata*) were strung together for rattles and fringes. In the Subarctic (especially) bird quills were split and dyed for use in the ornamentation of moccasins and equipment, as a supplement to the more usual porcupine-quill embroidery. The Eskimo combined utility with decorative effect by piecing together the feathered skins of sea ducks and divers (Anatidae, Gaviidae) into garments, or turned them singly into pouches (as did the Swedish Lapps).

Native American featherwork reached its apogee in classical Mexico, the land of the Feathered Serpent. Little has survived, but one or two brilliant examples of feather mosaic may still be seen in museums, and precolumbian codices and sculpture show both Maya and Aztec nobles wearing stupendous headgear based on the plumage of the Quetzal *Pharomachrus mocinno* and the *Xiuhtótotl* (*Cotinga* sp.). The sacred quetzal plumes bulked large in the tribute exacted from subject tribes.

The textile-orientated civilizations of the Andes made no great use of feathers, although the reigning Inca wore above his brow, in life and in death, a pair of sacred plumes taken possibly from a fork-tailed nighthawk, *Uropsalis lyra* or *U. segmentata*. It is in the forest areas of tropical South America that naked or near-naked peoples wed fine craftsmanship to controlled aesthetic sense to produce a variety of resplendent chaplets and diadems. Important among the many species exploited are the toucans (Ramphastidae), parrots and macaws (Psittacidae), curassows (Cracidae), and the Harpy Eagle *Harpia harpyja*. Feathers are also worn on arms, legs and necks, and thrust through perforated ears, lips, cheeks and the nasal septum. In coastal Brazil the Scarlet Ibis *Eudocimus ruber* was semi-domesticated to supply feather mantles. Sixteenth century travellers in the same region saw prospective victims of cannibal rituals whose skin was coated with crushed blue eggshell; the same cosmetic is worn today by girls in the Xingu tribal refuge, without culinary connotations. More widespread is the adornment of the body, overall or in patterns, with down or chopped feathers glued on with resin or latex.

Amazonia is the home of a process, known to ethnologists as tapirage, for altering the pigment of living birds. Typically, green parrots are partially plucked and the bared skin rubbed with the venomous secretions of the Giant Toad *Bufo marinus* or frogs, *Dendrobates* spp., sometimes mixed with a vegetable dye (usually *Bixa orellana*). The next growth of feathers is yellow or red. The biochemistry of the method is unclear, and made more so by the variety of unguents used in marginal areas, including fish fat, or dye alone, but its effectiveness is unquestionable.

Feather ornaments of more sober hue were worn south of the tropics, right to the tip of Tierra del Fuego, where a scrap of birdskin served as a pubic covering for Yahgan women. Here too bird-bone beads were worn. On the pampa feathers of rheas, *Rhea americana* and *Pterocnemia pennata*, and of herons (Ardeidae) took precedence.

Tribal Africa is in general much less feather-conscious than America. Predictably the Ostrich holds pride of place, its plumes decking heads and shields in East and South Africa, most strikingly in the great face-encircling feather 'manes' of such warrior tribes as the Masai and Emberre (who mixed them with those of the guinea-fowl *Acryllium vulturinum*), and surviving most extravagantly in the attire of modern Kaffir rickshaw boys. Ceremonial feather fans from the West African emirates recall those of dynastic Egypt. The wearing of ostrich feathers may indeed have been continuous from the ancient world to the modern, radiating from the Mediterranean and supplied until recently from birds in the North African-Middle Eastern range. About 1870 the European vogue for feathers led to the large-scale farming of ostriches in South Africa, soon carried over into Australia and the USA; early in this century ostrich feathers ranked fourth in value among South African exports. Despite vicissitudes, ostrich farming continues, reinforced by a steady demand for skins, which are converted into fine leather goods. Beads of ostrich-egg shell, ground into button-like discs, are worn up and down Africa, and appear in Libyan graves dated at 700 BC.

The Peacock *Pavo cristatus* and other phasianids are high on the list of species whose plumage is used for dress accessories and the like in the Orient. Flexible peacock feather shafts, stripped of the rami, are stitched into Indian embroideries; forewings of eagles (*Haliaeetus leucocephalus* and *Aquila clanga*) make fans in Manchuria—as in North America (*A. chrysaetos*); and cheap metal jewellery set with bright feathers is popular in China. The Naga tribesmen in Assam greatly value rectrices of the Racket-tailed Drongo *Dicrurus paradiseus*, and it is here that we first meet a preoccupation with the hornbills (Bucerotidae) which recurs at intervals to the limits of Indonesia. The bold black and white tail feathers are worn in the hair and on the war-coats of Dayak headhunters in Borneo, and the solid casque of the Helmeted Hornbill *Rhinoplax vigil* is carved into ornaments which include ear-plugs denoting the taking of a head. Wooden representations of hornbills, variously conventionalized, are important in Bornean ceremonial life. (See also HORNBILL).

A more significant focus on bird exploitation is found in New Guinea, where both men and women delight in disguising themselves behind startling face-paint, pig tusks and shells, topped by enormous structures built up of hair, fur, leaves and feathers—of eagle (*Harpyopsis novaeguineae*), parrots and lorikeets (Psittacidae), cassowary *Casuarius bennetti*, and above all birds-of-paradise. Cassowary plumes are thrust into pierced nostrils as well as through the septum, and cassowary-bone spatulae through the ears. Live cassowaries are kept for their plumage, and change hands as bride-wealth. Across the Torres Strait the northern Aborigines make some use of the Australian species, *C. casuarius*, along with Emus *Dromaius novaehollandiae* and smaller species, but featherwork is not prominent. Bird down is worn at corroborees, affixed sometimes with the wearer's blood. Patriotic plumes for regimental slouch hats seem to be the emu's one tiny contribution to white Australian adornment.

In the western Pacific featherwork, tasteful generally, achieved a brilliant climax on Hawaii. Its most characteristic manifestation everywhere is the feather cloak. The New Zealand Maoris make them of Kiwi *Apteryx australis* feathers tied into a groundwork of native flax, and may trim them with those of the New Zealand Pigeon *Hemiphaga novaeseelandiae*, Kea *Nestor notabilis*, and others. Chiefs used to supplement the cloak with one or two tail feathers of the extinct Huia *Heteralocha acutirostris* in the hair.

The most precious sources of feathers in Polynesia however were the honeyeaters (Meliphagidae) and Hawaiian honeycreepers (Drepanididae). On Santa Cruz Island fibre belts over 6 m long, covered with the scarlet body feathers of the Cardinal Honeyeater *Myzomela cardinalis*, were currency. On the Hawaiian group half a dozen species contributed splendour to the high-born in the form of *leis*, plumed staves, helmets and, most notably, robes. Leis were feather garlands more durable than those of flowers which are draped over modern tourists. The official staves, *kahili*, were emblems of authority. The helmets, *mahiole*, were astonishingly like Graeco-Roman models in outline, with high, broad keels, but made of wicker and entirely covered with tiny feathers set almost as closely as on the bird itself. So too were the robes, *ahuula*, varying in size from shoulder capes to full-length cloaks. The basic colour was normally yellow, counterpointed by triangles or lozenges of red or black. The yellow came from the small axillary tufts of the mainly black O-o *Moho nobilis*, red from the Iiwi *Vestiaria coccinea* and Apapane *Himatione sanguinea*, and black and orange from the Mamo *Drepanis pacifica*; some other species were utilized to a lesser extent. To make a robe, tufts of up to 20 tiny feathers were tied in so thickly and evenly that the foundation of *Touchardia* fibre is quite invisible. A full-sized robe may have some 100,000 such tufts.

Examples of this work survive to dazzle the eye and the imagination, but no more can be made; O-o and Mamo, like the New Zealand Huia, have gone, killed off not by feather-hunters (the rarer birds were released to grow new feathers) but by the destruction of habitats. Elsewhere however conscience has prevailed over commerce in time to save the egrets and birds-of-paradise, and the taking of eagles for latterday Indian festival gear in the USA is forbidden by laws which the Indians brand as discriminatory.

This article is based mainly on a long acquaintance with museum collections. The subject is touched on in innumerable ethnographies but the 4 books listed below are particularly relevant. The present tense used herein may soon, or already, be rendered inappropriate in some contexts by the advance of Progress and denim; feather ornaments are worn often in inverse ratio to the amount of other covering, in the jungle just as in the cabaret. G.E.S.T.

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ORNIS: Greek word (plural 'ornithes') for bird, used scientifically (in the singular)—but seldom nowadays—in the sense of AVIFAUNA.

ORNITHIC: pertaining to birds.

ORNITHICHNITE: geological term for a bird's footprint preserved in stone.

ORNITHOGAEA: name for a zoogeographical region (not one of the classical divisions) considered to include New Zealand and Polynesia. Reasons are given elsewhere for treating New Zealand as a subregion of the Australasian Region, and for excluding oceanic islands from any such scheme (see AUSTRALASIAN REGION; DISTRIBUTION, GEOGRAPHICAL).

ORNITHOLITE: geological term for the fossilized remains of a bird (see FOSSIL BIRDS).

ORNITHOLOGICAL SOCIETIES: organized groups of ornithologists with a collective interest in watching, studying or enjoying birds; or in their protection and conservation (see BIRD-WATCHING; CONSERVATION; ORNITHOLOGY).

Probably more than in any other branch of zoology, progress in ornithology depends on wide participation. Trained scientists in universities, museums and similar foundations and research institutes play their part, especially in more complex fields such as physiology or behaviour, but many studies of distribution, biology, ecology and migration are founded on this general enthusiasm for collective participation by amateurs, pursuing ornithology as a hobby.

Typifying the potential scientific achievement of such collaborative effort is the *Atlas of Breeding Birds in Britain and Ireland*, published in 1976 (see ATLAS). The project to map the breeding season distribution, based on survey visits to the 10 km squares of the British National Grid, was initiated by the British Trust for Ornithology (BTO) and Irish Wildbird Conservancy (IWC) and ran for the 5 years 1968–1972. It has been estimated that up to 15,000 observers took part, contributing immeasurable hours of field-work to visit every one of 3,862 squares, resulting in an invaluable *Atlas* of a precision unthinkable by any other approach.

The senior ornithological body in Britain is the British Ornithologists' Union founded in 1858, a learned society publishing the journal *Ibis* and devoting some of its subscription income to supporting ornithological expeditions, research and publications in Britain and overseas.

Concerned with the practicalities of the study of all types of birds is the BTO (founded 1933; journals *Bird Study, BTO News, Ringing and Migration*), whose members are able to participate actively in a wide and ever-changing spectrum of censuses, surveys, biological studies and bird ringing. The extensive data collected from these co-operative ventures is analyzed either by an amateur enthusiast or by the Trust's professional headquarters staff. The Wildfowl Trust (journal *Wildfowl*), founded by Sir Peter Scott, has a network of reserves directed at waterfowl conservation but is better known internationally as a centre of waterfowl research, ranging from population estimation, movements and ecology to the captive breeding of the Ne-ne *Branta sandvicensis*.

In Scotland the Scottish Ornithologists' Club (SOC) with its journal *Scottish Birds*, and in Ireland the Irish Wildbird Conservancy (journal *Irish Birds*) fulfil national roles, often co-operating with the BTO and the Royal Society for the Protection of Birds (RSPB; magazine *Birds*) in research covering all Britain and Ireland. There is as well a remarkable regional and local network of societies. In 1982, excluding branches of the RSPB, there were 170 organizations devoted to birds against only 46 catering for all other aspects of zoology.

Most counties have their own society, providing meetings and excursions to inform and interest their members and maintaining records of the status of the county avifauna. Most countries in northern Europe have an infrastructure of regional and local societies and clubs broadly similar to, but rarely so extensive as the network in Britain.

There are 3 major scientific ornithological societies in North America: American Ornithologists' Union (journal *Auk*), Wilson Ornithological Society (journal *Wilson Bulletin*), and Cooper Ornithological Society (journal *Condor*). The National Audubon Society provides leadership in conversation issues. There are also many state and province societies. In Australia, the Royal Australasian Ornithologists' Union publishes *Emu*. In Europe, most countries now have a national society (for example, Société Ornithologique de France, journal *L'Oiseau*; Nederlandsche Ornithologische Vereenigung, journal *Ardea*; Deutsche Ornithologen Gesellschaft, *Journal für Ornithologie*). The oldest society in Asia, the Bombay Natural History Society, celebrated its centenary in 1983. (The journal *British Birds*, published monthly since 1907, is an exception in not being the organ of a particular society or institute.)

These periodical journals are the prime means of disseminating ornithological information and it is generally within their pages that additions to our knowledge of birds are published. Relatively little is found in more general journals connected with animal ecology, physiology or behaviour, a situation distinct from most other disciplines save perhaps entomology. Many of the specialist journals are now regularly abstracted by the various international biological data retrieval systems, and an annual guide to the past contents of the majority can be found in the *Zoological Record* published by the Zoological Society of London. Of the 36 most-cited journals devoted to birds, 13 are specifically named after birds. J.J.M.F.

ORNITHOLOGY: the scientific study of birds; that branch of Zoology concerned with the Class Aves. (See AVES; BIRD-WATCHING; CONGRESSES, INTERNATIONAL; ORNITHOLOGICAL SOCIETIES; and articles on general subjects.)

Birds are fascinating objects for scientific study: their feathers, respiratory and circulatory systems are unique and extremely effective in relation to their great mobility. Flight has opened up new horizons in the form of migration, but has also imposed some strictures. The forelimb is given over to flight, so the food-gathering 'hand' has been lost, but this in turn has led to the enormous adaptive radiation shown by birds' BILLS. Research on birds may be considered under main discipline headings, though, as in all branches of Natural Science, the boundaries between disciplines are not clearly defined: indeed one may often augment another.

Systematics. Deals with the identity and relationships of birds, both of the present time and those of the fossil record, and is based largely on anatomy but with an increasing input from elsewhere e.g. protein analysis. There is a natural connection to studies of evolution.

Anatomy and physiology. Birds as a Class are regarded by general zoologists as remarkably uniform compared with other animal groups. Thus the subtle distinctions between the different anatomical and physiological adaptations that fit each species or group to its way of life are particularly interesting.

Ecology and distribution. Studies which relate birds to their total environment, for example in terms of food or population dynamics, come under this heading. So too does MIGRATION, an ability widely and well developed in birds, and a fertile study area where several key questions remain unanswered.

Behaviour (or **ethology**) **and vocalization.** Deal with the habits, e.g. courtship and aggressive displays, of birds and their songs and calls, including their causation and biological function.

Applied ornithology. Deals with the interactions between birds and men. At one extreme fall the economic aspects of bird damage to crops and its prevention, and at the other lie studies of species threatened by habitat loss or pollution at man's hand. Between lies the role of bird populations as indicators of environmental change.

While ornithology has benefited widely from research in other branches of zoology—for example from studies of migrating fish—there are many cases where ornithological investigations have been the foundation stones of research throughout zoology. Charles Darwin's studies of the Galapagos finches (see DARWIN'S FINCHES) contributed to the formulation of his theories on the ways in which new species originate—views that were to revolutionize all subsequent biological thinking. P.L. Sclater's work on the geographical distribution of birds, propounded in 1858, opened this field of study to all zoologists, and Sclater's zoogeographical regions were largely adopted by Alfred Russel Wallace, 18 years later, for animals in general. More recently, V.C. Wynne-Edwards and David Lack have been pioneering theorists at the forefront of studies of the factors regulating animal populations. J.J.M.F.

ORNITHOMANCY: divination from observations of the flight of birds—the words 'augury' and 'auspice' both owe their origin to this superstitious practice, being derived from the Latin 'avis' (see OMENS, BIRD AS).

ORNITHOPHILOUS: botanical term applied to plants fertilized through the intermediacy of birds (see POLLINATORS).

ORNITHOSCOPY: same as ORNITHOMANCY.

ORNITHOSIS: term (plural 'ornithoses') applied to diseases identical with, or closely related to, psittacosis (occurring in birds not necessarily of psittacine species)—see PSITTACOSIS.

OROPENDOLA: substantive name of species in the tropical genus (*Psarocolius*) of Icteridae (see ORIOLE (2)).

ORPHANED BIRDS: see CARE OF SICK, INJURED AND ORPHANED BIRDS.

ORTHONYCHINAE: see RAIL-BABBLER.

ORTOLAN: name, alternatively 'Ortolan Bunting', of *Emberiza hortulana* (for subfamily see BUNTING); the gastronomic application of the name is wider than its specific one.

ORTSTREUE: fidelity to home area, used especially for the tendency of migrants to return to a previous breeding or wintering area. A German term that has been widely used in English publications. See DISPERSAL.

OSCINES: see under PASSERIFORMES.

OSPREY: *Pandion haliaetus*, in America often called 'Fish-hawk' (see HAWK). Also a plumage trade misnomer for egrets (Ardeidae).

OSSIFICATION: see AGE; SKELETON, POST-CRANIAL; SKULL.

OSSIFRAGE: archaic name for the Lämmergeier *Gypaetus barbatus* (see VULTURE (1); also BIBLE, BIRDS OF THE).

OSTRICH: the largest living bird, *Struthio camelus*, the only species of the Struthionidae (Struthioniformes), which are placed in the group of large flightless birds known as 'ratites'. Now confined to some of the more arid areas of Africa; 'American ostrich' is an outdated term for the RHEA.

Characteristics. Adult Ostriches stand about 2.5 m high and weigh up to 150 kg. The eyes are large, surrounded by conspicuous eyelashes, and give very acute vision. The neck is flesh-coloured and appears bare, being covered only with minute downy feathers. It and the bare thighs develop a bright red or blue colour (depending on the race) in breeding males. The feathers covering the body lack barbules, giving them a soft appearance. The adult male is jet black, with beautiful white primary plumes in the wings and tail, although the latter usually become stained dark, perhaps deliberately. The female is grey or grey-brown all over, and is slightly smaller than the male. The legs are long and powerful, ending uniquely in only two toes; they can carry the ostrich at a running speed of up to about 50 km/h.

Ostrich *Struthio camelus*. (*K.J.W.*).

Habitat. Ostriches inhabit a range of open habitats from desert to savanna; they do not occur in thick bush or forest. They occasionally reach densities of more than 1 per km^2, but in most places they are much less abundant.

Distribution. Only 4 races of Ostrich are now both recognized and still extant. The nominate race *S.c. camelus*, the North African ostrich, stretches along the southern side of the Sahara from Morocco to Ethiopia. The so-called Dwarf Ostrich *S.c. spatzi* from Mauritania was mistakenly classified on inadequate information. In the Horn of Africa lives the Somali Ostrich *S.c. molybdophanes*, the males of which have bright blue-grey skin on neck and thighs. There is very slight hybridizing and overlap in eastern Kenya with its southern neighbour, the Masai Ostrich *S.c. massaicus*, which has bright red skin during the breeding season. This race stretches south as far as the Katavi plain in south-west Tanzania.

The South African Ostrich *S.c. australis* is found south of the Zambesi river in suitable open arid country. The Arabian Ostrich *S.c. syriacus* once abundant, has become extinct since 1941 (or possibly 1966). Populations elsewhere are declining in range, but are generally not unduly persecuted or threatened.

At Oudtshoorn, in the Cape Province of South Africa, Ostriches have been farmed as domesticated birds since 1860, originally for the feathers only but now also for leather, meat and tourism. Hybridization with imported North African Ostriches at the end of the last century improved the quality of the feathers of the domestic stock; this mongrel variety has been released and become feral in parts of South Africa and Australia (see DOMESTICATION).

Movements. In the less arid regions of East Africa, ostriches are largely resident, the same individuals remaining in the same area throughout the year. In desert regions they are reported to migrate more, and probably cover considerable distances in search of food and water.

Food. Ostriches are clearly well adapted to feeding on scarce high-quality foods—they can stride effortlessly over a sparsely vegetated landscape, lowering the beak on the end of the long neck to pluck off selected food items. They are almost entirely herbivorous, choosing leaves, flowers and seeds of a wide variety of plants. There are only occasional reports of their eating insects and other animals in the wild, despite their well-deserved reputation in captivity for swallowing anything. When feeding, the food from many pecks is stored at the top of the neck and then all visibly passes as a single large bolus down the elastic neck.

Behaviour. The groupings of Ostriches vary with race, place and season. They are often seen singly, often in pairs, and often in small groups of up to 5 or 6 birds. In arid regions larger aggregations may occur at particular feeding or drinking places. The small groups typically seen in East Africa are loose and temporary, as individuals join and depart from others in an apparently casual way. Their exceedingly acute eyesight, and their conspicuousness, especially of the males, clearly helps them to locate other members of their species.

Within the loose groups, both or all the individuals tend to be engaged on roughly the same activity at the same time—feeding, standing alert, walking, preening, or dustbathing. Preening is a frequent activity, but apparently directed as much towards snapping at pestering flies as towards care of the feathers.

Motivation and dominance relations are expressed by different body postures and wing movements. During aggressive encounters, males draw themselves up to their full extent, erect the body feathers, raise the tail, and flap their wings up and down on each side alternately. Much time is spent on threats and chases between breeding adult males, but actual fights are rare. The feet are their only, but extremely effective, weapon; an ostrich can deliver a fearsome forward kick at its opponent's chest. Threat or mild aggression towards a group member is accompanied by raising both wings and opening the beak wide.

Voice. During the breeding season, male Ostriches utter a loud 3-note booming sound, which has been likened by Livingstone and others to the roar of a lion. It is used in proclaiming ownership of a territory and attracting females.

Breeding. In East Africa, Ostriches breed during the dry season, but in more arid regions elsewhere, at the onset of the rains. The males' necks acquire their bright coloration, and territorial defence begins. The males boom, chase out intruding males, and court any females which come through their large territory. The courtship display is spectacular. The male draws himself up high, raises and erects his tail, and approaches the female at a trot. Suddenly he drops to a squat and rocks from side to side, his black and white wings extended and waving in the air alternately. Meanwhile his neck, even brighter red (or blue, according to subspecies) than usual, writhes from side to side. He may wave his wings as many as 70 or more times in front of the female, who is usually in the submissive or soliciting posture with head and both wings lowered and quivering. The male stands, approaches the female, raises both his wings high above his back, and mounts the squatting female. The mating itself is accompanied by further wing waving.

The male prepares a number of shallow scrapes somewhere within his territory. One of these is accepted by a female (the 'major' hen) who lays the first egg in it and continues to lay there at regular 2-day intervals. Up to 5 other females (the 'minor' hens) lay in the same nest, also on alternate days. The male has usually mated with these minor females, and he leads them to the nest with a wing-lowered display like that of submissive females.

The eggs are almost round, usually between 1,300 and 1,900 g in weight. The shell is about 2 mm thick, pitted with small pores, and shiny creamy white in colour.

Nest destruction is frequent, caused by Egyptian Vultures *Neophron percnopterus* which throw stones at the eggs, and by jackals and hyaenas. After the first few days, an adult ostrich may attend the nest to protect it against both heat and nest predators.

The major female lays about 10 eggs in her nest before incubation begins, and the minor hens may between them have laid between 10 to as many as 30 or more eggs there. At the start of incubation, the major hen pushes out a number of surplus eggs into an outer ring 1–2 m away where they are not incubated and are doomed. She rarely pushes out any of her own eggs, but retains them among the 20 or so which she can cover and incubate in the centre of the nest.

Incubation takes about 42 days. It is done by the major female during the day and by the male at night. The minor females take no part in it. The chicks are nidifugous, and leave the nest with the adult pair soon after hatching. Over the next few weeks the brood often merges with the broods from other successful nests, resulting in large aggregations of chicks attended by only one set of adults. The chicks grow very fast and are almost full height within a year. They reach sexual maturity at 3–4 years old, and probably live for at least 40 years.

See photo HEAT REGULATION. B.C.R.B.

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OTIDES; OTIDIDAE: see under GRUIFORMES; BUSTARD. (The spelling 'Otidae' is patently erroneous.)

OU: *Psittirostra psittacea* (for family see HAWAIIAN HONEYCREEPER).

OUTER TOE: see LEG.

OUZEL: substantive name, also spelt 'ousel', of the Ring Ouzel *Turdus torquatus*, but formerly applied to the Blackbird *T. merula* (cf. German 'Amsel')—see THRUSH. 'Water-ouzel' is a popular name in Britain for *Cinclus cinclus* (see DIPPER).

OVARY: female gonad, in birds usually developed only on the left side (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

OVENBIRD (1): substantive name of several species of Furnariidae (Passeriformes, infraorder Furnarii); in the plural, serves as a general term for the family but applies particularly to the nominate subfamily. The woodcreepers or woodhewers (Dendrocolaptidae) are often treated as a subfamily of the Furnariidae, but are here treated as a distinct family. The family is purely Neotropical and predominately South American; and it comprises about 221 species, in 58 genera, although many genera are considerably oversplit.

The Furnariidae are probably more diverse than any other avian family. Most systematists recognize subfamilies and these groupings may be usefully introduced here. The Furnariinae (confined to South America), besides true ovenbirds or horneros of the genus *Furnarius* (which build a mud nest like an old fashioned earth oven and thus give the family its name), include a variety of divergent genera such as the miners (*Geobates*, *Geositta*), the groundcreeper (*Clibanornis*), the earthcreepers (*Upucerthia*), the Tococo (*Chilia*), and shaketails or cinclodes (*Cinclodes*). Next and equally important are the Synallaxinae or spinetails, typified by the genera *Synallaxis*, *Cranioleuca* and *Asthenes*, which are rather less variable and tend to be characterized by peculiar tail structure and the building of relatively enormous enclosed nests, for this reason sometimes being called castle-builders. The genera of treerunners (*Margarornis*) and the Barbtail (*Premnoplex*) are often placed in a separate subfamily Margarornithinae, but are perhaps best included with Synallaxinae.

The third large and diverse subfamily, the Philydorinae, includes treerunners (*Pygarrhichas*), treehunters (*Thripadectes*), Hookbill (*Ancistrops*), Pointed-tail (*Berlepschia*), cachalotes (*Pseudoseisura*), xenops or recurved-bills (*Megaxenops* and *Xenops*), and the foliage-gleaners (*Philydor*, *Automolus*, etc.). The Philydorinae represent the ovenbird subfamily closest to the woodcreepers (Dendrocolaptidae) and may be considered with certainty to represent a transitional group to the woodcreepers. The affinities of the Sclerurinae, genera *Sclerurus* (leafscrapers) and *Lochmias* (Streamcreeper), are uncertain.

Characteristics. Most of the family consists of small brown birds which is as much as can be said by way of generalization. The largest members are about 25 cm in total length, e.g. cachalotes, species of *Pseudocolaptes*, and the large *Cinclodes*. The colour of nearly all members of the Furnariinae is dull, being shades of brown sometimes tending to rufous or chestnut or with rufous parts, usually paler or even white below, and often with a striking wing bar. The miners, earthcreepers, and shaketails, which are all grey-brown or dark brown birds, perhaps paler and somewhat mottled below or with a white wing bar (*Cinclodes*), reach the acme of drabness. The true Ovenbird *Furnarius leucopus* ('El Hornero' of the South Americans) differs in being essentially bright chestnut above and white below. The spinetails tend to be less drab and uniformly coloured, being mostly variegated on the upper parts with brown, chestnut, and almost black, and sometimes with dark streaking on the throat and breast (otherwise usually almost white). Some members even have some bright colour, e.g. the White-cheeked Spinetail *Schoeniophylax phryganophila* with a bright yellow chin, and *Asthenes* spp. with a touch of reddish chestnut on the throat. Species of *Margarornis* are rufous above and dark olive below, heavily marked with pear-shaped drops of light buff, somewhat resembling a woodcreeper. Similarly, the Sclerurinae are generally dark coloured and may be scalloped with white below. Many of the Philydorinae resemble woodcreepers, again, with their characteristic streaking on head and under parts, e.g. *Berlepschia rikeri* and *Pseudocolaptes* spp., while the genus *Philydor* has bright orange underparts.

The wing is as variable as other features of the family, from soft, short, and rounded, to long and somewhat pointed. The tail may be normal, or rather short as in *Furnarius* and *Geositta*, but is remarkably diverse among the spinetails. In that subfamily there is a tendency for it to be graduated or forked, long and attenuated, with the feather barbs breaking down and the webs becoming degenerate so that the naked quills project. For instance, *Leptasthenura* spp. have long tails with tapering rectrices, and *Synallaxis* spp. have graduated tails with the ends of the rectrices frayed and broken down so that the shafts project. Most remarkable of all is Des Murs' Spinetail *Sylviorthorhynchus desmursii*, with a tail 2 or 3 times as long as the rest of the bird, of very thin feathers with poorly developed webs. On the other hand, 'softtails'—*Metopothrix* and *Xenerpestes*—have normally developed rectrices, but with the shafts not at all strong, while the rectrices of *Berlepschia* are sharply tapered. Those forms which resemble dendrocolaptids (*Pseudocolaptes, Syndactyla, Anabacerthia*, and *Philydor, Xenops*, etc.) are distinguished from members of that family by not having the shafts of the rectrices stiffened.

A very few species are crested, such as the Plainrunner *Coryphistera alaudina* and the Brown Cachalote *Pseudoseisura lophotes*. The bill is mostly rather short, straight and pointed, and is normally wide; but many variations occur, the bill being long and decurved in *Upucerthia*, short and slightly curved in *Geositta*, moderate in both respects in *Furnarius*, long and straight in *Sclerurus*, laterally compressed in *Xenoctistes*, and short, wedge-shaped with upturned mandible in *Xenops*. The legs and feet are usually medium to short, but are strongly developed in terrestrial forms such as the true ovenbirds and cachalotes.

Habitat, ecology and behaviour. Most genera and species inhabit thickly wooded habitats or areas with plenty of good cover, and this applies particularly to those within the tropics (where the majority of the family live); but even so there are differences in habitat and behaviour. The foliage-gleaners (*Anabacerthia, Automolus*) are birds of the canopy and forest trees, where they hunt through the leaves like warblers (Sylviinae). *Heliobletus contaminatus* has the habits of a treecreeper (Certhiidae) or woodcreeper (Dendrocolaptidae), as have the treerunners. The leafscrapers inhabit the densest undergrowth, are great skulkers, and have the habit of rooting through leaves and tossing them in the air in their search for food. The Sharp-tailed Streamcreeper *Lochmias nematura* is equally unobtrusive, and it shows such a preference for sewage effluent that the Brazilians have aptly named it 'president of filth'. More widely distributed birds such as the true ovenbirds and many spinetails are inhabitants of less densely wooded areas; the former, being largely terrestrial, prefer fairly open country yet with plenty of trees, while spinetails characteristically skulk unobtrusively in thickets or low cover even in treeless lands.

In the southern part of its range, and to a limited extent in the Andean highlands as far north as Colombia, the family shows the greatest measure of adaptive radiation. In the open pampa of Argentina and the mountainous fjord areas of Chile, different genera and species have invaded every possible habitat. The miners and earthcreepers are entirely terrestrial and typical both of barren mountainous country and of the flat pampa. The Patagonian Earthcreeper *Upucerthia dumetaria* is even unwilling to fly, preferring to escape by running.

The Brown Cachalote is also largely terrestrial and tends to run off behind trees and other obstacles rather than fly when disturbed. Species of *Cinclodes* occupy the niche of dippers (Cinclidae) and are always found near water, from mountain torrents in the high Andes down to sea level; they are even known to feed off-shore on the floating masses of giant kelp. The White-throated Treerunner *Pygarrhichas albogularis* of Chile and Argentina fills the niche of a nuthatch (Sittidae). The Black-faced Spinetail is a bird of the marshes, as is the Curved-billed Reedrunner *Limnornis curvirostris*. *Aphrastura* and *Leptasthenura* are arboreal genera. For the most part, members of the family are active yet unobtrusive birds, even in open country, keeping well to cover, constantly creeping about in bushes, reeds, or thick grass, and even running off like mice rather than flying; and they show a great tendency to remain in pairs. The Greater Thorn-bird *Phacellodomus ruber* in Argentina is exceptional in being not at all restless and never making an effort to hide.

Distribution. The family, like the Formicariidae (see ANTBIRD), ranges from the montane and lowland forests of southern and central Mexico through Central to South America; likewise it reaches Trindad and Tobago, but is not found in the Antilles. In the south its range is greater than that of the antbirds, being over the whole of the continent to Cape Horn and Tierra del Fuego, as well as the Falkland Islands, with a tremendous Andean radiation. Many specialized forms have developed in the open, barren lands of the extreme south, and the monospecific genus *Chilia* is confined to Chile, where it inhabits semi-arid country. In Argentina a few species, such as the Black-faced Shaketail *Cinclodes fuscus* and perhaps the Patagonian Earthcreeper, are said to be migratory. As with the antbirds, no comprehensive account of the family has ever been written, and the majority of species are known only by their appearance.

Food. Most species are insectivorous, but *Cinclodes* spp. also take small crustacea and aquatic animals, as would be expected, while some miners and the Tococo feed on seeds and vegetable matter.

Voice. Like all other characters, the voice varies considerably. Generally, the spinetails and many other genera have short, harsh, rattling and jarring calls; but miners have clear ringing reiterated cries, likened to the laughing of a child; the Ovenbird *Furnarius leucopus* has a sequence of clear, resonant notes produced as a duet or harmonious singing; the Black-faced Spinetail *Phleocryptes melanops* gives wooden-sounding raps and creaks; Hudson's Spinetail *Asthenes hudsoni* has a plaintive four-note song audible for 900 m or more; and the cachalotes are especially noisy with jay-like screams (Brown Cachalote) or a piercing chorus (White-throated Cachalote *P. gutturalis*).

Breeding. The breeding habits are known mostly from species inhabiting the open lands of the southern parts of South America, but even within these limits the diversity is astonishingly great. The only constant feature is that all lay white eggs—except the Black-faced Spinetail, which lays bright blue eggs, and a few others which lay slightly bluish or off-white eggs. Clutch size is usually 3–5, but as many as 9 eggs are mentioned for the White-throated Spinetail *Synallaxis albescens*, and tropical species probably tend to have smaller average clutches. Terrestrial forms such as miners and earthcreepers nest in holes in the ground, either natural cavities or tunnels dug by the birds themselves or by mammals, e.g. the Common Miner *Geositta cunicularia* nesting in the burrows of the Vizcacha *Octomys mimax* on the Argentinian pampa. *Cinclodes* spp. nest in rock cavities or dig their own holes. Leafscrapers and the Streamcreeper also nest in holes or burrows in banks, and the leafscrapers have an odd habit of flying out of the hole and clinging to a tree-trunk when flushed from the nest. *Aphrastura* and *Leptasthenura* nest either in holes in trees, behind bark, or in the abandoned nests of such birds as *Asthenes* spp.

In contrast, the true ovenbirds build very substantial, domed mud-ovens on the branches of trees well above the ground. The spinetails in general build vast nests, remarkable for such small birds. The Firewood-gatherer *Anumbius annumbi* (a bird about 21 cm long) makes its big structures of large twigs, even in tall trees to which it may have difficulty in carrying up the material. The White-throated Cachalote perhaps makes the largest nest of the family, an enclosed structure with a cavity big enough for an eagle or vulture, and strong enough for a man to stand upon without damaging it; the Brown Cachalote also makes a nest the size of a barrel. The Black-faced Spinetail makes a perfectly roofed nest, domed and impervious to the wet, with entrance near the top, out of grasses and leaves daubed together with mud and probably saliva. Species of *Phacellodomus* place their castles at the ends of branches that are at first several m from the ground, but as the structure grows the boughs bend down and the nest may eventually rest on the ground. Hudson's Spinetail makes domed nests on the ground under the thickest cover, such as the giant cardoon thistles. On the other hand, the Striped-crowned Spinetail *Cranioleuca pyrrhophia* and the Wren-like Spinetail *Spartonoica maluroides* make open cup-shaped nests, which is quite exceptional for the Synallaxinae.

Owing to the impossibility of observing the nests of most species of Furnariinae and Synallaxinae without destruction or excessive disturbance (the nests of these 2 subfamilies are much better known than those of the rest of the family), breeding details are virtually unknown in spite of the fact that these huge nests are such a conspicuous feature of the countryside in the open parts of South America. The incubation and nestling periods are very superficially known, for only 6 species, being 15–20 days and 13–18 days respectively. The abandoned castles of the spinetails and the ovens of El Hornero are often used by other birds such as cowbirds (Icteridae), swallows (Hirundinidae), wrens (Troglodytidae), and parrots (Psittacidae); sometimes the owners are even expropriated after building their nest. (S.M.) A.F.

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OVENBIRD (2): *Seiurus aurocapillus* (see WARBLER (2)).

OVERFLOW ACTIVITY: a behaviour pattern appearing in the absence of the usual external triggering stimuli, e.g. Canaries in the appropriate physiological state will show nest building responses even in the absence of nest material. Overflow activities (also called vacuum activities) have been interpreted as evidence for spontaneous generation of behaviour patterns in the nervous system. (See BEHAVIOUR, HISTORY OF).

OVERSHOOTING: movement beyond the normal limits of a bird's area of distribution by continuance in the usual direction of migration beyond the proper destination.

OVERWINTERING: see MIGRATION.

OVIDUCT: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; LAYING.

OVIPARITY: the characteristic of laying eggs in which the embryos develop outside the maternal body; universal in birds. See also under DEVELOPMENT, EMBRYONIC; EGG; LAYING.

OVIPOSITION: see LAYING.

OVOTESTIS: in virtually all birds only the left ovary is functional. The right ovary remains minute but if the left one is removed, or destroyed by disease, it can develop. Depending upon when this occurs the right gonad may turn into an ovary or a testis, or on occasion into a structure combining the germ cells of both sexes: an ovotestis. In such situations seminiferous tubules are visible in one part of the organ whilst the other contains growing follicles. The potentially ambisexual nature of birds is not confined to one group but is most well known in chickens. Sex changes were described by Aristotle and up to this century were often thought to be associated with the supernatural.

OVULATION: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; also LAYING.

OVUM: the female germ-cell (plural 'ova')—see DEVELOPMENT, EMBRYONIC; EGG; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; GENETICS.

OWL: substantive name of all species of Strigiformes and in the plural, general term for the order. With very few exceptions owls look like nothing but owls, i.e. they are soft-plumaged, short-tailed, big-headed birds with large forward-facing eyes, surrounded by a broad facial disc. Owls probably have the most frontally situated eyes of all birds. This, together with their ability to blink with the upper eyelids, gives owls a semi-human appearance, in which lies much of their appeal to man.

Owls have often been regarded as nocturnal counterparts of the diurnal birds-of-prey (Accipitriformes and Falconiformes), but most likely the Caprimulgiformes (oilbirds, potoos, nightjars and nighthawks) are the owls' nearest living relatives, which have evolved from a common, nocturnal ancestor, perhaps not more than 100 million years ago.

Barn Owl *Tyto alba*. (*K.J.W.*).

General and systematic characteristics. Although the members of the Strigiformes may be easily distinguished from members of other orders, the familial, subfamilial and generic relationships within the order are much less certain. According to present knowledge there are about 134 species divided between 25 living genera and 2 families: the typical owls, the Strigidae, and the barn owls, the Tytonidae. The barn owls differ only in minor osteological details from typical owls. Barn owls have proportionately smaller eyes and are easily recognizable by the heart-shaped facial disc and the long slender legs. The family comprises 10 species: genus *Tyto* consisting of 8 species and genus *Phodilus* 2 species, one occurring in south-east Asia (Oriental Bay Owl *P. badius*) and the other in Africa (African Bay Owl *P. prigoginei*). The facial disc of the Strigidae is circular and the legs are usually rather strong and in most cases thickly feathered. This family contains about 124 species, distributed over about 23 genera, of variable size, coloration, and habits. However, owl taxonomy is currently in a state of flux, and anything approaching a final tally of species or genera must await revision now in progress.

Owls are mostly birds of medium size with some species fairly large or fairly small. The largest are some eagle owls *Bubo* spp., reaching 73 cm in length, and the smallest the Least Pygmy Owl *Glaucidium minutissimum*, 12–14 cm long. Like many birds of prey the female is often larger than the male (see SEXUAL DIMORPHISM).

Owls have dense, soft plumage which makes them look much bigger than they are and helps to keep them warm during long periods of inactivity between hunting forays. The colour of the plumage is often cryptic, which makes the bird less conspicuous when it is resting during the day. Woodland owls tend to be brown or grey in basic coloration; owls living in open habitats are typically paler and those inhabiting desert country are distinctly sandy-coloured (e.g. Hume's Desert Owl *Strix butleri*). In many species, markedly different colour phases occur, e.g. the most common British owl, Tawny Owl *Strix aluco*, is typically brown but also has a rarer grey phase (see POLYMORPHISM). Sexual colour dimorphism is usually absent but there are a few exceptions; for example, the female of the Snowy Owl *Nyctea scandiaca*, is barred, whereas the male is pure white. Differences between juvenile and adult plumage are normally slight, but many species tend to become paler or more whitish in old age (e.g. Short-eared Owl *Asio flammeus*). Most owls have relatively large, rounded wings, shorter in those species which hunt in cover and much longer in those which hunt in open country or are migratory. Owls are light in relation to their wing area (in aeronautical terms they have a low wing-loading) which explains why they can fly buoyantly and effortlessly, with relatively little wing-flapping (see FLIGHT).

Owls show a number of adaptations which enable them to operate with outstanding efficiency as nocturnal predators. First of all they have well-adapted eyes to hunt their prey in poor light; in absolute darkness they cannot see. The huge eyes are shaped like tapering cylinders to provide the largest possible expanse of retina, and a notably thickened cornea acts as an additional lens (see VISION). Forward-facing eyes give a considerable degree of binocular vision, but the eyes themselves are almost immobile. The owl must turn its whole head to look sideways, but it has an exceptional ability to rotate its head; the head of the Long-eared Owl *Asio otus* has been reported to be capable of turning through at least

Tawny Owl *Strix aluco*. (*K.J.W.*).

270°. The number of light-sensitive elements (mostly rods) in the retina is very high, particularly in definitely nocturnal species such as the Tawny Owl, and these species sometimes appear to be blinded by very strong sunlight. But many owls are able to hunt in daylight, and none is really helpless during the day. This is made possible by an exceptional range of aperture (pupil size) controlled by the iris. It is always difficult to prove whether an animal can perceive colour. As owls have some cones in their retina, it seems likely that they can do so when the light is good. Experiments on the crepuscular Little Owl *Athene noctua* have shown that it can perceive at least yellow, green and blue; red and the darkest grey were confused (see VISION).

The owl's sense of hearing is no less remarkable than its exceptional sight. The inner ear of owls is very large, and the auditory region of the brain is provided with many more nerve cells than in other birds of comparable size. Aural abilities are aided by a wide outer ear tube and in some species by the presence of large conchae, which, surrounded by the feathers of the facial disc, can be erected at will. In some species a striking asymmetry in the shape and relative position of the external part of the ear, including the bones surrounding the tympanic region and the operculum, has been described. Asymmetrical ear openings are thought to help the owls to locate the source of sound with precision. In laboratory experiments Barn Owls *Tyto alba* have been capable of locating and striking an unseen living prey in complete darkness, using only their acute sense of hearing (see HEARING AND BALANCE). The high frequency squeals of small prey and the rustle of dry leaves contain all the information the owl needs to locate its intended prey. Assertions that the owl is visually sensitive to infra-red radiation given out by the body of a prey animal have been proved incorrect. Also in the wild many owls rely only on their remarkable auditory powers, at least in hunting rodents and shrews during the winter when these mammals often move under the snow cover. The Great Grey Owl *Strix nebulosa* is able to localize from the air invisible small mammals and to catch them blindly on the right spot below the snow-surface. Those owl species not having the ears so highly developed can always combine their acute visual and aural abilities, because there is never total darkness in a place where an owl is likely to hunt. The 'ear tufts' which many species possess have nothing to do with the auditory organ; they express mood and act as night-time recognition signals, and may also be an aid to camouflage by breaking up the outline of the owl's head. Softened flight feathers together with the low wing loading help an owl to move silently through the air—to hear other sounds while flying itself, and to avoid giving alarm to its prey. Fishing owls of the genera *Ketupa* in Asia and *Scotopelia* in Africa do not fly soundlessly, but, as they take underwater prey, the noisy wing beats do not seem to be of importance.

The bill and claws of owls are clearly suited to their predatory way of life. The bill is hooked, usually short and not conspicuously strong, directed downwards—a modification to reduce obstruction of the already limited visual field. As in the diurnal birds-of-prey, the nostrils are placed in a soft cere at the base of the bill, which is partly hidden by the feathers of the facial disc. The feet are always 4 toed, with the fourth toe reversible. The legs and toes are usually feathered, a protection against possible bites from prey. The fish-eating owls, *Scotopelia* and *Ketupa*, have bare legs and feet with rough spiny soles. All owls have sharp, strongly hooked, raptorial claws.

Habitat. As a group of birds owls are able to occupy all kinds of habitats: tundra, deserts, grasslands, marshes, swamps, woods, luxuriant rain forests, mountains and islands, but the majority of the species live in woodlands or forest edges. Only a few species, like the Arctic Snowy Owl and the desert-living species of North America (e.g. Elf Owl *Micrathene whitneyi*) prefer habitats where trees cannot grow. Some species are terrestrial and live in flat country or among rocks. Long-legged terrestrial species are known both in the Tytonidae (Common Grass Owl *Tyto capensis*, found in Africa and from India to Australia) and in the Strigidae (Burrowing Owl *Athene cunicularia*, found in North and South America). The recent decline of many owls with arboreal habits can be associated with the destruction of forest habitat. Some insular owls, e.g. Madagascar Owl *Tyto soumagnei*, Seychelles Owl *Otus manadensis insularis*, Sokoke Scops Owl *Otus ireneae* (living in a fairly small 'island' of inland forest on the Kenya coast), Anjuan Scops Owl *Otus rutilus capnodes* and Forest Little Owl *Athene blewitti*, are even threatened with total extinction, because of habitat destruction now occurring.

Distribution. On the whole, owls are successful birds, which have dispersed to all continents except Antarctica and several remote oceanic islands. The great majority of species occur in the tropics and subtropics. North America and the Palearctic zone of the Old World are inhabited by 33 species of owls, of which 8 species occur in both North America and Eurasia. The most common owl in the world is probably the Barn Owl which has almost world-wide distribution with at least 34 recognizable geographical forms. Barn Owls have been released in some Indian Ocean islands to control rats, and recently they have also colonized Malayan oil palm plantations. The Short-eared Owl is the other owl with a very wide range, mainly inhabiting boggy and marshy places in open country. The Marsh Owl *Asio capensis* is an ecological equivalent of the Short-eared Owl in Africa. The Snowy Owl is distributed throughout the Arctic tundra regions of the Northern Hemisphere. Throughout the zone of boreal coniferous forests of Europe, Asia and North America quite a number of other species are found; some of them are restricted to this zone, such as the Great Grey Owl, the Hawk Owl *Surnia ulula*, Tengmalm's Owl *Aegolius funereus* (known in North America as the Boreal Owl), the Ural Owl *Strix uralensis*, the Long-eared Owl, and the Pygmy Owl *Glaucidium passerinum*. The last two have a number of closely related forms in tropical America and Africa. The Eagle Owl *Bubo bubo* of Europe and Asia, ranging from the cold northern forests to the hot southern deserts, has allied species also in America (Great Horned Owl *B. virginianus*) and in Africa (Cape Eagle Owl *B. capensis* and Spotted Eagle Owl *B. africanus*). The Little Owl has a mainly Palearctic distribution, the Burrowing Owl from the steppe and desert regions of America being its present closest relative. The Little Owl has been introduced into Great Britain and New Zealand. The Tawny Owl and European Scops Owl *Otus scops* have both only Old World distribution. The Tawny Owl belongs to a widely distributed genus *Strix* which is absent only from Australia. *Otus scops* is the only European representative of the scops owls, which form a widespread group of about 33 species mostly living in the tropical regions of the world, except in Australasia where the genus is replaced by the hawk owls *Ninox* spp.

Populations. Studies of the territorial Tawny Owl (Southern 1970) have shown that there is a limit to the owl density in a given habitat, this being determined by territorial behaviour. In England Tawny Owl pairs had a territory of about 13 ha in closed woodland and 20 ha in mixed woodland and open ground (see TERRITORY). Fluctuations in food resources did not lead to changes in the number of adult owls in the woods. Failure to breed, the laying of fewer eggs than potentially possible, failure to hatch laid eggs, and mortality of the young in autumn and winter were the main factors keeping the numbers virtually constant from one year to the next. But quite the opposite population dynamic applies to the nomadic species. For instance, the Short-eared Owl alters the size of its territory from month to month according to the abundance of its main prey, *Microtus* voles. If food is scarce the species becomes nomadic and seeks new breeding and hunting areas.

Movements. Owls are mainly sedentary; regular migrations are known in respect of only a relatively few species. Among European owls some populations of Scops Owl migrate regularly to tropical Africa, while the northern populations of the Striated Scops Owl *Otus brucei* migrate to the Indus Valley and the Bombay region. Within eastern Asia the Oriental Scops Owl *Otus sunia* as well as the Oriental Hawk Owl *Ninox scutulata* migrate between temperate and tropical regions. The two most migratory species in Eurasia are some northern populations of the Long-eared and Short-eared Owls which are partially migrant also in North America. In several species (e.g. Snowy, Hawk and Great Grey Owls), nomadic winter movements or even irruptions occur more or less cyclically, triggered by fluctuations of rodent populations (see IRRUPTION).

Tengmalm's Owl *Aegolius funereus* has evolved a strategy of partial migration, adult males being resident and females and young being migratory. The periodical food scarcity favours the migration of females and young, and the urgency of guarding the nest-holes of good quality favours residence by the adult males.

Food. It has been fairly easy to analyse in detail what owls are eating at different seasons, because the smaller prey are generally swallowed whole, indigestible matter such as fur, feathers, bone, and chitin being regurgitated some hours later in the form of large PELLETS. Owls feed exclusively on animals. Small mammals like rodents and shrews predominate as food items for the majority of owls. Some species feed on birds, reptiles, amphibians, fish, crabs, earthworms and insects. Hunting methods vary according to the prey. A few species hunt actively on the wing, taking moths and other small creatures in flight. Semiaquatic fish-eating owls catch fish in their talons from the surface of rivers, or hunt crabs on shores and river shallows. But most owl species quarter the ground in silent flight, or scan it from a convenient perch, waiting and intently listening for ground-living insects and small mammals. Food is mainly consumed in the fresh-caught state; carrion is only occasionally eaten.

Behaviour. Most owls seem to be highly territorial, but some nomadic species, such as the Great Grey Owl and the Short-eared Owl, sometimes form loose colonies. Highly territorial owls (e.g. Eagle and Tawny Owls) are very aggressive towards other birds-of-prey, especially during the breeding season; birds of prey and smaller owls form often as much as 3–5% of the total food of the Eagle Owl.

Owls are generally monogamous, nesting in individual pairs, which are apparently permanent. But some males are known to be polygynous: at least, bigamous males of Tawny, Eagle, Snowy, Short-eared and Tengmalm's Owls have been discovered.

Owls usually hide away by day in holes, or in dark places in thick foliage, taking advantage mainly of their protective plumage. At least 80 species out of 134 hunt by night; others are known to be active at dusk or in full daylight. In northern latitudes the Snowy Owl and the Hawk Owl hunt during the light nights of the Arctic summer and in winter during the short hours of daylight. Some species seem to enjoy sun-bathing (Little Owl, Burrowing Owl).

Voice. Several species of owls sing, some very musically. In temperate regions it is the owls which in late winter or early spring fill the night with music, and in the tropics owls are just part of a formidable chorus of animal songs and calls. Throughout the world they have an extraordinary repertoire of shrieks, hoots and caterwaulings, in a range of frequencies which carry far on the night air. These announce their presence and the existence of occupied territories. Calls are completely diagnostic of species, and owls are as likely to recognize other individuals by voice as by sight during their travels in the dark. Individual Tawny Owls can be identified from sonagrams of their hooting.

Breeding. The weather and the food available influence the start of breeding activities and many species appear to make an assessment of rodent abundance; during good vole years they lay earlier and larger clutches than in poor ones. Late snowfalls may cause even advanced broods to be abandoned, while an abundant food supply and high temperatures can encourage reproduction by Barn and Short-eared Owls even in winter.

With minor exceptions, owls make hardly any nests themselves; instead, they use other birds' nests—such as the abandoned nest of a raptor or corvid—and holes in trees or rocks and a great variety of other places, including human habitations. Eagle Owls sometimes dig their nest cavities into uninhabited anthills. Owls of taiga and tundra nest on open ground or in low vegetation; they make a shallow scrape and even add some lining material to their nests (e.g. Snowy and Short-eared Owls). Desert species tend to live underground, taking over abandoned rodent burrows to escape the heat of the sun. Owls' eggs are chalky-white and roundish, the number varying from 1–14. Clutch-size is dependent on the food supply available, the differences from one season to the other being most notable in species which feed on rodents subjected to cyclic population fluctuations. Hence, in years of abundance, the Snowy Owl may have clutches of 10–14 eggs, and in years of food scarcity it may have clutches of 2–4, or not breed at all. Owls lay their eggs several days apart, and incubation starts with the first egg laid, resulting in marked differences in the size of the young in the nest. In good years all the young may survive, whereas in bad years the oldest progeny compete with their siblings for scarce food, and the clutch produces one well-fed fledgling instead of 3 or 4 starved weaklings. Such flexibility maximizes success in good years, while minimizing the risk of total failure in bad years.

Usually only the female incubates, while the male forages and brings food to the female; both sexes care for the young. The incubation period is long, being 32–34 days in the Barn Owl, 26–28 in the Long-eared Owl, and 34–36 in the Eagle Owl. The young are nidicolous after hatching, with ears and eyes closed and body lacking independent means of temperature regulation. After the natal down, the young acquire the so-called mesoptile feathers, which are followed by true feathers appearing on the same feather papillae (see PLUMAGE). Young owls become capable of breeding at about the age of one year; i.e. in the first spring after the year of birth. Owls have the reputation of reaching a great age, but records of their longevity are still inadequate. The life expectation of ringed Barn Owls in Switzerland has been found to be surprisingly short, being on average 16 months; only a few individual birds are known to have reached the age of 9 years. But in captivity one Tawny Owl has lived for 22 years and 2 Eagle Owls for 53 and 68 years respectively.

See photo VISION. (K.H.V.) H.M.

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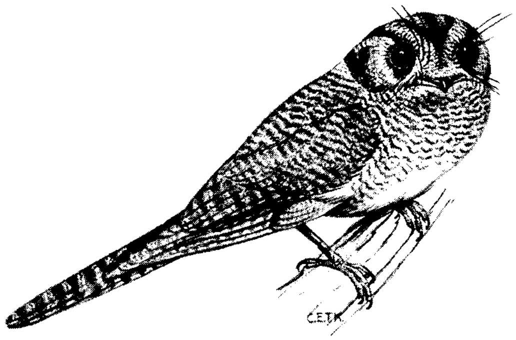
OWLET: term for a nestling OWL.



Owlet-frogmouth *Aegotheles cristatus*. (*C.E.T.K.*).

OWLET-FROGMOUTH: substantive name of the species of Aegothelidae (Caprimulgiformes, suborder Caprimulgi): in the plural, general term, alternatively 'owlet-nightjars', for the family.

Systematics and distribution. The group is related to the frogmouths (Podargidae) and consists of a single genus of small arboreal nightjars (in the ordinal sense) almost restricted to the Papuo-Australian area. One species has penetrated to the Moluccas and another is found in New Caledonia. New Guinea is inhabited by 5 species, of which *Aegotheles cristata* occurs widely in Australia. Extensive fossil remains of a closely allied form have been found in the Pleistocene to Recent in New Zealand, described as *Megaegotheles novaezealandiae* by Scarlett (1968).

Structurally, *Aegotheles* resembles *Podargus* but with several differences. The features in which it resembles *Podargus*, but which are not shared with true nightjars, include the desmognathous palate and the bronchial syrinx; the sternum has two foramina on each side instead of being double-notched. However, it possesses the two carotids normal in the order and an oil gland, and it lacks the powder-down tufts found in *Podargus*. It is unique in the order in not having caeca.

Characteristics. The body length is 20.5–24 cm. Plumage characters of mottled brown are similar to those of the frogmouths and true nightjars (Caprimulgidae). The frogmouth-like bill is shorter and weaker than in *Podargus* or *Batrachostomus*, and it is largely obscured by the forehead feathering. Stiff and partly erectile filoplumes occur on the forehead and lores, with a few softer recurved filoplumes on the chin. The bird sits with an upright, owl-like stance, but it does not adopt the rigid 'broken branch' stance, when alarmed, which is characteristic of *Podargus*. Generally, it is a more active bird than the comparatively lethargic *Podargus*.

Habitat. *Aegotheles* lives in forested and semi-open country, and has the same arboreal habits as *Podargus*.

Food. The feeding habits appear to be intermediate between those of the frogmouths and the true nightjars. Aerial hawking for flying insects has been described, but most hunting is done from the ground, the bird sometimes rising to take flying insects; most of the stomach contents analysed suggest that the bird feeds predominantly on terrestrial prey. Rich and Scarlett (1977) infer that the fossil New Zealand *Megaegotheles*, which tended to gigantism and 'may have been well on its way to becoming another of New Zealand's flightless birds', was a terrestrial insectivore.

Voice. The calls include a loud hissing note and a repeated churring call.

Breeding. Nesting takes place in hollow trees or occasionally in tunnels in banks. No actual nest may be constructed, or the eggs may be laid on a mat of dry leaves or mammal fur. The colour of the shell is white, as in *Podargus*, and the clutch is 3 or 4. The fledgling is covered with dense white down. The birds are readily flushed from their roosting or nesting hollows by tapping likely limbs or tree trunks. D.L.S.

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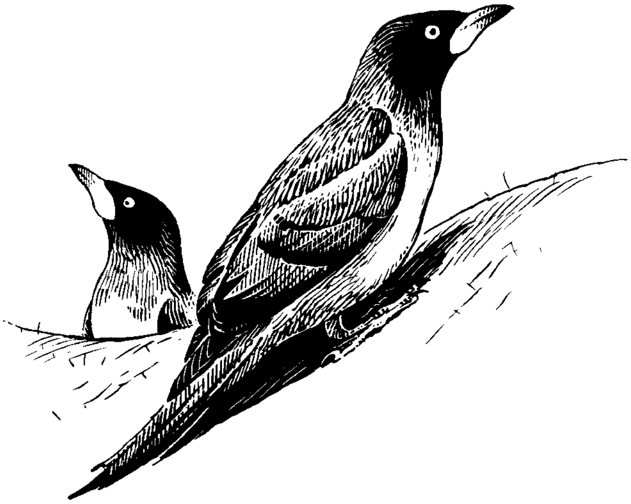
OXPECKER: substantive name of the 2 species constituting the subfamily Buphaginae of the Sturnidae (Passeriformes, suborder Oscines) (see STARLING); in the plural, general term for the subfamily. They are also called 'tickbirds'. The 2 species are similar (starling-like but with short legs) in size (18–19 cm long), and are very much alike with dull brown plumage; the sexes are similar, and the bill colouring is fully developed only in adults.

Characteristics, habitat and distribution. The Yellow-billed Oxpecker *Buphagus africanus* which has the terminal half of its broad bill red and the rump paler than the back occurs from west Africa through to western Ethiopia, east Africa and south to southern Africa. It became extinct in South Africa before 1914. The slightly smaller Red-billed Oxpecker *B. erythrorhynchus*, which has the whole narrow bill red and the back and rump concolorous, has a more restricted geographical range, from Eritrea and the south-eastern Sudan to South Africa and across to northern Namibia. It is an eastern species, its western limit being approximately 30°E except in the south of its range. In broad terms, therefore, *B. africanus* occupies the region west of the Rift Valley system, crossing it only in the area immediately to the north of Mount Kenya and in western Tanzania; it is absent from areas of dense forest, as is *B. erythrorhynchus*, though penetrating the open parts of the Congo. Both species are typical inhabitants of the African savanna.

Oxpeckers are notable for their special association with indigenous African ungulates and also domestic livestock (Artiodactyla and Perissodactyla). The birds are wholly dependent on their mammalian associates. Although the geographical ranges of the two species overlap in parts, their distribution and density are often patchy in accordance with their mammalian associates. In areas of sympatry the Yellow-billed Oxpecker associates more commonly with naked or sparsely furred mammals (e.g. the African Buffalo *Syncerus caffer*) than with mammals with moderately dense fur, including cattle, to which the Red-billed Oxpecker is then restricted. Both species, however, associate with a wide variety of mammals, including rhinoceros, giraffe, warthog, zebra and various antelopes, and both species prefer less densely furred mammals. The association is influenced by the behaviour of the mammals as well as that of the birds. Most ungulates are remarkably indifferent to the birds clambering over their bodies. However, waterbuck, reedbuck, hartebeest, tsesseby and steenbuck, for example, are intolerant of oxpeckers. Despite their naked skins, elephants, which are not ungulates, are not used by oxpeckers, apparently because elephants are intolerant of them.



Yellow-billed Oxpecker *Buphagus africanus*. (*D.A.T.*).

Populations. In the last few decades the distribution and numbers of oxpeckers have been greatly reduced, with the extension of regular dipping of cattle to control ticks. Successful reintroduction into a game reserve in Zimbabwe has been accomplished.

Food. Oxpeckers obtain nearly all their food from the skins of their mammalian associates. Despite the differences in bill morphology, both species seem to use the same techniques for foraging. Ticks, chiefly members of the genera *Amblyomma, Boophilus* and *Rhipicephalus*, comprise their main food and flies are a supplement. The birds progress on their hosts by walking and hopping, using their sharp, curved claws; their stiff, rather long tails are employed for bracing support when clinging to vertical surfaces. The birds' beaks are laterally flattened, facilitating a 'scissoring' feeding action in which the bill is opened and closed rapidly while being pushed through the pelage or over the skin of the mammalian host. This is the normal method of foraging. Plucking and pecking are also used in capturing ticks, and in feeding on scurf and open sores. The birds occasionally hawk flying insects, but are not very adept at this. At least in the case of the Red-billed Oxpecker, they feed mainly in the morning and late afternoon, resting in the middle of the day. They drink regularly, the host being used as a platform from which the birds descend to waterholes.

Voice. In addition to a variety of harsh starling-like calls, oxpeckers have a distinctive hissing alarm call given when disturbed on a mammal or at the nest. It is believed that they act as sentinels for their mammalian associates, particularly rhinoceroses, but this has yet to be critically evaluated.

Behaviour. More than a dozen birds can be found on a single large animal, such as a giraffe, but individual foraging groups generally are smaller. The birds roost communally, at traditional sites in trees, reeds, cliffs, buildings etc., the roosts, at which other species of starlings often also roost communally, comprising one or more individual groups of oxpeckers. The roosts decline in size with the onset of the wet season which is the start of the annual breeding cycle.

Breeding. Oxpeckers nest in tree cavities. All searching for nest holes is done from the mammalian hosts. Animal hair, dung, grass and rootlets are used for the nest. Up to 5 birds constitute a co-operative breeding group, and all collect nest material. Copulation occurs on the backs of the mammalian associates or on the ground. Only one female and one male actually breed, in that this pair is responsible for the production of fertile eggs (1–5 per clutch, most often 2 or 3) and their incubation (about 12 days). The eggs are pinkish white, with small red-brown, purple and lilac spots. In the daytime, the incubating birds relieve each other approximately every hour; the female incubates at night. All members of the group feed the nestlings which continue to be given food once they have left the nest, at about 30 days if undisturbed, and until they are about 3 months old. Up to 3 broods are raised in a season. Breeding overlaps with moult which is exceptionally long; the primaries are replaced over an 11-month period in the Red-billed Oxpecker. W.R.S. and R.K.B.

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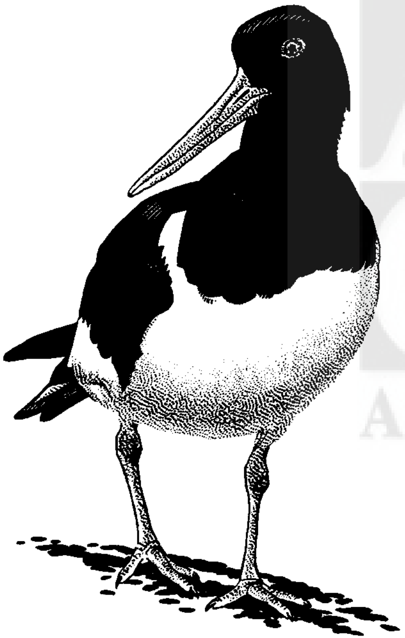
OXYRUNCIDAE: family of PASSERIFORMES, suborder Deutero-Oscines; SHARPBILL.

OXYURINI: see DUCK.



Oystercatcher *Haematopus ostralegus*. (*R.G.*).

OYSTERCATCHER: substantive name of all the species of Haematopodidae (Charadriiformes, suborder Charadrii); in the plural, general term for this small cosmopolitan family.

Characteristics. Oystercatchers, sometimes called 'sea-pies', are large waders (40–45 cm long) with either black-and-white or wholly black plumage. The powerful bill is characteristic—being long, stout, laterally compressed, and bright orange-red. It is specially adapted for opening the shells of bivalve molluscs but is also used for probing in mud, sand or turf. The rather thick legs are reddish; and each foot has 3 toes, slightly webbed. The tail is short; the wings are long and pointed. There are some slight seasonal and sexual differences, and the juveniles are more dark brown than black and have less brightly coloured bills and legs.

On the ground the birds normally walk but can run swiftly. They can swim well on occasion. The flight is rapid and direct, with rather shallow wing-beats. Oystercatchers are noisy and restless birds, often by night as well as by day, the characteristic call being a loud clear *klee-eep, klee-eep*.

Habitat. Oystercatchers are mainly birds of the seashore, and outside the breeding season they gather in flocks, sometimes of many thousands. Flocks of immature birds persist throughout the year, especially in certain favoured areas, for instance, in the British Isles, the northern coasts of the Irish Sea. It has been shown that the birds (at least of the European species) do not breed until 3 years old.

Distribution and populations. The family has no representatives breeding in very high latitudes or in tropical Africa or southern Asia. Otherwise, the distribution includes the coasts of most of both Old and New Worlds, and also certain inland areas to be mentioned below. Populations in higher latitudes tend to be migratory.

There is only a single genus, and the numerous forms comprised in it are grouped by different authors in from 3 to 6 or 7 species. The taxonomic position is complicated by the existence of melanistic populations, by some regarded as consisting of black mutants and by others as constituting distinct species. The Oystercatcher *Haematopus ostralegus* in various subspecific forms, some pied and some black, breeds from Arctic Europe to the coasts of the Aegean, Black, and Caspian Seas; on the Canary Islands and the coasts of temperate South Africa; and in Australasia from New Guinea to Tasmania and New Zealand. Further, the race *H. o. longipes* breeds mainly about inland waters from Kiev eastwards through southern and eastern Russia and Siberia to the Cis-Altai steppes, and is probably the race found breeding on the tributaries of the R. Euphrates in eastern Turkey, up to 1,900 m. The British race *H. o. occidentalis* has bred inland in Scotland for centuries and has recently begun to spread along the river valleys in the north of England. The form *H. o. unicolor* (*H. 'finschi'* of some authors) breeds far inland along the courses of the snow rivers of South Island, New Zealand. All these inland breeding birds apparently winter on the coasts.

Certain of the New World forms are treated by some as races of *H. ostralegus*. By others they are assigned to separate species, such as the Black Oystercatcher *H. bachmani* of western North America and the widely distributed American Oystercatcher *H. palliatus*.

Other species which have been recognized are the Sooty Oystercatcher *H. fuliginosus* of the coasts of Australia and two which both inhabit the coasts of southern South America and the Falkland Islands; of these last, *H. ater* is a black form while *H. leucopodus* is pied but with a black chest and under wing coverts, yellow (not crimson) eyelids, and other peculiarities of plumage.

Food. The food consists chiefly of molluscs, crustaceans, annelid worms, and insects, varying with the particular habitat (rocky or sandy shores, estuaries, river gravels, moorland, farmland). With their powerful bills, they can knock limpets off rocks. There is some evidence that birds on inland territories breed more successfully than those on coastal territories, probably because they can gather food for the chicks, which are dependent on their parents, unrestricted by the tides.

Behaviour and voice. The species present in Europe has an elaborate 'piping' ceremony in which 3 or more birds run about with 'shoulders hunched' and bills held pointing to the ground, while they utter together a rapid high-pitched trill. This behaviour is probably concerned with the separation of breeding pairs from the flock; both sexes take part and either may initiate it—and, apparently, immature birds do not pipe. As Makkink (1942) says, this ceremony is 'a mechanism which first enables the sexes to arrange themselves into pairs, and subsequently creates opportunities for the formed pairs to take up a position' against their fellows. Although this performance usually takes place on the ground, it sometimes occurs when the birds are in flight.

Breeding. The nest is a mere scrape in the ground, which is often decorated—rather than lined—with white shells, bones, stones, and other objects. The 2–4 eggs (usually 3 in the European species) are yellowish buff, heavily marked with dark brown or black. One clutch is laid and both sexes take part in incubation. The cryptic coloration of the eggs is highly effective, and the old birds avoid betraying the position; DISTRACTION BEHAVIOUR ('injury feigning') occurs, and also 'false brooding' at spots where no eggs lie. Incubation, in the European species, normally lasts for 26 or 27 days. The chicks run as soon as their cryptic down is dry; they are, however, fed by their parents for at least 6 weeks; they take about 5 weeks to fledge.

See photo FLOCKING. E.J.M.B.

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P

PACHYCEPHALIDAE; PACHYCEPHALINAE: family and subfamily of PASSERIFORMES, suborder Oscines; THICKHEAD.

PADDLING: see FEEDING HABITS.

PADDY: alternative name (plural 'paddies') for *Chionis* spp. (for family see SHEATHBILL).

PADDY-BIRD: otherwise the Indian Pond Heron *Ardeola grayii* (see HERON).

PAINTED SNIPE: substantive name for the 2 species of Rostratulidae (Charadriiformes, suborder Charadrii): the Old World Painted Snipe *Rostratula benghalensis* (colloquially 'painter') and the American Painted Snipe *Nycticryphes semicollaris* (called 'sleepyhead' in Argentina). Both superficially resemble snipe *Gallinago* spp. and, like the Jacanidae and Gruidae, have two notches on the posterior edge of the sternum.

Characteristics. Both species are unmistakable. Skulking and difficult to flush, they often run with lowered head, stopping to bob the head and neck if alarmed. They seldom fly far, with slow wingbeats and dangling legs, before diving into cover.

The plumage is spectacular, particularly in the females which are some 10% larger than the males. *R. benghalensis* (25 cm long) has longer legs, shorter bill and tail and broader wings than snipe. The bill is decurved at the tip, the nostrils lying in deep narrow grooves which extend over half-way along the mandible. The eyes lie towards the front of the skull, and the toes are un-webbed. The female has a chestnut face and black crown divided by a thin, buff stripe; diagnostic white spectacles surround the eyes. A white stripe over the shoulder separates the dark head and neck from the bronzy-green upperparts, whose dark vermiculations are only discernible at close range. The rump and rounded tail are browner, and marked with white spots, and the underparts are white, a black band running across the chest. The male is similarly patterned, though the colours are more subdued and less uniform. The chest, neck and coverts are barred, and the spots more obvious, creating a disruptive effect. The bill colour varies; generally it is pale brown, darker at the tip, becoming greenish towards the base. Juveniles resemble males and the downy nestling is striped. *N. semicollaris* (21.5 cm long) is smaller, with a more curved, terminally flattened bill. It has a slight web between the middle and outer toe, and the tail is wedge shaped. The sexes are similar, being deep chocolate brown above, finely barred with black. The head lacks spectacles, having superciliary stripes in addition to that on the crown. Two buff streaks form a V over the back and the coverts bear conspicuous white spots; the primaries are white on their outer edges. The underparts are white and the bill greenish or pink, tipped with red. Immatures are paler and more variegated.

Habitat. Low, swampy areas are preferred, with patches of open water interspersed with dense vegetation, as well as paddy fields and freshly flooded land. Birds may leave cover at dawn and dusk to forage on grassland and ploughed fields.

Distribution and movements. *R. b. benghalensis* inhabits Africa, the Middle East and southern Asia; *R. b. australis*, Australia; and *N. semicollaris* southern South America. Both species are generally sedentary, though *R. b. benghalensis* may make short migrations to follow the rains.

Voice. *R. benghalensis* is usually silent outside the breeding season. The voice of the female is deeper than that of the male due to a longer, convoluted trachea, which, during the breeding season, becomes less firmly held in the fat of the neck. The low mellow *vot* notes given during her display flight carry over long distances. When displaying on the ground to a male, mellow *booo* notes are given, reminiscent of the sound produced by blowing across a bottle. When confronting a rival or predator, throaty hissing and growling sounds are given by both sexes, and flushed birds may give a somewhat sharper alarm note.

Food. Omnivorous diet includes invertebrates, particularly Orthoptera, molluscs and earthworms, and seeds. They feed by probing soft mud or with scything movements of the bill in shallow water.

Behaviour. Being so secretive, few behavioural observations have been made, particularly on the American species. *R. benghalensis* usually occurs solitarily or in pairs, though after breeding flocks comprising several family groups may form. Males outnumber females and polyandry is the general rule, although in sparse populations, such as those in South Africa, monogamous bonds may form. Breeding is during the rainy season and the females take up territories within which they court several males in succession. They declare their territories and attract males with an advertisement flight not unlike the roding of Woodcock *Scolopax rusticola*. On the ground, one display is used both to woo males and during territorial disputes with other females. At low intensity the female stands sideways on, the far wing raised or extended, the tail fanned or depressed. At higher intensity she faces her opponent or mate, lowers her breast and extends and pronates both wings, bill pointed downwards and tail fanned. Females may actually fight each other in defence of their mates.

Breeding. The nest is a pad of woven plant material concealed in dense vegetation and is built by the male, though the female may be in attendance. The normal clutch is 4 (occasionally 5 or 6) pointed oval eggs, glossy cream or yellow marked with bold black blotches, speckles or lines. After laying the female leaves the male to incubate for *c.* 20 days and rear the young, and goes to court another mate. Bonds form rapidly, the second clutch often being laid before the first is hatched. The nests of one female usually form a loose group 4–10 m apart, and in Japan 2–4 clutches per female are usual. The males attend the nidifugous young and may use the head-on form of display to frighten off predators, as well as occasionally employing a rudimentary form of distraction display to lure observers from the chicks.

In the less well-known *N. semicollaris* the female incubates the eggs, though polyandry appears also to be normal and the male escorts the young. Single nests may be found, usually during July, though groups of 5 or 6 in an area of a hectare are most usual. The nests are also of woven plant matter, and the 1 or 2 eggs are white, evenly mottled with black, sometimes so densely as to appear wholly black. The call is a plaintive whistle. A.S.R.

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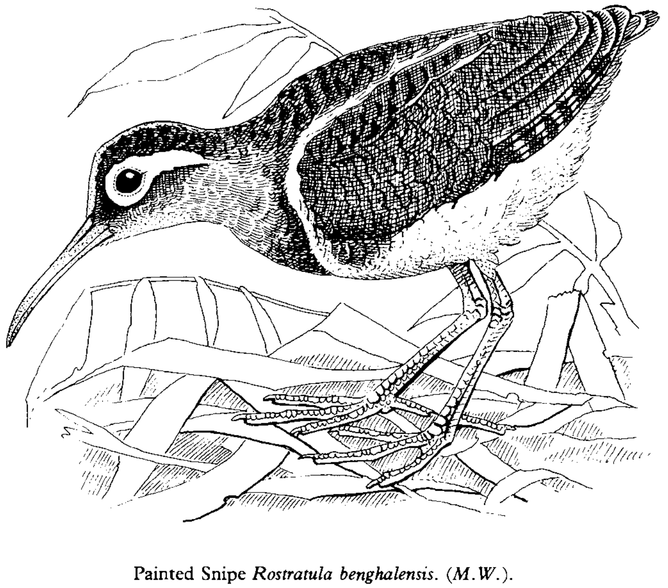

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PAIR: collective noun for, inter alia, two birds of opposite sexes, ordinarily used of adults (normally of the same species) believed to be mated together.

PAIR FORMATION: establishment of a special relation between two birds of opposite sex. Practically every type of relationship between the sexes occurs among birds. Some species, e.g. 'lek birds', have merely a temporary pair bond, the sexes meeting only for copulation (see LEK). More usually there is a lasting relationship, which may endure for days, weeks, or even years, and which may be monogamous, polygamous, or polyandrous (see MATING SYSTEMS; POLYANDRY). Monogamous relationships are most frequent, and it is with that type that this article is primarily concerned. Such relationships are of course normally heterosexual; although pairing between individuals of the same sex is common in captive birds, it is rare in the wild.

Pair formation implies that a number of social responses, potentially elicitable by any member of the species, become more or less limited to one individual; at the same time other responses (e.g. aggressive ones) become inhibited towards the partner. When paired, the mates often tend to keep together for much of the time, and may show a special type of searching behaviour if they lose contact.

Pair formation depends on an exchange of signals between potential mates over a period of time. These may be visual (e.g. colours or structures, often exhibited by courtship displays—see DISPLAY), or auditory (e.g. song—see VOCALIZATION). Since hybrids are usually at a selective disadvantage compared to their parental types, it is important that pairing should be intraspecific (see HYBRID). For this reason the signals usually differ markedly between closely related species living in the same area (see ISOLATING MECHANISM). Specific differences in courtship postures are shown in every comparative study, and the relevant plumage patterns usually differ between species more than the displays themselves. Sympatric closely related species also often differ markedly in song (e.g. Willow Warbler *Phylloscopus trochilus* and Chiffchaff *P. collybita*). The study of hybrids shows that such interspecific differences are usually polygenic, and are thus likely to be of adaptive value. That this value lies in the prevention of hybridization is suggested by the following types of evidence.

1. Divergence is most marked in those characters important in pair formation. Thus amongst cardueline finches, where there may be an interval of some weeks between pair formation and copulation, the early courtship displays differ between species more than do those immediately preceding copulation (see COPULATION).

2. Divergence is often greatest where hybridization is most likely, for instance in the overlap zone of potentially sympatric species.

3. Species characteristics often tend to disappear on oceanic islands, where no closely related species are present.

4. Divergence is more marked in males than in females. This is in harmony with Dobzhansky's view that since gamete loss is more serious for females than for males, it is primarily female preference that will be selected for; but the fact is also explicable in other ways, such as the maintenance of female uniformity by selection for cryptic coloration.

Mayr (1942) has shown that hybrids are more common in genera in which copulation is not preceded by an 'engagement' period (e.g. Paradisaeidae; some Tetraoninae), although hybrids do of course occur in groups that form lasting pair bonds. On the whole, however, hybrids are extraordinarily rare in nature, even among species that hybridize readily in captivity when conspecific mates are not available (see HYBRID).

Pair formation has been most studied in territorial song-birds (see TERRITORY). Where territorial establishment precedes pair formation and this occurs some time before copulation (e.g. Robin *Erithacus rubecula*, Snow Bunting *Plectrophenax nivalis*, Chaffinch *Fringilla coelebs*), the female is usually first attracted by the song or appearance of the male. The male normally responds aggressively to all intruders on his territory. If the intruder is a male, he flees or fights back. If it is a female not yet ready to pair, she flees. If, however, it is a female in condition, she usually stays around, often showing a 'submissive' posture, and the male's attacks gradually cease. The male then gradually ceases to be aggressive and begins to show courtship behaviour. The range of variations on this theme is of course enormous. For instance, the process may take anything from minutes to days; the stimuli to which each sex responds may be primarily structural, behavioural, or both; and the male's aggressiveness may cease almost at once or persist right up to copulation. Where pair formation precedes territorial establishment, it may start with the male's behaving aggressively to other members of the flock, although the process is fundamentally similar. Usually the increasing tendency of the male to behave sexually as the season advances is associated with a reduction in his aggressiveness towards his partner, who may then become dominant. Outside territorial song-birds, the diversity of behaviour is even greater. For instance, in some crows and ducks pair formation seems to involve a social ceremony. In most cases that have been studied in detail (e.g. Laridae), however, there seems to be a similar interplay between tendencies to attack, to flee from, and to behave sexually (or socially) towards the mate. The term sexually is, of course, to be interpreted rather widely, since in the early stages the consummatory situation is proximity to the mate rather than copulation, and the relation between male and female is little different from that between flock companions. It will be clear that the dominance relations during pair formation may be very complex; indeed many species pass through a phase in which the female attacks the male during courtship, but the male attacks her at other times, so that a distinction can be made between sexual and social dominance. Although pair formation is usually associated with changes in dominance, it is very difficult to make useful generalizations about the role that dominance plays (see DOMINANCE (2)).

Because of the diversity of the processes of pair formation, it is impossible to classify species into a limited number of types. Lorenz (1935) attempted a classification that depends primarily on whether the displays of the sexes are similar or different, on whether one or both sexes show 'releasers', and on whether males respond initially to other members of the species by aggression or courtship. Although his classification has been criticized by N. Tinbergen, D. Lack, and others, and it is clear that his categories do not represent inclusive groups, they are useful as types. R.A.H.

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PALAEOGNATHAE: a formerly recognized superorder.

PALAEOGNATHOUS: also 'palaeognathine' (Pycraft)—see PALATE.

PALAEOMONTANE: belonging to the fauna of the alpine or snow (nival) zones of the high mountains of the Palearctic Region.

PALAEONTOLOGY: the study of fossilized remains of animals and plants (see ARCHAEOPTERYX; EARLY EVOLUTION OF BIRDS; FOSSIL BIRDS).

PALAEOSPECIES: a species existing at an earlier level of geological time, possibly ancestral to one or more species of the present day but distinct from any of them; the ordinary criteria of a species are purely contemporary.

PALAEOTROPICAL: inclusive term used by Sclater for his three southern zoogeographical regions in the Old World, contrasted with the Palearctic Region (and on the other hand with the Neotropical); more generally, a term implying wide distribution in the tropical parts of the Old World (see DISTRIBUTION, GEOGRAPHICAL).

PALAEOXERIC: belong to the fauna of the steppes and deserts of the southern Palearctic Region.

PALAEO-XEROMONTANE: belonging to the fauna of the arid slopes of the low mountains of the southern Palearctic Region.

PALAEOZOOLOGY: the part of palaeontology that is concerned with forms ascribed to the Animal Kingdom.

PALATABILITY OF BIRDS AND EGGS: regarded both from the subjective human standpoint and, so far as possible, from that of the observed preferences of other animals. The inverse relation that is commonly found between palatability on the one hand and vulnerability and conspicuous coloration on the other is particularly considered.

Palatability of the flesh. It is well known that the flesh of birds differs widely in palatability. Some enjoy a high reputation in this respect, e.g. Quail *Coturnix coturnix*, Partridge *Perdix perdix*, Red Grouse *Lagopus lagopus scoticus*, Golden Plover *Pluvialis apricarius*, Woodcock *Scolopax rusticola*, Snipe *Gallinago gallinago*, Teal *Anas crecca*, Canvasback *Aythya valisineria*, Corncrake *Crex crex*, Bittern *Botaurus stellaris*, and Skylark *Alauda arvensis*. Others are unfit for the table, e.g. Kelp Goose *Chloephaga hybrida*, Smew *Mergus albellus*, Shelduck *Tadorna tadorna*, Oystercatcher *Ostralegus haematopus*, Egyptian Plover *Pluvianus aegyptius*, Hoatzin *Opisthocomus hoazin*, and various hornbills, kingfishers, and drongos. (See also UTILIZATION BY MAN.)

Attempts to assess relative palatability more exactly by experiments with meat-eating animals, and by observations of tasting panels, have extended knowledge to include a wide range of species not normally eaten by man, and have shown that among relatively vulnerable species, cryptic coloration, whether in the female alone or in both sexes, is generally associated with edibility, and conspicuous coloration with distastefulness. For example, in a series of experiments in which hornets were used in Egypt as assessors of the acceptability of the flesh of 38 species, the two rated as most acceptable (Wryneck *Jynx torquilla* and Crested Lark *Galerida cristata*) are also the two most cryptic in appearance; and those of lowest edibility (White-rumped Black Chat *Oenanthe leucopyga*, Mourning Chat *O. lugens*, Hooded Chat *O. monacha*, Pied Kingfisher *Ceryle rudis*, Masked Shrike *Lanius nubicus*, and Hoopoe *Upupa epops*) are all conspicuous and include the only three species in the series examined having exclusively black-and-white coloration. On available evidence other and quite unrelated tasters, such as cat and man, show generally similar preferences and aversions. Nauseousness is a common but not invariable attribute of conspicuous birds, for many highly conspicuous species are nevertheless relatively palatable, e.g. various albatrosses (Diomedeidae), storks, egrets *Egretta* spp., swans *Cygnus* spp., cranes, gulls, and macaws and cockatoos (Psittacidae); but such birds have no need of a nauseous deterrent, being otherwise protected—by large size, fighting strength, social habits, or ability to escape.

Tests recently carried out by members of a tasting panel in Zambia (Department of Game and Tsetse Control) confirm the above general conclusions. Samples of flesh were assessed on a scale from 9.0 (excellent) to 2.0 (inedible). Of 191 species examined, the 19 rated higher than 7.0 include 15 cryptic species, and in 10 of these the female or both sexes are highly cryptic (Quail *Coturnix coturnix*, the Kaffir (or African Water) Rail *Rallus caerulescens*, Corncrake *Crex crex*, African Crake *Crecopsis egregia*, Water Dikkop *Burhinus vermiculatus*, Senegal Bustard *Eupodotis senegalensis*, Black-bellied Bustard *Lissotis melanogaster*, Double-banded Sandgrouse *Pterocles bicinctus*, Yellow-throated Sandgrouse *P. gutturalis*, and Fiery-necked Nightjar *Caprimulgus pectoralis fervidus*. In contrast, of 14 species with plumage that is black, white, or a combination of both, only the White-breasted Cormorant *Phalacrocorax carbo lugubris* (7·0) was rated as palatable, and Little Egret *Egretta garzetta* (6.3), and Openbill Stork *Anastomus lamelligerus* (6.0) as moderate. Nine of the remainder are relatively or markedly distasteful, notably Pied Crow *Corvus albus* (4.9), White-winged Black Tit *Parus leuconotus* (4.8), Black (or Sooty) Chat *Myrmecocichla nigra* (4.5), Whiteheaded Black Chat *Thamnolaea arnotti* (4.5), Pied Kingfisher *Ceryle rudis* (4.1), Southern Black Tit *Parus niger* (4.1), and Black Cuckoo *Cuculus cafer* (3.0). The relation between visibility and distastefulness is also seen within the limits of restricted groups, for example: among 6 crakes examined, the only conspicuous species (Black Crake *Limnocorax flavirostra*) has the lowest edible rating (5.1); of 6 chats, the 3 most conspicuous are also the 3 most distasteful (all 4.5); the same relationship is found in 5 plovers, of which 2 (Blacksmith Plover *Vanellus* ('*Hoplopterus*') *armatus*, 5.1, and Long-toed Water Plover *Vanellus* ('*Hemiparra*') *crassirostris*, 4.8) are both relatively conspicuous and distasteful.

Colour conflict. The inverse relation between acceptability of the flesh and visibility of the plumage is of special interest in a connection with the concept of 'colour conflict'. It has been shown elsewhere (see COLORATION, ADAPTIVE) that concealing (cryptic) and revealing (phaneric) characters subserve many and diverse functions of adaptive value in the struggle for survival. Yet for optical-psychological reasons the two types of coloration, although both advantageous, are generally antagonistic and tend to be mutually exclusive.

The conflicting needs of effacement and of advertisement are reconciled in various ways. (*a*) Conspicuous characters, in birds of which the coloration is predominantly cryptic, may be revealed at special times by the momentary display of bright ornaments normally hidden (as in deflection displays, social recognition marks exposed only in flight, and the buccal feeding releasers of nidicoles, etc.). (b) Again, in many species, cryptic coloration is confined to the more valuable or vulnerable individuals, e.g. females in sexually dimorphic species where the males are conspicuous, e.g. many Anseriformes, Galliformes, and some territorial Passeriformes; and nidicolous young, where adults of both sexes are conspicuous, e.g. oystercatchers, some plovers (Charadriidae), gulls, and terns. (*c*) Relatively non-vulnerable species otherwise protected have no need for concealment; for them the road to conspicuousness lies open and has generally been taken by both sexes, e.g. cassowaries, gannets, pelicans, flamingos, some birds-of-prey, cranes, swans *Cygnus* spp., many gulls, and parrots. Such birds are not protected by distastefulness. (*d*) In many small and otherwise vulnerable birds the advantages of concealment have over-ridden those of visual advertisement, and cryptic coloration is developed in both sexes, e.g. in partridges *Perdix* spp., francolins *Francolinus* spp., quails *Coturnix* spp., coursers *Cursorius* spp., thickknees, nightjars, pipits *Anthus* spp., larks, warblers (Sylviinae). The palatability of such birds tends to render cryptic coloration of paramount importance. (*e*) Another line of evolution has led in the opposite direction, towards conspicuousness in both sexes, e.g. various plovers (Charadriidae), auks, turacos, Hoopoe *Upupa epops*, wood-hoopoes, kingfishers, barbets, shrikes, drongos, starlings, chats *Oenanthe* spp. etc. and tits. But this trend has been possible only for relatively defenceless species when it is associated with the counter-deterrent of repugnant taste. The advertising coloration of such birds is (in part) warning (proaposematic) in function.

Palatability of eggs. Experiments with egg-eating mammals of several orders (cat, ferret, mongoose, hedgehog, rat), and observations by members of a tasting panel (Low Temperature Station, Cambridge) afford results parallel in many respects to those considered above. Edibility and coloration are related to various factors that influence the availability of eggs to predators. Thus, eggs laid by larger birds, or in colonies, or in sites difficult of access, are in general more palatable than those laid by smaller birds, or by solitary nesters, or in accessible sites. Among otherwise vulnerable species, many eggs in the higher edibility grades are protected by cryptic coloration or are covered by a close-sitting cryptic parent, e.g. in many ducks, game-birds (Galliformes), bustards, rails, waders (Charadrii), sandgrouse. On the contrary, conspicuousness of the shell is often associated with a repugnant taste.

In a series of 212 species examined, the shells of the most ill-flavoured eggs were commonly either immaculate white or white with reddish spots: Red-faced Mousebird *Colius indicus* (3.5), Green Woodpecker *Picus viridis* (3.5), Verreaux's Eagle Owl *Bubo lacteus* (3.3), House Wren *Troglodytes aedon* (3.2), Wren *T. troglodytes* (2.7), Speckled Mousebird *Colius striatus* (2.5), Black Tit *Parus leucomelas* (2.0). Among eggs of low-grade edibility, the most widespread distasteful property is bitterness, which is highly developed in the flavour-pattern of Columbiformes, Cuculiformes, Strigiformes, Coliiformes, Coraciiformes, Piciformes, and Passeriformes. H.B.C.

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PALATE: the bony palate (Fig. 1) is made up of the same elements as are found in reptiles, except that the ectopterygoid or transpalatine is absent. Anterior are the premaxillae, which have shelf-like palatal processes fused in the midline at the front of the bill. Farther back these processes may be separated from each other by a cleft. There is often a large vacuity between them and the palatal processes of the maxillae, or

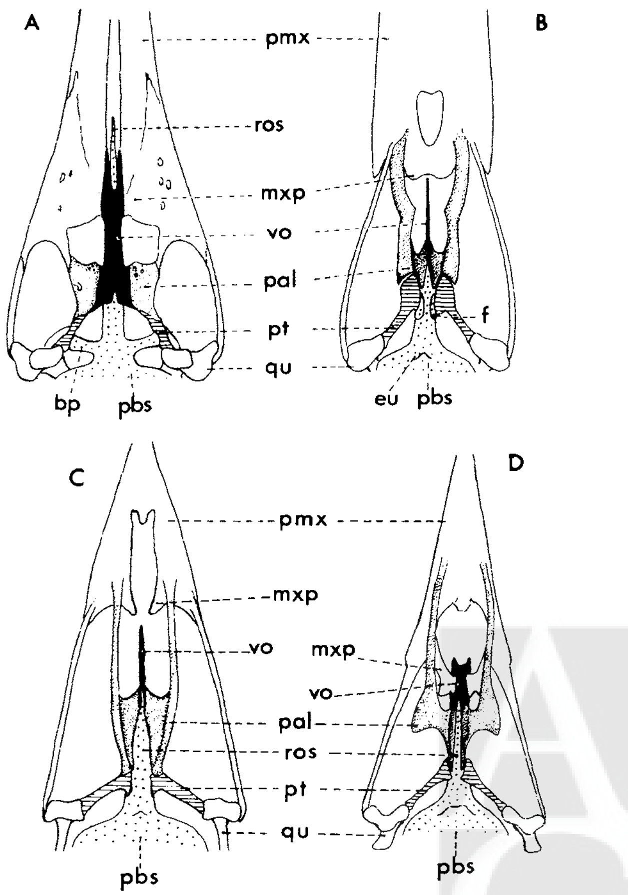

Fig. 1. Palate bones, seen from below, in A, *Rhea* (palaeognathous); B, duck *Anas* (desmognathous); C. fowl *Gallus* (schizognathous); D, crow *Corvus* (aegithognathous). In A the contact between pterygoid and vomer is on the dorsal surface of the palate. (*A.d'A. Bellairs*).
bp. basipterygoid process; **eu.** opening of Eustachian tubes; **f.** facet for pterygoid on rostrum; **mxp.** maxillopalatine; **pal.** palatine; **pbs.** parasphenoid and basisphenoid fused; **pmx.** premaxilla; **pt.** pterygoid; **ros.** rostrum of parasphenoid; **qu.** quadrate; **vo.** vomer.

maxillopalatines, which may or may not be fused or closely approximated in the midline.

The vomers are usually fused into a single bone in the adult. On either side of these, and often separated by a gap on each side, are the palatines; behind these are the pterygoids, articulating posteriorly with the quadrates.

The internal nares lie between the palatines, the vomers and the maxillopalatines; but in kiwis *Apteryx* spp., where the palate is exceptionally complete, the internal nares are bordered by the palatines and vomers only, which approximate in front of the choanal opening.

Deeply placed in the midline of the palate is the rostrum of the parasphenoid. Posteriorly this bone widens out and is fused with the lower surface of the basisphenoid. The usually common opening of the Eustachian tubes (Tubae pharyngotympanicae) can be seen at the base of the rostrum.

In many birds the pterygoids articulate with the parasphenoid rostrum by means of movable joints. Movements of the quadrates are transmitted through the pterygoids and palatines to the BILL, which is thus raised or lowered (kinesis; see SKULL).

Taxonomic significance. Since T.H. Huxley's work (1867), the structure of the bony palate has been used as a basis for classifying birds into major groups. The following types of palate have been distinguished:

1. Palaeognathous, or dromaeognathous, characteristic of 'ratite' birds and tinamous (Fig. 1A). Vomers large and imperfectly fused, articulating anteriorly with the premaxillae and the maxillopalatines and posteriorly with the palatines and pterygoids (except for *Struthio*). Pterygoids in contact with the palatines along an unmovable suture and separating these from the parasphenoid rostrum. Well-developed basipterygoid processes set well back on parasphenoid. Complex pterygoid—quadrate articulation, involving the orbital process of the quadrate.

2. Neognathous, characteristic of carinate birds. Vomers often small and completely fused, sometimes absent. Palatines and pterygoids usually in contact with parasphenoid rostrum, and articulating with each other at a movable joint. Typical basipterygoid processes usually absent, but often replaced by facets on rostrum farther forwards (Fig. 1B).

Neognathous palates have been further subdivided as follows: (i) Desmognathous (Fig. 1B), as in Anseriformes, Pelecaniformes, Psittaciformes, most Accipitriformes and Falconiformes, Strigiformes, and some other groups. Vomers small and tapering. Maxillopalatines broad and meeting each other or the vomers in the midline. (ii) Schizognathous (Fig. 1C), as in Columbiformes, Galliformes, Sphenisciformes, Charadriiformes, and others. Vomers tapering in front. Maxillopalatines not meeting each other or vomers in midline, so that there is an extensive longitudinal cleft in the bony palate. The palate of woodpeckers (Picidae), to which the term saurognathous was applied to cover the (erroneously supposed) condition of paired and separated vomers is not distinguishable from the schizognathous condition (de Beer 1937). (iii) Aegithognathous (Fig. 1D), as in Passeriformes and a few other groups such as swifts (Apodidae) and nightjars (Caprimulgidae). Maxillopalatines separated, fused vomers truncated and broad in front, and forked behind, embracing the parasphenoid rostrum.

Today the taxonomic value of the different bony palate patterns is open to question. The various subdivisions of the neognathous condition partly merge into one another, and while these palatal types may be of value as a guide to the systematics of the smaller groups, they do not provide a reliable basis for major group classification.

McDowell (1948) denies that the distinction between the palaeognathous and neognathous types may be upheld any longer. Several authors have pointed out that during embryonic development some neognathous birds show an arrangement similar to the palaeognathous condition, with the pterygoid extending forward so as to articulate with the vomers. Later the front end of the pterygoids becomes detached from the rest as the 'hemipterygoid' and fuses with the palatine. Consequently the criterion of a palatine separating the vomer from the pterygoid, formerly thought to be characteristic of neognaths, is in some cases illusory.

The similarity in the embryonic arrangement of some neognathous birds may be interpreted as a recapitulation of an ancestral stage, or the palaeognathous palate in the ratites may be a neotenic structure, comparable to other features thought to be neotenic in these birds (see EARLY EVOLUTION OF BIRDS).

Fossil evidence adds no light to the problem. *Archaeopteryx* is claimed to be neognathous (schizognathous). The reconstruction of the skull of *Hesperornis* by Gingerich suggests a somewhat similar arrangement of the bony palate as in the palaeognaths, yet the vomer does not articulate with the pterygoid, and there is not the complex pterygoid-quadrate articulation.

In contrast with McDowell, Bock (1963) has clearly shown that in palaeognaths there is indeed a common morphological pattern and that

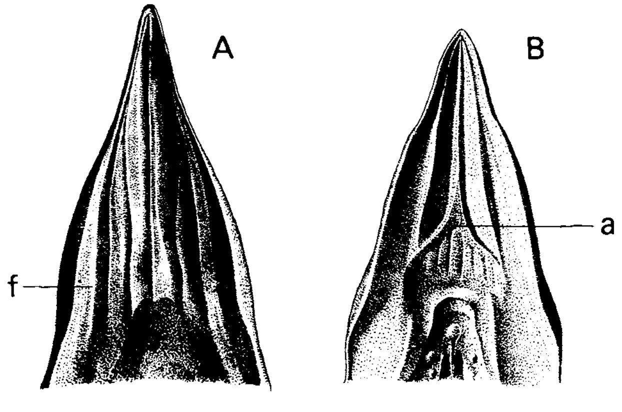

Fig. 2. View of the horny palate of *Fringilla coelebs* (A) and *Passerina ciris* (B). **a.** abutment; **f.** furrow.

the palaeognathous palate can be defined by the criteria mentioned above. He stresses its function in transmitting great forces for rhynchokinetic movements of the bill. Thus, the palaeognathous palate may indeed be of crucial importance for understanding of ratite evolution and relationship.

Horny palate. Apart from the bony palate there is a horny palate (Fig. 2) on the inner side of the rhamphotheca which covers the upper mandible. Normally this horny palate is a simple vault, but in several dietary specialists such as birds which remove the husks from the seeds before swallowing them (e.g. the granivorous songbirds and the parrots), the horny palate is highly structured with a characteristic system of furrows and longitudinal or cross tuberosities. The furrows lodge the seeds when they are cut open, the tuberosities serve as an abutment when the seeds are pressed off (Ziswiler 1965). In the granivorous songbirds and the parrots (Homberger 1980) the structure of the horny palate is species-typical and therefore of considerable taxonomic importance.

(A.d'A.B.) V.Z.

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PALATINE: a paired bone of the SKULL.

PALEARCTIC REGION: or 'Palaearctis', name of zoogeographical region proposed by Philip L. Sclater (1858) (see DISTRIBUTION, GEOGRAPHICAL), comprising the whole of Europe, Africa north of the Sahara, and arctic, boreal and temperate Asia north of the Himalayas. The concept of a 'Holarctic Region' for all cold and temperate land masses of Eurasia and North America was introduced by Alfred Newton and followed widely, reducing the Palearctic and Nearctic (cold and temperate New World) to the rank of subregions. In spite of this, for the sake of convenience the term Region is still generally used. In zoogeography the stress has shifted from the static concept of a 'region' with fixed boundaries to the dynamic and more realistic state of a 'fauna'.

Features and boundaries. The main physical features of the Palearctic Region are a basically circumpolar arctic or tundra Zone, a virtually continuous belt of boreal, mainly coniferous woodland known as the taiga from Norway to eastern Siberia, an almost continuous chain of mountains from the Pyrenees, Alps, Carpathians, Caucasus, Elburz, to the Himalayas, and an almost continuous belt of desert from Morocco to Sinai, Arabia, Iran, Turkmenistan, Uzbekistan, Tibet, and Gobi. These features and their histories during the Pleistocene ice-age have exercised a profound influence on bird-life and its distribution.

The boundaries of the Palearctic Region are broadly defined in the west, north and east by the Atlantic, Arctic, and Pacific Oceans, separating it from the Nearctic. But in the south there is no clearly defined boundary with either the Afrotropical or the Oriental Regions.

Greenland, although geographically part of North America, is, on the evidence of plants, insects, and birds, biologically part of the Palearctic, probably in consequence of the ice-free condition of the arctic deserts in north-eastern Canada at least during the last glacial period and the amount of sea-ice in the North Atlantic in the post-glacial. Only 5 Nearctic species out of 55 have established themselves in Greenland as regular breeding birds, whilst 3 species have reached Iceland (Great Northern Diver *Gavia immer*, Harlequin Duck *Histrionicus histrionicus*, Barrow's Goldeneye *Bucephala islandica*).

The Atlantic has been an efficient barrier to avian dispersal. It is remarkable that no purely Palearctic passerine species has reached North America within the memory of man, save perhaps the Wheatear *Oenanthe oenanthe* in north-eastern Canada, whilst but a single non-passerine—the Cattle Egret *Bubulcus ibis* has recently established itself in the New World by crossing the Atlantic. In addition, the Black-headed Gull *Larus ridibundus* and the Lesser Black-backed Gull *L. fuscus* are busy establishing a foot-hold in eastern North America (via Iceland). Despite the hundreds of North American birds blown across the Atlantic or assisted by ships every year, not one species has yet established itself in Europe, though the Spotted Sandpiper *Actitis macularia* and Wilson's Phalarope *Phalaropus tricolor* have recently made an attempt.

In southern Europe the Mediterranean has been a less efficient barrier to dispersal than the Sahara. The northern and central Sahara are still predominantly Palearctic; but at both ends we find Palearctic species seeping down (e.g. Spoonbill *Platalea leucorodia* in the west and east, and Little Owl *Athene noctua* in the east) and Afrotropical species seeping up—some along the coast of Morocco and spreading east to Tunisia and even to Spain, e.g. the Little Buttonquail or Andalusian Hemipode *Turnix sylvatica* and the Crested Coot *Fulica cristata*, and several up the Nile Valley and into Lower Egypt and the Jordan Valley, e.g. the Palestine Sunbird *Nectarinia osea*. The bird faunas of the Canary Islands, Madeira, and the Azores are definitely Palearctic; so is the majority of the birds of the Cape Verde Islands.

Sinai is pure Palearctic. In Arabia many Palearctic forms reach the Yemen, as do a few Oriental forms across southern Arabia. At present, mountainous south-west Arabia is included by most biogeographers in the Afrotropical Region. In south-west Asia there are two remarkable cases of interrupted distribution, both Oriental kingfishers—the White-breasted Kingfisher *Halcyon smyrnensis* reaching westernmost Asia Minor and probably even south-eastern Europe, and the White-collared Kingfisher *H. chloris* reaching the southern Red Sea (outside the confines of the Palearctic), the latter's nearest relative being 3,200 km distant in India.

The avifaunas of the Persian Gulf and Iran are predominantly Palearctic with slight Afrotropical and Oriental elements; but farther east we find a more exact boundary between the Palearctic and the Oriental regions in the mountains of northern Baluchistan, the Afghan-Pakistan frontier, and then east along the higher levels of the Himalayas and into China about Szechuan and Hupeh, where the Yangtsekiang is usually considered a faunal boundary, but where in fact there is a large transition zone. North of the Hwang-ho the fauna is definitely Palearctic, as are those of Korea and Japan.

In Kamtschatka we find a close relationship with northern Alaskan birds. The narrow Bering Strait, which was land during each of the glacial periods, hardly acts as an efficient barrier for birds. Several Nearctic species have spread to eastern Siberia, e.g. the Grey-cheeked Thrush *Catharus minimus*, and some true Palearctic species have spread to Alaska, e.g. the Yellow Wagtail *Motacilla flava*, Wheatear and Arctic Warbler *Phylloscopus borealis*, while the Dotterel *Charadrius morinellus* has occasionally bred there.

Effects of Pleistocene glaciations. A large part of the north-western Palearctic has been subjected to arctic and sub-arctic conditions during the series of at least four alternating Pleistocene glaciations, which terminated some 10,000 years ago after persisting for almost 2,000,000 years. In fact, the present climatic condition of the Holarctic can be described as a post-glacial or even as a recent inter-glacial period. However, only small areas of the Palearctic were actually covered by ice-caps involving the complete extermination of bird-life. These included the whole of north-west Europe south to the British Isles, the Netherlands, the southern shores of the Baltic, central Russia, north-east to the Taimyr Peninsula, but not central and east Asia. (See also GEOLOGICAL FACTORS). There were minor ice-caps in the Atlas, Pyrenees, Alps, Himalayas, and mountains of north-east Asia. But even in glaciated regions small pockets of unglaciated land persisted as they do today in Greenland.

Far the greater part of the Palearctic Region was ice-free, though tundra and wind-swept cold deserts reigned in extensive peri-glacial areas. Warmer climates and more luxuriant vegetation prevailed, particularly in the east and south-east. In the western Palearctic all climatic vegetation zones were shifted south by a few thousand kilometres. Notably arboreal and forest birds were forced east, south-east and south, and this phenomenon has its counterpart in the post-glacial general return (expansion) westwards, north-westwards and northwards, continuing even today. During the last 100 years more than 28 Eurasiatic species have extended their range westwards and north-westwards, following the retreat of the Fenno-Scandinavian ice-cap and the surrounding tundra and steppes, the most spectacular extensions being those of the Grey-headed Woodpecker *Picus canus*, Greenish Warbler *Phylloscopus trochiloides*, and Scarlet Rosefinch *Carpodacus erythrinus*.

There are 66 species of birds breeding regularly in Britain that do not do so regularly in Ireland; the Magpie *Pica pica* reached Ireland only in 1676, the Stock Dove *Columba oenas* as recently as 1877, and the Black-necked Grebe in 1906 (but no longer breeds there).

Glaciation was the major influence in transforming many continuous into discontinuous distributions. Today we find the Blue or Azure-winged Magpie *Cyanopicus cyanus* in south-west Spain and again in China and Japan, the Twite *Carduelis flavirostris* in north-west Europe and again in the Caucasus and central Asian highlands; the Marsh Tit *Parus palustris* has two disjunct ranges in Europe and east Asia, the White Stork *Ciconia ciconia* has three disjunct ranges, in Europe, Turkestan, and east Asia. Also it was almost certainly the effect of glaciation that drove the Magpie *Pica pica* into Yemen, and some Palearctic species into tropical Africa; they left behind isolated populations when conditions in Eurasia allowed them to spread once more into the northern areas where the bulk of their numbers are now found. Examples are the Chough *Pyrrhocorax pyrrhocorax* in the Ethiopian highlands and the Bittern *Botaurus stellaris* in southern Africa.

Subdivisions. Bird-life in the Palearctic Region is by no means uniform; there are only 41 species in Korea that also breed in the British Isles; and there is still less uniformity among birds from Scandinavia and the eastern Himalayas. It may therefore be useful to suggest at least 7 zones of bird-life in the Palearctic Region, based on B. Stegmann's concept of faunal elements or faunal types.

1. Arctic Zone, with many circumpolar species, some of them extending south to the alpine levels of the European and Asian mountains, including the Tien Shan, but absent from the Himalayas and the Caucasus. The Ptarmigan *Lagopus mutus*, Snow Bunting *Plectrophenax nivalis* and numerous waders and waterfowl are typical of this zone. By its circumpolar nature and extreme climatic conditions the Arctic Zone is sometimes considered an independent Region or Sub-region. The Arctic Zone includes a more arid and colder high arctic and a moister and less extreme cold low arctic zone; characteristic species are Brent Goose *Branta bernicla*, King Eider *Somateria spectabilis*, Glaucous Gull *Larus hyperboreus* (part-arctic), Knot *Calidris canutus*, Sanderling *Calidris alba* (high arctic), Steller's Eider *Polysticta stelleri*, Bewick's Swan *Cygnus columbianus bewickii* (low arctic). The Arctic may include a sub-arctic zone, which is sometimes considered to have its own, independently derived vegetation and fauna. It is the zone of the low birch forest with fascinating tortured stems; characteristic species are Lesser White-fronted Goose *Anser erythropus*, Red-breasted Goose *Branta ruficollis*, Spotted Redshank *Tringa erythropus*, Pechora Pipit *Anthus gustavi*.

2. Siberian Zone, characterized by boreal coniferous forest, known as taiga, occupying a continuous belt from eastern Siberian into Scandinavia, with a gradual reduction of the number of species from east to west. Again there are isolated pockets of a Siberian fauna, including the Capercaillie *Tetrao urogallus* and the Nutcracker *Nucifraga caryocatactes*, in the sub-alpine zones of mountain ranges in Asia and Europe, such as the Alps and the Pyrenees. The Hawk Owl *Surnia ulula*, Siberian Jay *Perisoreus infaustus*, Redwing *Turdus iliacus*, and Brambling *Fringilla montifringilla* are typical species of the Siberian Zone.

3. European Zone of deciduous forests, narrowing to the southern Urals. A few species typical of this zone extend to Scandinavia, south-west Siberia, and recently even as far east as Baikal. Characteristic species are the Green Woodpecker *Picus viridis*, Robin *Erithacus rubecula*, Song Thrush *Turdus philomelos*, and Chaffinch *Fringilla coelebs*. The oak forests of North Africa and the mixed deciduous forests of the Caucasus and Turkestan contain others, such as the Jay *Garrulus glandarius*, several species of tit *Parus*, nuthatch *Sitta*, treecreeper *Certhia*, and thrush *Turdus*.

4. Mediterranean Zone, typified by xerophilous shrubs, steppe and semi-desert, and extending through most of lowland southern Europe, North Africa and south-west Asia to Iran and Afghanistan, with a few species extending north to southern England (Dartford Warbler *Sylvia undata*), central Europe and the steppes of southern Russia. The Cream-coloured Courser *Cursorius cursor*, bustards *Otis* and *Chlamydotis*, and many species of larks *Melanocorypha, Calandrella*, and warblers *Sylvia* are typical of the Mediterranean Zone.

5. Old World Desert or Eremian Zone, including the high Mongolian and low Turkestanian deserts, those of Iran and the Near East, with northern Arabia and Sinai, extending into Asia Minor and the northern half of the Sahara. Typical of this zone are sand partridges *Ammoperdix*, ground jays *Podoces*, various species of larks *Ammomanes, Alaemon, Ramphocorys*, wheatears *Oenanthe*, rock nuthatches *Sitta*, and the Trumpeter Finch *Bucanetes githagineus*. In the south-west of this zone there are many infiltrations from the Afrotropical Region, such as the Ostrich *Struthio camelus* in north Arabia and north-west Africa until quite recently, and several species of sandgrouse *Pterocles*.

6. Tibetan Zone, including the northern slopes of the high Himalayas. With the probable exception of the boreal forest zone there is no other continental area of the size of Tibet with such a distinct fauna. Typical are the Snow Partridge *Lerwa lerwa*, snowcocks *Tetraogallus*, Blue Grandala *Grandala coelicolor*, and various species of rosefinches *Carpodacus* and snowfinches *Montifringilla*; only the latter are restricted to the Tibetan highlands, the others include also Sino-Himalayan species, of which there are many.

7. Chinese Zone typified by the mixed broad-leaved forests of east Asia prevailing in southern Manchuria, Korea, Japan, and China and extending in the Himalayas as far as Kashmir and the Pamirs. Both the flora and the fauna of this area have maintained a high degree of diversity dating from pre-glacial times. The bird-life includes numerous forms and species that have died out in other parts of the Palearctic through the influence of the Pleistocene glaciations. Typical of the Chinese Zone are many species of pheasants *Ithaginis, Pucrasia, Lophophorus, Crossoptilon, Syrmaticus, Chrysolophus* and laughing thrushes *Garrulax* and *Pomatorhinus*.

Comparison with other regions. In size the Palearctic is roughly one and a half times as large as the Nearctic (*c.* 34 million km^2 against *c.* 21). However, computed per million km^2, the numbers of species occurring in these regions are almost alike, viz. *c.* 30 and 35, respectively. Compared with other continents and regions the numbers are low, as there are 85 species per million km^2 in the Afrotropical Region and up to 135 in South America (R.E. Moreau). These numbers may roughly indicate the relative diversity of ecological niches available, which is more restricted in the less hospitable temperate and cold areas than in the—for birds—more friendly humid tropics.

Of non-passerine species *c.* 443 occur in the Palearctic Region; of these 102 occur also in the Nearctic, 112 in the Afrotropical, and 105 in the Oriental Regions. Of passerine species *c.* 500 occur in the Palearctic Region; of these 16 occur also in the Nearctic, 30 in the Afrotropical, and 101 in the Oriental Regions.

There are 194 genera of non-passerine birds and 135 of passerine birds occurring regularly in the Palearctic Region. In the Nearctic Region these numbers are 180 and 111, respectively.

Characteristic forms. If we omit infiltrations from other regions, the Palearctic is more easily characterized by what it has not than by what it has; this applies particularly to its western half in which the devastating influence of the Pleistocene glaciations has been most severe. If we take the buntings *Emberiza*, we find 9 species in western Europe and 19 in Eastern Asia. We have 5 flycatchers *Ficedula* and *Muscicapa* in Europe and 14 in Palearctic Asia. On the other hand, of the 16 species of warblers *Sylvia* breeding in Europe and south-western Asia, not one occurs east of the Yenesei or in Japan; of the 6 species of *Phylloscopus* this number is, however, 4. Still, the Palearctic has 71 genera peculiar to it, and of these 27 are non-passerine (e.g. pheasant *Phasianus*, ruff *Philomachus*) and 44 passerine (e.g. crested lark *Galerida*, redstart *Phoenicurus*, long-tailed tit *Aegithalos*, wall creeper *Tichodroma*, chaffinch *Fringilla*).

A few groups require especial mention. Of the kingfishers (Alcedinidae) there are *c.* 87 species in the world and of parrots and parakeets (Psittacidae) *c.* 340; of these only 7 and 1, respectively, occur in the Palearctic, and 2 and 2 respectively, in the Nearctic. Among the larks (Alaudidae) only one species (Horned or Shore Lark *Eremophila alpestris*) occurs in the Nearctic, 24 in the Palearctic, and 49 in the Afrotropical Region. In the pipits and wagtails (Motacillidae) there are 5 species of wagtail *Motacilla* in the Palearctic, 3 in the Afrotropical Region, and only one, a geologically recent arrival, Yellow Wagtail *M. flava* in the Nearctic. There are 13 species of pipit *Anthus* in the Palearctic, 11 in the Afrotropical Region, and only 2 regularly in the Nearctic. The accentors (Prunellidae) with 13 species are virtually endemic to the Palearctic Region; none of them occurs in the Nearctic and only one marginally (Yemen, Arabia) in the Afrotropical Region.

The Horned Lark and Raven *Corvus corax* are noteworthy examples of truly Holarctic distributions: both species encompass the globe in its Northern Hemisphere, both extend from the Arctic to the tropics, and both breed from 5,500 m to below sea level.

Few birds have become extinct in the Palearctic in recent times.

Notable examples are Pallas' Cormorant *Phalacrocorax perspicillatus*, Great Auk *Pinguinus impennis*, a thrush *Cichlopasser terrestris* and a grosbeak *Chaunoproctus ferreorostris* from the Bonin Islands, Japan. (R.M.) K.H.V.

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PALILA: *Loxioides bailleui*, one of the HAWAIIAN HONEYCREEPERS.

PALLIUM: the mantle (see TOPOGRAPHY).

PALMAR: pertaining to the ventral surface of the manus, or sometimes of the whole wing.

PALMATE: having three toes connected by webs (see LEG).

PALMCHAT: *Dulus dominicus*, sole member of the Dulidae (Passeriformes, suborder Oscines). It is confined to Hispaniola, West Indies. Some investigators place it in the same family as the WAXWINGS (Bombycillidae) and their presumed relatives the SILKY FLYCATCHERS (Ptilogonatidae)—others prefer classification as a separate family, principally because of the 'communal' nests but also because of the harsher plumage, which lacks the silky quality and blended coloration of waxwings.

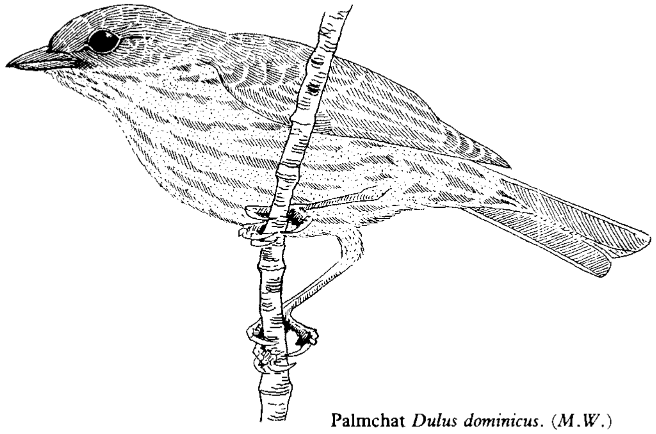
The total length is about 18 cm. The sexes are alike—greyish-olive (or brownish in worn plumage) above, and longitudinally striped with dark brown on a white base below. The head is darker than the back, the feathers having dark shafts; the rump is dark green. The tail is relatively long, the wings short and rounded, and the tenth primary rather long and thin, when compared with waxwings. Likewise the bill is stronger, more curved and compressed, and the nostril is exposed. The juvenile differs in having the throat and foreneck almost entirely dark brown, with only faintly paler edges, and a buffish rump.

The species is locally abundant throughout the island of Hispaniola (comprising Haiti and the Dominican Republic) except in rain-forest and at higher altitudes. On nearby Gonave Island the birds are slightly more local in distribution.

New nests are built, or old ones repaired or added to, during the spring months (March–June). These are usually large bulging structures—sometimes 1 m in diameter—of sticks and twigs, woven all about the smooth trunks of Royal Palms *Roystonea* and the bases of their fronds; when the fronds die, the nests fall. Pines are also used, but to a lesser extent, and nests built in them are smaller—used by one or two pairs.

Likening such nests to a block of flats is perhaps more apt than the word 'communal'. Pairs occupy their own compartments, to which they alone have access by passages from the outside. Each nest is lined with fine grass and shredded bark, and here the eggs are laid. Nests with central chambers and passages have been described. About 4 eggs are to be found in a clutch; they are white, heavily spotted and blotched with dark purplish grey or with a ring of this colour at the large end.

Berries (perhaps especially those of palms), as well as flowers of *Cordia* and other plants, are known to be staple foods. The birds are sociable and gregarious, even drawing together on the tree-limbs when roosting. No song has been recorded, but rather a noisy chattering in chorus as well as a variety of more or less pleasing notes. (J.C.G. Jr.)



Palmchat *Dulus dominicus*. (*M.W.*)

Greenway, J.C. Jr. 1960. Family Dulidae. *In* Mayr, E. & Greenway, J.C. Jr. (eds.). Check-list of Birds of the World vol. 9. Cambridge, Mass.
Wetmore, A. & Swales, B.H. 1931. The birds of Haiti and the Dominican Republic. U.S. Natl. Mus. Bull. 155: 345–352.

PALMCREEPER: substantive name of *Berlepschia rikeri*, a South American furnariid strictly associated with *Mauritia* palms (for family see OVENBIRD (1)).

PAMPA (PAMPAS): an environment of prairie type characteristic of southern South America (see PRAIRIE).

PAMPRODACTYL: having all 4 toes directed forwards or (the first being movable) capable of being so directed (see LEG).

PANCREAS: an unpaired organ lying within the loop of the duodenum (see ALIMENTARY SYSTEM). In addition to secreting digestive juices into the duodenum, it secretes insulin internally, i.e. into the blood-stream (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; NUTRITION).

PANDIONIDAE: family of ACCIPITRIFORMES; HAWK.

PANIC: in a special sense, a sudden wave of alarm that—often for no reason apparent to the observer—spreads very quickly through a flock of birds (especially waders) or colony (especially gulls Laridae and terns Sternidae). The birds rise and fly off together, usually returning soon; also called a 'dread'.

PANTROPICAL: of widespread distribution in the tropical parts of the world (see DISTRIBUTION, GEOGRAPHICAL).

PAPILLA, FEATHER: see FEATHER.

PARADIGALLA: substantive name of the 2 species of BIRDS-OF-PARADISE of the genus *Paradigalla*.

PARADISAEIDAE: a family of the PASSERIFORMES, suborder Oscines; BIRD-OF-PARADISE.

PARADISE BIRD: see BIRD-OF-PARADISE.

PARADISE-CROW: substantive name of *Lycocorax pyrrhopterus* (see BIRD-OF-PARADISE).

PARADOXORNITHINAE: see TIMALIIDAE; PARROTBILL.

PARAKEET: substantive name of some smaller species of Psittacinae with long, pointed tails (see PARROT).

PARALECTOTYPE: see TYPE SPECIMEN.

PARALLELISM: evolution in related stocks, producing similarity in ways which are not shown by the common ancestor, but derive from its genetic potential. Parallelism may in practice be difficult to distinguish from CONVERGENCE, which is never a sound basis for classification.

PARAMO: term applied to an altitudinal zone in the Andes, just above the limit of trees.

PARAPATRIC: occupying different but contiguous geographical areas.

PARAPHYLETIC: of a single evolutionary ancestry, but not including all the descendents of the common ancestor (see MONOPHYLETIC; POLYPHYLETIC). The term is necessary only in CLADISTICS, in which a monophyletic group is further defined as one which does include all the descendants.

PARASEMATIC: see under SEMATIC.

PARASITE: an organism that lives at the expense, so to speak, of another species and commonly in or upon it, without reciprocal advantage to the host—and indeed often with disadvantage. Birds have many parasites (see ECTOPARASITE; ENDOPARASITE; also DISEASE). No bird is itself wholly parasitic. A few, however, are parasitic in respect of parental care (see BROOD-PARASITISM); others are in a sense parasitic, as distinct from predatory, in their feeding habits (see PIRACY). True parasitism, in which the advantage is all on one side, is to be distinguished from associations that tend to be either neutral or mutually beneficial; thus, in 'commensalism' two species of organisms share the same food, while 'symbiosis' denotes a more intimate partnership (see NESTING ASSOCIATION).

PARASITISM: the exploitation by one organism of the resources of another. As a rule the relationship is between a more highly organized host and a less highly organized parasite; thus birds support many 'lower' parasites (see ECTOPARASITE; ENDOPARASITE), but are rarely parasites themselves. There are birds, such as skuas, which pirate the food catches of other birds (see PIRACY), while some other species such as the Cut-throat Finch *Amadina fasciata* (Estrildidae) usurp the nearly completed nests of ploceids such as the Masked Weaver *Ploceus velatus*, and a facultative parallel exists in the occupation of Black Woodpecker's *Dryocopus martius* nest-holes by Jackdaws *Corvus monedula*, or the burrows in Prairie Dog colonies by the Burrowing Owl *Athene cunicularia*. In south-east Asia some ploceids such as the Scaly-breasted Munia *Lonchura punctulata*, the Javan Munia *L. leucogastrioides* or the Java Sparrow *Padda oryzivora* regularly breed (sometimes several pairs together) in the side-walls of large raptor nests such as those of the Changeable Hawk-eagle *Spizaetus cirrhatus*, the Grey-headed Fish-eagle *Ichthyophaga ichthyaetus* or the White-bellied Sea-eagle *Haliaeetus leucogaster*, often when these nests contain eggs or young (see NESTING ASSOCIATION). A much more highly developed form of exploitation is found in birds which lay their eggs in the nests of birds of other species, and have evolved special adaptations, morphological and behavioural, promoting the acceptance and survival of their eggs and young in the hosts' nest (see BROOD-PARASITISM).

PARASPHENOID: a paired bone of the SKULL; PALATE.

PARASYMPATHETIC: see NERVOUS SYSTEM.

PARATHYROID GLAND: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

PARATREPSIS: term for DISTRACTION BEHAVIOUR.

PARATYPE: see TYPE SPECIMEN.

PARDALOTE: substantive name, alternatively 'diamond-bird', of *Pardalotus* spp. (for family see FLOWERPECKER).

PARDALOTINAE: see FLOWERPECKER.

PARENTAL ANTI-PREDATOR STRATEGIES: see DISTRACTION BEHAVIOUR; PARENTAL CARE.

PARENTAL CARE: the protection, feeding, and general care of young by one or both of the parents from the time of hatching to independence. For care of eggs see EGG; INCUBATION.

The amount of parental care expended by adults depends strongly on the mode of development of the young (see GROWTH). At one extreme are the ALTRICIAL species whose young are born naked (or nearly so) and unable to leave the nest. They therefore depend completely on the adults for food, brooding and defence from predators until they develop to independence. At the other extreme are such fully PRECOCIAL species as the megapodes, whose young lead an independent existence from the moment of hatching. Between are a series of intermediate forms of various abilities in respect of locomotion and thermo-regulation, of food finding and acquisition and of predator avoidance.

Hatching. Much of the hatching process is performed by the chick itself and the parents rarely assist. However, Eastern Bluebird *Sialia sialis* females have been seen to speed the hatching process by eating part of the shell and membranes of the pipping egg. Sanderlings *Calidris alba*, Stone-curlews *Burhinus oedicnemus* and other waders have also been recorded assisting hatching in this manner.

Eggshell removal. The majority of birds remove or eat the eggshell after hatching. Only in large ground-nesting species with large and precocial broods e.g. geese, ducks, game-birds and in some of the terns, are the shells left on the nest which is itself soon abandoned by the family. In large tree-nesting species, e.g. herons, the shells may be dropped over the nest edge. Stouter-billed passerines may eat some or all of the shell but slender-billed species and most of the Charadriiformes carry them away. The young Flamingo *Phoenicopterus ruber* is fed fragments of its shell by the parent, probably to increase its calcium intake for skeletal growth.

Eggshell disposal probably serves primarily as an anti-predator func-

Bittern *Botaurus stellaris* removing eggshell from nest. (*Photo: E.J. Hosking*).

tion. Field experiments show that nests with empty eggshells alongside attract predators e.g. crows, more frequently than do nests without shells. Study of the factors eliciting eggshell removal by Black-headed Gulls *Larus ridibundus* shows that the behaviour is not as simple as it first appears; rather it is under close control of a series of responses to the characteristics of the hatched eggshell which together ensure that the parent neither attempts to remove the shell prematurely whilst the young bird is still hatching or is so wet as to be vulnerable to cannibalism by conspecifics, nor tardily, exposing the nest to unnecessary predation risks. Such predation risks are particularly high for many ground-nesting species with precocial young and in these species eggshell removal tendencies peak around the time of hatching. Predation risks are often lower for species with altricial young, either because the parents sit tightly on the nest (thus concealing the hatched eggshells), as in doves, or because the nest sites are relatively inaccessible, e.g. hirundines. Nevertheless, eggshell removal occurs in such species and the removal tendency increases through the laying cycle. One possibility is that hatched eggshells in such species may otherwise slip over and encase the eggs not yet hatched, thereby reducing hatching success: in one study of Barbary Doves *Streptopelia risoria* 5 of 24 shells not removed within an hour of hatching interfered with other eggs in this way.

Nest sanitation. Disposal of the faeces by the parents, either by removing them or by swallowing them, is largely confined to the Passeriformes and the orders immediately related to them. The large broods of nidicolous young require a warm dry nest in the interests of hygiene and insulation and their vulnerability to predators requires distant disposal of excreta. In these species, therefore, the faeces are excreted within tough mucous sacs which can easily be carried away by the parent. Faeces are almost invariably produced only after feeding, the adult waiting for the nestling to lift its tail and produce the sac. The parent may prod the young bird near the vent to stimulate excretion. With very tiny young the sacs are immediately eaten by the adult, perhaps because digestion of ingested food is incomplete at this stage and the adult is tied to the nest by brooding requirements. With older young the sacs are carried away and disposed of. Passerines often wipe the material on to tree branches but some, such as swallows and martins, tend to drop them into water. Few go to the lengths of the female Lyrebird *Menura novaehollandia* which submerges the faeces in a nearby stream if she can and otherwise digs a hole and buries them. Young gulls and terns move away from the nest to defaecate but some tern species void their faeces around the nest where bird and substrate (e.g. sand dunes) are both white.

As the nestlings age, sanitation practices change. Sacs may be deposited on the nest rim or, in a roofed nest, in the entrance hole and are carried away by the parent after a feeding visit. In hirundines and other species with inaccessible nests, the young vent their faeces over the nest edge, leading to mounds of sacs outside or on the ground below. Young Kingfishers *Alcedo atthis* likewise have considerable competence in ejecting liquid faeces through the entrance of their tunnel nest. Woodpeckers and hornbills may void the faeces on to the floor of the nesting cavity where they are absorbed in the litter, to be periodically cast out by the female or young and the litter renewed.

Many of the larger species nesting in inaccessible sites, such as eagles, simply void their faeces in liquid form over the nest edge and do so from an early age. Some other species, notably the herons, have a nest of loose construction through which the liquid faeces fall. In hot climates this practice may be adaptive, the moist faeces falling on the twigs evaporating and keeping the nest cool. In broods of well-grown Blue Tits *Parus caeruleus* the faeces are also left in the nest; perhaps because the water they contain helps cool the crowded nest.

The young of some species are able to move from the nest although fed and cared for by their parents there, and some (e.g. Montagu's Harrier *Circus pygargus*, Nightjar *Caprimulgus europaeus*) do so to defaecate.

Brooding. Most young, altricial or precocial, are unable fully to regulate their body temperatures for some or many days after hatching (see GROWTH) and therefore require warming or brooding by the parents. Precocial young require only intermittent brooding but altricial young require almost constant brooding until their own temperature control develops. Figure 1 shows the typical pattern of brooding time in such species. Brooding frequency declines sooner in large than in small broods, because the large broods can conserve their body heat by huddling together.

The brooding rhythm of the adults is not endogenously controlled but depends on stimuli from the young. When Pied Flycatchers *Ficedula hypoleuca* were experimentally replaced by older nestlings, brooding frequency decreased, whilst when the growing young were successively replaced with younger ones brooding was substantially prolonged.

Fan-tailed Warbler *Cisticola juncidis* removing faecal sac from nest. (*Photo: E.J. Hosking*).

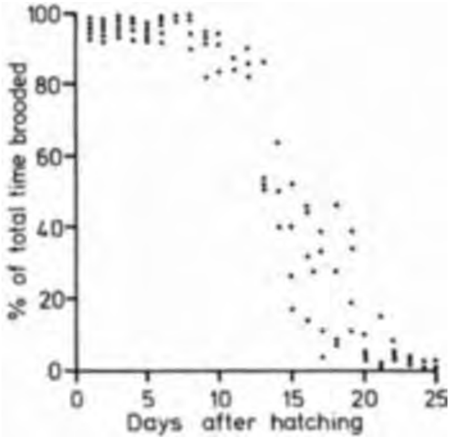


Fig. 1. Variation in brooding attentiveness of Peregrine Falcon *Falco peregrinus* in relation to nestling age during typical June–July weather. (Modified from Enderson *et al* 1972.)

Doubled-banded Courser *Cursorius africanus* defending egg. (*Photo: G.L. Maclean*).

Protection from the weather. Adult birds normally shelter their young from rain, either by brooding them when small or by standing over them with spread wings when large. Precocial young may also seek shelter from their parents during rain. In prolonged rain the adult is unable to leave the young unattended and the chicks may suffer from starvation. In a few species, principally the aerial insectivores e.g. swallows, swifts, the adults may themselves be forced by starvation to leave their young unattended. Such species usually have sheltered nests (roofed, in crevices or tunnels, etc.) and the young are exposed to chilling rather than to wetting. Such young may have considerable tolerance of low temperatures, becoming torpid until the adults return. The European Swift *Apus apus* can survive a week or more in this fashion, from an early age.

Young birds have poorer physiological responses to overheating than to cooling and are dependent on their parents for shading during exposure to excessive insolation. Some herons defaecate over their young in extremes of sunlight, the resulting evaporative heat losses serving to cool the young. Tropical seabirds, notably terns, often dip to the sea surface to wet the breast feathers before sitting on the nest, thereby cooling eggs and young (see also BELLY-SOAKING).

Protection from predators. A very few species have young equipped to defend themselves against predators: the oil squirting of Fulmars *Fulmarus glacialis* and other Procellariformes, the odour glands of Hoopoes *Upupa epops* and the massive talons of young eagles being examples. Most young depend on their parents for warning and protection. Most will crouch and 'freeze' on hearing a parental alarm call. Mobile young may run and hide in the surroundings and gull chicks, for example, have individual refuges in the vicinity of the nest. Occasionally, adults may remove the young from danger by leading or carrying them to a safer site but their main tactics are to attack the predator directly or to attempt to distract it from the nest or young.

Direct attack on the predator is particularly common in colonial nesting species and many birds may combine to harass the intruder by swooping and screaming at it and even striking it with beak or claws. More solitary species, notably Charadrii, may rely on DISTRACTION BEHAVIOUR in which the bird appears to have been injured or otherwise incapacitated and flutters about near the predator but always just out of reach, until it has led the enemy far enough from the young for safety, whereupon it resumes its normal behaviour.

Hole-nesting species are occasionally threatened on the nest and may use a 'hiss' display to deter the predator at the nest entrance. The behaviour apparently simulates a hissing snake either by vocal means (Wryneck *Jynx torquilla*) or by wing movements (various tits). Adults disturbed on the nest may also adopt threatening postures and may attack the intruder with bill and claws or with regurgitated (and evil-smelling) food or oil secretions (Fulmars; coucals *Centropus* spp.) During dive-attacks, gulls and terns may defaecate on the intruder; and Fieldfares *Turdus pilaris* are notable exponents of this method of defence, their attacks sometimes leading to the death of the faeces-plastered victim.

Parents may also carry the young away from danger. A variety of waterfowl carry their young on their backs when swimming or with their beaks in flight, Woodcock *Scolopax rusticola* carry their young between their legs and body whilst in flight, and other species carry young using their feet (Red-tailed Hawk *Buteo jamaicensis*, Moorhen *Gallinula chloropus*). The American Finfoot *Heliornis fulica* has special pockets of skin under each wing in which to carry its young whilst swimming or in flight. Other species can walk away from danger carrying their young in their beak (*Rallus* spp.) or under their wings (African Jacana *Actophilornis africanus*).

Chinstrap Penguin *Pygoscelis antarctica* colony; Sheathbill *Chionis alba* eating penguin's egg. (*Photo: N. Rankin*)

Feeding. Some young receive no parental aid in food finding, the extreme being the megapode chicks which are fully independent from hatching. Amongst the more typical preococial species, however, the extent of parental involvement varies substantially. Most duck and shorebird (Charadrii) young are led to food sources but are left to feed themselves. Mute Swans *Cygnus olor*, however, will pull up submerged vegetation for their offspring and Quail *Coturnix coturnix* lead their young even to individual food items; they may also make food available by scratching the ground. Yet another group of semi-precocial species proffer food to very young chicks; older chicks of the same species feed at food regurgitated by the parents on to the ground in front of them. Fully altricial nestlings depend on their parents to deliver food into their open bills but semi-altricial raptor chicks can tear up and consume food brought to the nest after a period of fully altricial feeding by their parents.

Details of feeding behaviour are highly species-specific but a few broad generalizations are possible. Most parent birds feed their young on the same foods as they eat themselves but reserve the larger prey items for their young (except when feeding tiny young); they consume the smaller prey themselves. Presumably this trend reflects the relative economics of prey size and transport-to-nest costs. For the same reason various large seabirds with remote feeding grounds return to their young with a single large meal, often in conjunction with mate relief. Several seabird species feed their young by regurgitation of a thick stomach oil and doves and pigeons have evolved a similar ploy in the use of 'pigeon-milk' (see CROP MILK). In these and in other species, regurgitated food contains an increasing proportion of solid material as the young grow.

Feeding is most frequent in the early part of the day, presumably because the young are most hungry then after their overnight fast. But birds with unusually small broods have been noted to feed small young especially frequently in the middle and warmer part of the day, pre-

Blackbird *Turdus merula* female feeding young. (*Photo: E.J. Hosking*).

Sand Martin *Riparia riparia* feeding young at nest entrance. (*Photo: B. Huseby*).

sumably because they can then brood the young during the cooler mornings and evenings. The amount of food brought increases with the size of the brood but rarely proportionately, so young in large broods are frequently underweight and slower growing. This is apparently due to the inability of the parents to collect food fast enough over long periods: at one Great Tit *Parus major* nest studied, the parents of the over-large brood progressively 'tired' earlier each day as the nesting period progressed, collecting less food per unit time in late afternoon despite the greater food needs of their growing young.

Young are generally fed more frequently in cold weather, provided the food is available. This responds to the greater energy needs of the young. For other species cold weather results in reduced food availability and the parents may need to leave their young not only unfed but even un-brooded. In wet weather the general rule is to brood the young rather than to seek food for them.

Water supply. Most nestlings obtain their entire water requirements from the moisture content of their foods though, in the case of Bullfinches *Pyrrhula pyrrhula* and other species feeding their young by regurgitation, the young may well receive additional water in the mucus binding the food items together. Species breeding in hot areas, however, need large quantities of water for evaporative cooling and special behaviours have evolved to communicate these needs to the parents. Young Darters *Anhinga melanogaster*, for example, seek food by begging behaviours performed with the bill closed but seek water with the same behaviour performed after a feed and with the bill open; in response to such solicitation the adults fly to nearby water and return to regurgitate water into their offsprings' bills.

Most precocial young can travel to water but the Namaqua Sandgrouse *Pterocles namaqua* breeds in the Kalahari Desert 80 km or more from water. The adult male possesses specially modified ventral feathers with which to transfer a net 10–20 ml water from waterhole to chick over these distances. In this way the chick receives water over its 7 weeks of pre-flight life (see SANDGROUSE).

Care during nest departure. The extent to which the departure of the young from the nest receives parental care varies widely between species, from total absence in European Swifts to the elaborations of the 'water-call' and 'exodus call' of the Guillemot *Uria aalge* and Wood Duck *Aix sponsa* respectively. Young Swifts depart from their nest without parental attention, often doing so in the absence of the adult, and this is a common pattern amongst altricial species. Generally, however, fledglings are tended by their parents for the first few days of life outside the nest. In many such species nest departure is not synchronous and the parents may seek to encourage tardy young to fledge by withholding food: in Bluebirds *Sialia sialis* feeding rates are markedly reduced in the last day in the nest and more so when one young has left the nest, though feeding is resumed once the brood has fledged and re-united. In some cases adults seek to induce individual laggards to depart the nest by offering them food items from just outside it. In other species, however, the male and female divide the brood between them, one adult attending the new fledglings, the other those remaining in the nest.

Precocial young feed themselves to a large extent and the parents' major role is to warn and guard against predators once the brood has left the nest site after a short post-hatching period. In such species there may be a premium on the brood departing together, particularly where the chick feeding grounds are some distance from the nest-site. The adults frequently possess a distinctive nest exodus call, soft in terrestrial nesters but loud and well-developed where the chicks must jump from the nest, as in the tree-holes of the Wood Duck or the cliff ledges of Guillemots. Following a period of about 24 hours post-hatching during which she repeatedly utters the exodus call (thus familiarizing the young with her voice) the female Wood Duck reconnoitres the environs of the nest site and, if clear, summons the young from their cavity. Young Guillemots similarly leave their nest-ledges before developing full flight, descending on the 'lift' of their secondaries, and are prone to gull predation once away from the ledge. Hence the chicks 'fledge' predominantly at dusk following a session of reciprocal 'water-calling'—a loud clear whistling call—between parent and young, culminating in resumed contact between them on the sea below, the two swimming away through the dusk to offshore (and more gull-free) waters by dawn. The descent of the chick may be accompanied by an adult flying down behind it, providing physical obstruction to aerial predation.

Strength and duration of care. The duration and intensity of parental care are believed to represent a balance between (1) the reproductive potential of the parents on ceasing to tend the current young in favour of future broods and (2) their potential on continuing to invest further in the current attempt (giving the current young a better chance of surviving to reproduce). This has two consequences for the birds.

First, their willingness to provide care should increase through the nest

Great Crested Grebe *Podiceps cristatus* feeding feather to young on its back. (*Photo: E.J. Hosking*).

cycle since it will become increasingly difficult for them to get through a replacement cycle successfully. Thus, incubating eggs should be defended more vigorously than newly-laid eggs and hatched young should be defended more intensely than eggs. Empirical data testing these ideas are scarce but what are available support the hypothesis.

The second consequence of the theory is that fledglings should be cared for by the parents only whilst the return in reproductive output by doing so exceeds the return obtained by investing the same care into a fresh breeding attempt. In general terms this is the case, with species in which the young can quickly learn to forage for themselves having short periods of post-fledging care, as in small unspecialized passerines, whilst species with unusual (or very specialized) feeding techniques have long periods of post-fledging care. Terns have been found tending their British-born offspring whilst on their African wintering grounds, thus providing the young with the time and opportunity to acquire specialized fish-catching techniques with adequate levels of skill before being left to forage independently. However, another consequence of this inclusive FITNESS theory of parental care is that a period of conflict between parent and offspring as to the amount of care provided must arise, the offspring seeking more than the parent should optimally provide. Empirical data support this prediction for a variety of species. In a Bewick's Swan *Cygnus columbianus* study, for example, the proportion of cygnet movements going immediately unguarded by the adults increased from 52% to 87% over the first 4 weeks of cygnet life, even though the cygnets seek proximity to their parents for their protection during aggressive encounters.

Parental care and clutch-size. Precocial species have, on average, larger clutches than altricial species and this difference is frequently attributed to a supposed reduction in the need for parental care for self-feeding chicks. However, parental care in these species takes the form of guarding against predators and this has to be attained over the foraging area of the independently hunting chicks. When prey densities are low the chicks must hunt over larger areas than can in practice be adequately protected by the adults, thus limiting productive clutch size. For many arctic waders the clutch size is 4, suggesting some general limiting factor of this nature and, in one experimental test of the idea, artificially increased brood sizes of Semi-palmated Sandpipers *Calidris pusilla* fledged fewer young than did the natural broods of 4. Thus the provision of parental care even in the form of chick guarding can in practice be limiting to clutch size in the same way as can parental care through feeding (see also CLUTCH-SIZE).

Crèches. Chicks of several species normally spend part of their development period in groups or 'crèches' attended by a small number of adult birds which may or may not include the parents of the chicks present at the time. The behaviour was noted early in studies of penguins but also occurs in the 'crested' terns, pelicans, flamingos, and several waterfowl species, though the detailed features of the behaviour differ even within these species groups.

Sandwich Tern *Sterna sandvicensis* feeding fledged juvenile. (*Photo: D. Hosking*).

In some high latitude species the huddling together of the chicks into crèches undoubtedly serves to conserve heat by reducing the effective surface-to-volume ratio experienced by the chicks. But in the Eider *Somateria mollissima* and Shelduck *Tadorna tadorna* the chicks are actively guarded by the accompanying adults who are generally (perhaps always) successful breeders. On the Ythan Estuary in Scotland marked Eider ducks averaged only 4 days with their brood in a crèche before leaving to join adults feeding elsewhere on the estuary. These females have fasted to a substantial extent whilst incubating their clutches but the food they need to replenish their reserves—the edible mussel *Mytilus edulis*—is concentrated into parts of the estuary remote from the centres for the invertebrates required by their young—the amphipods *Corophium* spp., a

Great Black-headed Gull *Larus ichthyaetus* male, female and young. (*Photo: V. Siokhin*).

House Sparrow *Passer domesticus* male feeding fledged juvenile. (*Photo: J.B. & S. Bottomley*).

gastropod mollusc *Hydrobia* sp. and a winkle *Littorina* sp. Hence the ducklings in the crèches can be guarded only by the succession of females bringing their offspring to the brood-rearing areas over a period of time. Similar considerations have different consequences for local populations of Eiders on rocky (rather than estuarine) coasts; these do not form crèches but their young feed on the gammarids and other small crustaceans present in the seaweeds whilst the females take mytilids and littorinids present on the rock surfaces to which the seaweeds are attached.

Alternatively, crèching may have originated in normal parental caring at high brood densities. Broods then become mixed, either because both pairs of adults are fighting in defending their broods, which then scatter, or because a chick of one brood wanders closer to a foreign brood than to its own parents and joins the foreign brood when it is called together by its parents. Such mixing is most frequent when broods are less than a week old. Yet another explanation may lie with the adults resorting to crèching to share the costs of guarding young chicks amongst several adults: each adult can then spend a longer time feeding.

See photos BELLY SOAKING; CARRYING; DISTRACTION BEHAVIOUR; HEAT REGULATION.
R.J.O'C.

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Protection of eggs. As a general rule, breeding birds do not actively engage a predator—and thus put themselves at risk—unless it is relatively safe for them to do so, or as a last resort (though even then not to the extent of losing life or limb). Rather, they leave the eggs or young to the safety of their own camouflage or to that of the site as much as possible. In waders precautionary adaptations that enhance the camouflage of the eggs include siting them against a disruptive background (e.g. among cattle droppings) or concealing them, partly or completely, with nest debris; also the adoption of inconspicuous routines at the nest and the speedy removal of egg-shells as each chick hatches. The parents may also nest in loose association with other species that actively demonstrate, etc. against predators when breeding (see DISTRACTION BEHAVIOUR). If a predator appears, but does not immediately threaten the safety of the eggs or young, the attendant adult may react by flushing sooner or later (the timing being adaptably variable according to circumstances) or by adopting a concealing posture; it will depart furtively if necessary—in some species (such as Kittlitz's Sand-plover *Charadrius pecuarius*) after first speedily covering the eggs or even newly hatched chicks—and then remain inconspicuously in the general vicinity or depart entirely.
K.E.L.S.

Hall, K.R.L. 1958. Observations on the nesting sites and nesting behaviour of the Kittlitz's Sandplover *Charadrius pecuarius*. Ostrich 29: 113–125.

Simmons, K.E.L. 1955. The nature of the predator-reactions of waders towards humans; with special reference to the role of the aggressive-, escape-, and brooding drives. Behaviour 8: 130–173.

Tinbergen, N. *et al* 1963. Egg shell removal by the Black-headed Gull *Larus ridibundus* L.: a behaviour component of camouflage. Behaviour 19: 74–117.

PARENTAL INVESTMENT: see PARENTAL CARE.

PARIDAE: a family of the PASSERIFORMES, suborder Oscines; TIT.

PARIETAL: a paired bone of the SKULL.

PAROTIA: substantive name sometimes used for the 4 species of *Parotia*, usually known as six-wired BIRDS-OF-PARADISE.

PARRAKEET: see PARAKEET.

PARROT: substantive name of most species of Psittacidae, sole family of the order Psittaciformes; in the plural, general term for the family and order.

Characteristics. Parrots share a number of characters which define the order: the upper mandible is strongly curved and fits over the shorter lower mandible; a cere surrounds the base of the upper mandible which articulates with the SKULL; the lingual and jaw musculature is highly developed and complex; the tarsometatarsus is short, the zygodactyl foot is covered with granular scales; the feather tracts are sparse among prominent bare areas; the moult of the primaries starts in the centre; the egg shell is white.

There is a wide variation in size from a total length of *c.* 8.4 cm for the Buff-faced Pygmy Parrot *Micropsitta pusio* to *c.* 100 cm for the Hyacinth Macaw *Anodorhynchus hyacinthinus*. In general, the male is slightly larger than the female; the opposite is true for some *Agapornis* spp. The plumage generally is brightly coloured, the prominent colour being most frequently green. Some species are less colourful, being mostly brownish-green, grey, black, or white. Most species are sexually monomorphic; in the dimorphic species the difference between the sexes varies from extreme, e.g. in *Eclectus roratus* to minimal, e.g. in the Budgerigar *Melopsittacus undulatus*. The juvenile is similar to the adult plumage, only somewhat duller; a distinct juvenile plumage is found in the ring-necked parakeets (*Psittacula* spp.), the Crimson Rosella *Platycercus elegans*, the Blue-crowned Lory *Vini australis* and others.

The wings can be elongated and pointed, as in the Swift Parakeet *Lathamus discolor*, or broad and rounded, as in the *Amazona* spp. Tails may be long and pointed or short and squarish. The central tail feathers are decorously elongated in the Papuan Lory *Charmosyna papou*; in the racket-tailed parrots (*Prioniturus* spp.) they extend beyond the tip of the tail as bare shafts terminating in spatules. Stiff shafts project from the tip of the tail feathers in the pygmy parrots (*Micropsitta* spp.) and *Nestor* spp. The crown feathers are elongated and form movable crests in cockatoos. Some lorikeets (*Vini* spp.) can ruffle their crown feathers, whereas the elongated crown feathers of the Horned Parakeet *Eunymphicus cornutus* cannot be moved. Elongated hind neck feathers are found in the Collared Lory *Phigys solitarius* and Hawk-headed Parrot *Deroptius accipitrinus*. The head is bare and covered only with bristles in the adults of Pesquet's Parrot *Psittrichas fulgidus* and the Vulturine Parrot *Gypopsitta vulturina*. Bristles are also found at the base of the bill of nocturnal parrots. The bill varies in length. It is very long and narrow in the Nestorinae, most Loriinae, the hanging parrots (*Loriculus* spp.), Pesquet's Parrot, the Long-billed Corella *Cacatua tenuirostris*, the Red-capped Parrot *Purpureicephalus spurius*, the Slender-billed Conure *Enicognathus leptorhynchus*, the Tepui Parrotlet *Nannopsittaca panychlora*, and *Brotogeris* spp. Short bills are found in the black cockatoos (*Calyptorhynchus* spp.), the pygmy parrots and *Poicephalus* spp., most broad-tailed parrots (Platycercini), *Ara* spp., and *Bolborhynchus* spp. The Palm Cockatoo *Probosciger aterrimus*, Great-billed Parrot *Tanygnathus megalorhynchus* and Hyacinth Macaw are known for their disproportionately large bills. The tongue is broad and fleshy. In pollen and nectar feeders, the tongue is elongated and bears epidermal papillae at the tip, e.g. in the lories, the Swift Parakeet, and the Philippine Hanging Parrot *Loriculus philippensis*. Most parrots have a well developed crop and a muscular gizzard. Both organs are reduced in pollen-nectar and fruit specialists.

Habitat. Parrots are found mainly in tropical regions but also in temperate zones. They are especially plentiful in lowland tropical forests. Some have conquered mountainous regions, e.g. the Derbyan Parakeet *Psittacula derbyana* in Tibet, or the Kea *Nestor notabilis*. Others inhabit more open country, mostly keeping close to waterholes and water courses in arid regions. A few species live on the sea shore, e.g. the Rock Parakeet *Neophema petrophila*, some subspecies of the Red-fronted Parakeet *Cyanoramphus novaezelandiae*. Three species are terrestrial, the

Kakapo *Strigops habroptilus*, the Australian Ground Parrot *Pezoporus wallicus*, and the Night Parrot *Geopsittacus occidentalis*.

Distribution. Parrots are found around the world, mainly in the Southern Hemisphere, i.e. Australasia, Pacific Islands, Africa, South and Central America, and the Caribbean Islands. The northernmost point of the distribution is reached by the Slaty-headed Parakeet *Psittacula himalayana* in Afghanistan, the southernmost point by the Austral Conure *Enicognathus ferrugineus* in Tierra del Fuego. The easternmost island of the Pacific, Henderson Island, is reached by Stephen's Lory *Vini stepheni*.

Movements. Most parrots are more or less sedentary, except for daily local movements between roosting and feeding places. Nomadic behaviour is especially common among inhabitants of arid regions, e.g. the Budgerigar and Cockatiel *Nymphicus hollandicus*. A few cases of seasonal migratory behaviour are known, e.g. the Swift Parakeet and the Orange-bellied Parakeet *Neophema chrysogaster*.

Food. The diet of parrots is mainly vegetarian and includes seeds, nuts, berries, fruit, tubers, roots, nectar, pollen, insects, and lichens. Specializations on either food have often been evolved several times independently. However, all parrots (except Pesquet's Parrot) eat some seeds (or nuts) which they always husk before swallowing. Food is often held in the foot when feeding.

Behaviour. Most parrots are gregarious. Many species live in pairs during the breeding season. The social behaviour of parrots is very complex with play behaviour, courtship and ritualized fighting. Mating is for life, and the pair bond is maintained (except in cockatoos) by mutual preening and partner feeding. The Kea is polygamous.

Voice. Parrot calls are mostly screeching, loud, metallic, and unmelodic. High-pitched whistles are characteristic for the Loriinae. Many species emit chattering vocalizations. Some parrots have a soft, almost melodic voice, e.g. the Purple-bellied Parrot *Triclaria malachitacea*, Bourke's Parakeet *Neopsephotus bourkii*. Vocal mimicry has been observed only in captivity.

Breeding. Nesting generally takes place in hollow trees without litter material. *Loriculus* and *Agapornis* spp. build a nest within tree holes. The Monk Parakeet *Myiopsitta monachus* builds huge colonial twig nests in trees. The Rock Parakeet and the Patagonian Conure *Cyanoliseus patagonus* nest in cliffs. The Australian Ground Parrot nests in tufts of grass. Some species nest in termite nests, e.g. the Golden-shouldered Parrot *Psephotus chrysopterygius*, the Red-faced Lovebird *Agapornis pullaria*, and the pygmy parrots. Depending on the species, 2–5 eggs are laid on alternate days, incubation, usually (except in cockatoos) by the female only, starting with the second egg. The chicks hatch after 16–32 days. The hatchlings are blind, naked or have sparse down. They are fed and brooded by the female during the first 5–10 days; later the male assists in the care of the young. After leaving the nest, the young usually remain with their parents until the next breeding season.

From early times parrots have been valued as pets because of their playfulness and mimicry of the human voice. In recent years, the lucrative pet trade has become, together with habitat destruction, a major threat to the survival of many species.

Systematics. Relationships of the Psittaciformes to other orders are unclear and hypothetical; most likely is a common ancestry with the pigeons. The first fossil parrot is known from the lower Miocene in France. The family comprises about 82 genera and 332 species. Eight subfamilies can be recognized.

Nestorinae. The single genus *Nestor* is endemic to New Zealand and adjacent islands. The 2 species are large, stocky birds. The Kea inhabits sub-alpine regions, whereas the Kaka *N. meridionalis* inhabits forests.

Strigopinae. The single species *Strigops habroptilus* is endemic to New Zealand. This heaviest parrot of all is flightless and nocturnal. The males display lek-behaviour (see LEK). The recent rediscovery of a small population on Stewart Island may save the Kakapo from imminent extinction.

Psittrichadinae. The single species *Psittrichas fulgidus* is endemic to New Guinea and inhabits high elevations. Its diet consists of fruit. It is the only parrot not known to eat seeds or nuts. It drinks with a suction-pump action of the tongue.

Cacatuinae. The cockatoos are found in Australia, New Guinea, and the islands adjacent to the Philippines. They are large birds with a movable crest, a short and high bill, and a narrow, stubby tongue. The plumage is white, pink, grey, or black, with various red or yellow markings. They are specialized seed and nut eaters and drink by scooping up water with their lower mandibles. The Cockatiel is much smaller than the rest of the group and has evolved in convergence to the broad-tailed parrots.

Rosy-faced Lovebird *Agapornis roseicollis*. (*K.J.W.*).

Micropsittinae. The pygmy parrots are endemic to New Guinea and the adjacent islands. These smallest of the parrots live in dense forests, climbing along the tree trunks. The bill resembles that of the cockatoos. The tarsometatarsus and the claws are long. Their food consists of lichens and, probably, insects.

Loriinae. The lories are found on the Pacific Islands, Australia, New Guinea and adjacent islands. They are medium-sized to small birds with extremely colourful plumage. They are pollen and nectar specialists, but eat also seeds and insects, and drink by dipping their brush-tipped tongue into the liquid.

Psittacinae. This group comprises 58 of the 82 parrot genera. It can be divided into 4 well-defined tribes, although the exact systematic position of some particular genera is not yet clear. The subfamily includes species of widely varying sizes, colours, appearances and feeding specializations. The group is characterized by a broad fleshy tongue with a spoon-shaped tip and by a drinking mechanism in which the tongue ladles water and swallows it by pushing the tongue against the palate.

(1) Platycercini. The broad-tailed parrots are restricted to Australia, New Zealand, New Caledonia, and Fiji. The group consists mostly of seed-eaters, but includes also the pollen feeding Swift Parakeet and the frugivorous shining parrots (*Prosopeia* spp.) All species have long tails.

(2) Psittaculini. This group has the most extensive distribution, from Australia to Africa. Size varies from the small *Agapornis* spp. to the large *Eclectus* sp. The appearance varies from stocky parrots with short tails to slim parakeets with extremely long tails. Most species have a coral-red bill.

(3) Psittacini. This African group consists of only 2 genera. The Grey Parrot *Psittacus erithacus* is more frugivorous than the seed and nut specialist *Poicephalus* spp. to which the Senegal Parrot belongs.

(4) Arini. This group is endemic to South America and comprises all Neotropical parrots (141 species of all 332 parrot species).

Loriculinae. Previously thought to be closely related to the *Agapornis* spp., the hanging parrots form a distinct group with the single genus *Loriculus*. They are small, green birds with a brilliantly red rump. Most species are highly specialized fruit, pollen, and nectar feeders. They drink with a suction-pump action of the tongue. They often roost and rest during the day hanging upside down, hence their name.

See photo NEST SITE SELECTION. D.G.H.

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Schmalbindenloris, *Trichoglossus haematodus massena* Bonaparte. Zool. Garten N.F., Leipzig 42: 51–94.

PARROTBILL (1): substantive name of most of the species of the subfamily Paradoxornithinae of the Timaliidae (Passeriformes, suborder Oscines); in the plural, a general term for the subfamily (sometimes called Suthoras or Crow-Tits). Certain aspects of the biology of this subfamily, including features of behaviour and moult, have prompted consideration that familial rank might be justified.

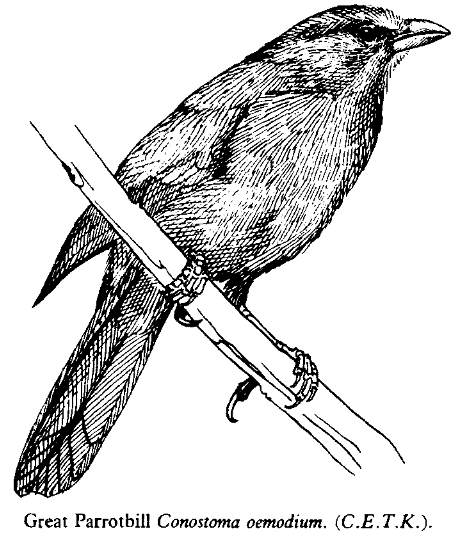
Characteristics. Parrotbills are small to medium-sized birds, ranging in total length from about 12–28 cm. Although somewhat like the tits (Paridae) in general appearance, they are with two exceptions distinguished from other Oscine birds by the peculiarly formed (usually yellowish) bill, which is shorter than the head, very much compressed, and with strikingly convex outlines. The culmen is curved strongly for its entire length, the gonys ascends sharply, and the cutting edges of both mandibles are more or less distinctly sinuous. The nostrils are completely covered in bristles, and the legs and feet are robust, with strong toes and claws. The plumage is very soft and loose.

Although numerous generic names have been proposed for the parrotbills on the basis of bill-shape, only 3, *Paradoxornis*, *Panurus* and *Conostoma* are currently accepted, the last 2 being monotypic. The Bearded Reedling or Bearded Tit *Panurus biarmicus* differs from the typical species in a number of particulars, e.g. in having a more normally shaped bill, in the sexes differing in plumage (with the juveniles resembling the female), and in laying larger clutches. The Great Parrotbill *Conostoma oemodium*, is much the largest of the subfamily, and has a bill intermediate in shape, though larger, between *Panurus* and *Paradoxornis*.

The sexes in *Paradoxornis* and *Conostoma* are alike in plumage, the coloration ranging from the almost uniform greys and browns of the larger species to complex patterns featuring orange-buff, pinkish-browns, and black and white. In most species the wings are short and rounded, but the tail is generally long and graduated. One species, the Three-toed Parrotbill *Paradoxornis paradoxus*, is remarkable among passerine birds in only having three toes, the outer one being a clawless stump attached to the middle toe.

Habitat. Parrotbills are birds of dwarf bamboo, rhododendron, and the lower levels of either deciduous or evergreen forest, while many of the smaller species prefer tall grass and reeds. The Bearded Reedling and one Chinese species are confined to reedbeds.

Distribution, populations and movements. The 19 species are essentially Sino-Himalayan birds, although several range widely in the Palearctic, and no less than 12 species extend into the mainland countries of south-east Asia, though not entering Malaysia. Amongst the typical parrotbills, the Vinous-throated *P. webbianus* is perhaps one of the most widely distributed, ranging in 7 races from Manchuria and Korea to Hainan and Burma. The Black-throated *P. nipalensis*, with 12 subspecies, ranges from Nepal to Taiwan and southwards into the Indo-Chinese countries. On the other hand, one of the most restricted species is *P. heudei*, a very distinctive intermediate-sized form, which only occurs in the reedbeds bordering an 80 km reach of the Yangtze river in the Chinese province of Kiangsu. The rather aberrant Bearded Reedling, is wholly Palearctic, and ranges in areas of reedbeds from England eastward into Manchuria. Most species are resident, though there is some seasonal and altitudinal movement in the Himalayas, and the western populations at least of the Bearded Reedling have, in the last 30 years, developed a new dynamism characterized by now annual eruptive dispersal and the colonizing of new sites.



Great Parrotbill *Conostoma oemodium*. (*C.E.T.K.*).

Food. Insects are commonly taken, as well as vegetable matter such as shoots, buds, berries and seeds, the strong and unusually shaped bill of many species also being well adapted for stripping bamboo stems.

Behaviour. All species are gregarious, and forage through tall grass or bamboo in small or large parties, keeping in touch with a continual twittering or cheeping. They fly reluctantly and rather feebly, but are quite agile and somewhat reminiscent of tits Paridae when foraging.

Voice. Some of the larger species are quite noisy, with both harsh chattering notes and more musical calls, and at least 2, including the Bearded Reedling, have rather metallic ringing notes. Most species have a variety of cheeping or chittering notes, and another is described by Stuart Baker as 'like . . . the plaintive bleating of a kid in distress.'

Breeding. The breeding habits of some species and subspecies remain undescribed; much is still to be learnt of the lives of some of the uncommon parrotbills of remote areas. Those whose nidification has been studied build compact cup-shaped nests of grass and strips of bamboo, often thickly lined with finer grasses and sometimes bound with cobwebs. The nest is placed in reeds or grass or among bamboo stems within 2 m or so of the ground. The eggs number 2–4, and may be unspotted blue, or white to creamy or fulvous with speckling and blotching of reddish, greenish-grey or purplish. Both sexes of the Bearded Reedling incubate the clutch of 5–7 eggs for 12–13 days; and the young, fed by both parents, may leave the nest in 9–12 days. Two broods are usual. (H.G.D.) M.W.

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PARROTBILL (2): term sometimes applied, in the plural, to the Psittirostriinae (for family see HAWAIIAN HONEYCREEPER).

PARROT-FINCH: substantive name of *Erythrura* spp. (see ESTRILDID FINCH).

PARROTLET: substantive name of the Neotropical *Forpus* spp. (Psittacinae, Arini) (see PARROT).

PARSON-BIRD: alternative name for the Tui *Prosthemadura novaeseelandiae* (see HONEYEATER) and in Trinidad for the tanager *Tachyphonus rufus*.

PARTHENOGENESIS: production of a new individual from an egg not fertilized by a male gamete; from Greek *parthenos* meaning virgin and *genesis* meaning birth. In application parthenogenesis may be regarded as any mitotic activity in unfertilized eggs, or more conservatively, the development of a macroscopically detectable blastoderm.

Parthenogenesis may result in at least two cytological forms. Generative parthenogenesis occurs in animal groups in which chromosomes of the egg are reduced (through meiosis). Individuals that are produced are thus haploid. Automictic parthenogenesis occurs in animal groups in which chromosomes are initially reduced but diploidy is ultimately restored. The hypothesized mechanism for this restoration is suppression or re-entry of the second polar body during the second phase of meiosis.

Parthenogenesis appears to be relatively widespread in the animal kingdom. Using a definition of any mitotic activity in unfertilized eggs, parthenogenesis is probably very common. However production of viable offspring is much less common. Of all known cases 90% occur among invertebrate species.

Among birds mitosis may be initiated in the unfertilized egg but organization of the blastoderm generally fails. Naturally occurring parthenogenesis is usually abortive. The only documented cases of production of offspring by parthenogenesis are from domestic varieties of the chicken *Gallus gallus* and the Turkey *Meleagris gallopavo*. Automictic parthenogenetic development has been observed in 1% of the unfertilized eggs of standard and cross breeds of chickens; the frequency among various strains of domestic turkeys averages approximately 10%. Selective breeding programmes have increased the frequency of parthenogenesis indicating a genetic basis for the phenomenon. The presence of viruses appears to increase the frequency of parthenogenesis. Fowl Pox, Rous Sarcoma and Newcastle DISEASE have all been shown to play an active role in parthenogenesis in turkeys. Vaccinations using live virus have proven more effective than the killed form. Vaccination/selection programmes have resulted in frequencies of parthenogenetic development approaching 50%. In most cases development is aborted and production of viable individuals is rare. Those that have hatched have been male and of those surviving to maturity only 20% have produced viable sperm.

Parthenogenesis resulting in viable offspring in the wild has not been documented in birds. It is suspected in wild Turkeys because of its unusually high level in captivity. However, laboratory experience has shown that the parthenogenetically produced turkeys suffer from malposition in the egg and are generally less vigorous during pipping and hatching than normal young. In addition to poor hatchability, the birds show difficulties with locomotion and feeding during the early post-hatch phases. The probability of successful parthenogenetic production of offspring in the wild appears to be exceedingly low. W.F.P.

Beatty, R.A. 1967. Parthenogenesis in vertebrates. *In* Metz, C.B. & Mulroy, A. (eds.). Fertilization: Comparative Morphology, Biochemistry and Immunology, vol. 1. New York.

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PARTIAL MIGRANT: term applied to species of which, in a given breeding area, some individuals are migratory while others are not, e.g. Song Thrush *Turdus philomelos* in Britain. (see MIGRATION).

PARTRIDGE: substantive name of species of Phasianidae in several genera (*Perdix*, *Ammoperdix*, *Alectoris*, etc.); also the tree partridges *Arborophila* spp. etc, the Snow Partridge *Lerwa lerwa*, and the bamboo partridges *Bambusicola* spp. etc. (see under PHEASANT).

PARULA: substantive name of the 2 species of *Parula* (see WARBLER (2)).

PARULIDAE: a family of the PASSERIFORMES, suborder Oscines; WARBLER (2).

PARVORDER: a taxonomic category which is a subdivision of an order, ranked between infraorder and superfamily. Used by McKenna (1975), Sibley and Ahlquist (in press). See also DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA.

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Sibley, C.G. & Ahlquist, J.E. In press. The phylogeny and classification of the passerine birds, based on comparisons of the genetic material, DNA. Proc. XVIII Int. Orn. Congr. Ilyichev, V.D. (ed.). Moscow.

PASSAGE MIGRANT: term, alternatively 'transient', applied to birds from the viewpoint of an observer in an area that they pass through on migration without remaining throughout either the summer or the winter; 'bird of passage' is sometimes used as an equivalent but is applied poetically to any migrant (see MIGRATION). For 'passage hawk' see FALCONRY.

PASSERES: used both as an ordinal name synonymous with 'Passeriformes' and (less commonly) as a subordinal name synonymous with 'Oscines' (see below). It was the name used by Linnaeus for his sixth order of birds.

PASSERIDAE: family of PASSERIFORMES, suborder Oscines, SPARROW (1).

PASSERIFORMES: an order comprising 2 suborders (1) the 'Deutero-Oscines' (with 12 families; name introduced by Voous, Ibis 119 (1977): 224); treated by Feduccia as an order of its own, Tyranniformes, with an independent origin from Coraciiform ancestors, and (2) the 'Oscines' (with 70 families) (see TABLE OF CLASSIFICATION). The families of 'Deutero-Oscines' are often referred to collectively as the 'Suboscine Passeriformes', but the name 'Suboscines' more precisely denotes the Australian Atrichornithidae and Menuridae which have syringeal differences in comparison to the remaining Oscines. The name 'Clamatores' is used alternatively for the Tyranni (but earlier had a wider connotation). The order can also be divided in accordance with the number and arrangement of the syringeal muscles (see SYRINX). In the terminology most lately used, the Tyranni or Clamatores (with which the Eurylaimi agree in the particular respect, although otherwise peculiar), are called 'Mesomyodi', and are subdivided into 'Tracheophonae' (= superfamily Furnarioidea) and 'Haploophonae' (= Tyrannoidea); the Menurae and the Oscines together constitute the 'Acromyodi'. There have been other variants of this scheme.

The Passeriformes, as an order, are often referred to as the 'perching birds', and the Oscines as the 'song-birds', and from the point of view of European ornithology these two common names are in practice synonymous, the Oscines being the only suborder represented in the Palearctic Region.

General characters. Perching and singing are functions reflected in the structure of members of the order. The foot is characteristic. There are always 4 toes, joined at the same level; the hallux is directed backwards and is not reversible. This form of foot is well adapted to perching by the method of gripping a slender branch, twig, reed, grass-stem or wire (see LEG). The toes are never webbed, even in the very few forms that have acquired aquatic habits (Cinclidae, and *Cinclodes* spp. in the Furnariidae). The syrinx is tracheal in a few (Tracheophonae—see above); otherwise it is in the common tracheo-bronchial position, but with various arrangements of its muscles as already mentioned. The quality of song varies greatly, even among the Oscines, but the order certainly includes the best musicians—and the most accomplished vocal mimics (see VOCALIZATION; and MIMICRY, VOCAL).

Among other morphological characters the wing is eutaxic and has either 9 or 10 distinct primaries. The tail most usually has 12 rectrices. The spermatozoa have a distinctive form, not found in other birds.

The form of bill shows various adaptations to the kind of food (see BILL). In body size, the members of the order range from very small to the moderate dimensions attained in the larger crows (Corvidae) and the lyrebirds (Menuridae). In feathering they range from inconspicuous drab hues and lack of adornment to brilliant colours and ornamental plumes.

Mode of life. The Passeriformes are land birds. Some particularly frequent the vicinity of fresh water, and a very few find their food in it; some live near, or visit, the seashore; but to them all the open sea figures only as a dangerous area to be crossed on migration. Many of them, especially insectivorous species breeding in high latitudes, are migratory in the highest degree; others perform shorter journeys, while others again are sedentary. Widely varying habitats are exploited, including desert, montane areas, man-made environments, roosting and nesting in buildings and making use of 'unnatural' food.

Breeding habits show a wide range of difference in nest sites, nests, eggs and so on. The young are nidicolous, being hatched blind, naked, and helpless. In general, parental care—by both sexes—is well developed; a few species, however, are parasitic in this respect (see BROOD-PARASITISM).

Distribution. The order is cosmopolitan, unrepresented only in polar latitudes and on the most forbidding islands. Indeed, its members predominate in the avifaunas of all but a few highly specialized types of environment. Some families of the Oscines are almost cosmopolitan, or are widespread in either the Old World or the New.

Familial taxonomy of the Oscines. This is a subject of the greatest difficulty and much speculation. The general resemblance is so high, and the effect of convergence on adaptive characters so great, that trustworthy evidence of relationships between groups is hard to find. As E. Mayr has pointed out, with the exception of the Alaudidae (absence of ossified pessulus in the syrinx) and the Hirundinidae (closed bronchial rings) none of the families can be defined unequivocally by anatomical characters—there is always a hint that these may be functional and not phyletic.

Many of the families are nevertheless reasonably distinctive—or at least appear to be so—and their validity as taxa has not been seriously challenged. Others are very unsatisfactory, and their boundaries are obscured by the existence of aberrant forms that may be included or excluded as a matter of opinion. Thus thrushes, warblers, flycatchers, and babblers have been considered by some authors to be so distinct as clearly to warrant the status of separate families, Turdidae, Sylviidae, Muscicapidae, Timaliidae, respectively. Many of the authors working on groups from the Old World Tropics, have treated them as subfamilies or tribes of the family Muscicapidae with all too numerous species and phenetic forms. Another classic area of special doubt includes the Fringillidae, Emberizidae, Thraupidae and other so-called nine-primaried (as opposed to the ordinary ten-primaried) Oscines. There are, in addition, instances which it is merely a matter of opinion, on degrees of difference, whether a few apparently nearly related groups should be treated as separate families or as subfamilies of one; such points are of minor importance.

Where it is difficult even to delimit many of the families, it is still more difficult to arrange them all in larger groups. Generally, the song-birds (again excluding the larks and swallows) are divided into 3 major assemblages; (1) Old World insect-eaters and relatives; (2) New World insect-eaters and finches; and (3) crows (Corvidae), birds-of-paradise (Paradisaeidae), and associated families. The remaining more peculiar and isolated families, as well as the Old World nectar-eaters, are then placed rather irregularly within this broad framework (see Mayr and Greenway 1956).

Whether or not any groups of families be expressly designated, it is necessary for practical purposes to arrange the families of the suborder in some sequence. Customarily, such a sequence purports to lead from the most primitive to the most specialized, or (chiefly in the past) vice versa. The same lack of real evidence, however, makes this equally in vain; the essential facts are just not known, and may perhaps never be ascertainable. In any event, even were it possible to construct an adequate concept of phyletic relationships, this could not be expressed in a linear sequence such as, for instance, the arrangement of any check-list or other systematic work requires. The most that a sequence can do is to keep together, here and there, a few families that are probably closely related; but it equally brings into juxtaposition other families between which no such near relationship can be supposed to exist.

Current views tend to favour a sequence that is traditional, and thus in some ways convenient. There may be reason for believing that the sequence is to some slight extent a 'natural' one, and that it at least serves to keep a few probably related families together—especially those that might perhaps equally well be brought under a single head as subfamilies, and are indeed so treated by some authors.

It should nevertheless be recognized and made abundantly clear that, apart from recent progress in biochemical and DNA research, the device is for the most part merely a convention. Thus, a conventional sequence of Passerine families was agreed upon by a committee appointed by the XI International Ornithological Congress (Basel 1954) and published by Mayr and Greenway (1956). This sequence has been followed by the editors and authors of the late James L. Peters' *Check-list of Birds of the World.* It follows the sequence (1), (2), (3) mentioned above and accepts the view that crows, as well as the whole corvid assemblage (group 3) are the most advanced and highly developed songbirds, a supposition which appears more or less based on the crows' intellectual capacities rather than on anatomical or fossil evidence and therefore has not failed to evoke refutation (Amadon 1957, Delacour and Vaurie 1957, Wetmore 1957, Mayr 1958, Storer 1959, 1971, Sibley 1970). Wetmore (1930, 1951, 1960) and most other Americans basically follow the sequence (3), (1), (2), whereas European authors, following Ernst Hartert's monumental work (1903–38) always have been more inclined to (3), (2), (1). As Storer's (1971) sequence, following (1), (3), (2), is thought to gain widest acceptance, it has been followed here with a few amendments as to the places of Motacillidae and Laniidae, in accordance with Voous (1977). It combines the views that the nine-primaried assemblage of New World insect-eaters, tanagers, finches, sparrows, cardinals and icterids are the most recently developed and diversified large group of birds. The evolution of the seed-crunching and seed-shelling fringilline and emberizine groups is thought to have been a geologically rather recent event, following the rapid and equally recent evolution of monocotyledonous plants. Sturnids, ploceids and allies are most advanced among the other groups of songbirds. The nectar-feeding birds form highly advanced groups of their own.

Among other authors, Sibley particularly (1976, 1983) has added a new aspect to the systematic arrangement of songbirds by expressing the view that many of the characteristic Australian songbirds have no direct relatives in the other continents, but instead represent ecologically diverse groups comparable to those found in the diversity of Australian marsupials. Similarities between many Australian birds and groups or families occurring in other continents therefore are to be considered as having resulted from parallel or convergent evolution. In addition to the main groups (1), (2), and (3), a fourth group of Old Australian Endemics (e.g. Maluridae, Acanthizidae, Neosittidae) has to be accepted. A secondary radiation of Australian crow-like Endemics (e.g. Callaeidae, Grallinidae, Cracticidae, Paradisaeidae) adds a further dimension to the basic group (3). Numerous details of this theory remain obscure, but the theory in itself is fascinating and illuminating. K.H.V.

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See also references under CLASSIFICATION.

PASSERINE: appertaining to the order Passeriformes; commonly used substantively for species belonging to that order, members of all others being collectively called 'non-passerines' (see PASSERIFORMES). The form of the word would also admit of its being applied in a restricted sense with reference to the subfamily Passerinae, but to obviate confusion this is better avoided.

PASTOR: substantive name of the Rosy Pastor (or Rose-coloured Starling) *Sturnus roseus* (see STARLING).

PATAGIAL TAG: see MARKING.

PATAGIUM: see METAPATAGIUM; PROPATAGIUM; WING.

PATELLA: the 'knee-cap', not present in all birds (see LEG; SKELETON, POST-CRANIAL.

PATRISTIC: term sometimes applied in taxonomy to resemblances between forms due to common ancestry, as distinct from resemblances due to convergent adaptation (see CONVERGENCE).

PAURAQUE: substantive name of *Nyctidromus* and *Siphonorhis* spp. (for family see NIGHTJAR).

PEACOCK: see below.

PEAFOWL: substantive name of *Pavo* spp. and also of *Afropavo congensis* (and there are also 'peacock pheasants' *Polyplectron* spp.)—see PHEASANT. 'Peacock' and 'peahen' are special names for male and female, but the former may also be used irrespective of sex.

PEALEA PHENOMENON: the occurrence of 'spotting or streaking as variations from the normal plumage pattern' in some species of storm-petrels (Hydrobatidae). Specimens showing this and at one time ascribed to a supposed form '*Pealea lineata*' were later found to belong to 3 otherwise well known species.

Murphy, R.C. & Snyder, J.P. 1952. The 'Pealea' phenomenon and other notes on storm petrels. Amer. Mus. Novit. no. 1596: 1–16.

PECKING: see BEHAVIOUR, DEVELOPMENT OF.

PECK-ORDER: see DOMINANCE (2).

PECTEN: a structure on the retina of the avian eye (see VISION).

PECTINATE: provided with a serrated (comb-like) edge, as on the inner aspect of the claw on the middle toe of some species and on the sides of the toes in certain Tetraoninae (see under LEG).

PECTORAL: pertaining to the breast (see TOPOGRAPHY); for pectoral girdle see SKELETON, POST-CRANIAL.

PEDIONOMIDAE: see under GRUIFORMES; PLAINS-WANDERER.

PEDIUNKER: name for the Grey Petrel *Procellaria cinerea*, see PETREL.

PEEP: see SANDPIPER.

PEEWIT: see PEWIT; PLOVER (1).

PELAGIC HABITAT: see OCEANIC BIRDS.

PELECANI; PELECANIDAE: suborder and family of PELECANIFORMES; PELICAN.

PELECANIFORMES: an order, alternatively 'Steganopodes', comprising 3 suborders: Phaethontes, Pelecani, Fregatae; 6 families: Phaethontidae (TROPICBIRD), Sulidae (GANNET), Phalacrocoracidae (CORMORANT), Anhingidae (DARTER), Pelecanidae (PELICAN), Fregatidae (FRIGATEBIRD).

The order is one of mainly fish-eating birds of substantial size, characterized by having all 4 toes connected by a web (totipalmate), the hallux being turned forward and connected with the second digit. Except in the families first and last named above, the 8th and 9th of the 17–20 cervical vertebrae are so shaped that they articulate at an angle with those in front and behind.

PELECANOIDIDAE: family of PROCELLARIIFORMES; PETREL.

PELICAN: substantive name of all species of *Pelecanus* of the family Pelecanidae (Pelecaniformes, suborder Pelecani).

Pelecanus includes 7 species, divided into 3 groups: (1) Great White Pelican *Pelecanus onocrotalus*, Dalmatian Pelican *P. crispus*, Australian Pelican *P. conspicillatus*, and American White Pelican *P. erythrorhynchos*, all large, feed in groups, nest in dense colonies on ground, and never roost in trees; (2) Grey or Spotted-billed Pelican *P. philippensis* and Pink-backed Pelican *P. rufescens*, both smaller, usually feed singly, normally nest in trees in loosely packed colonies, and perch at roost in trees; and (3) Brown Pelican *P. occidentalis* which dives for its food. Sometimes *P. crispus* is included with *P. philippensis* but differences in nesting, feeding behaviour and morphology make this invalid.

Characteristics. Pelicans are large (140–180 cm) aquatic birds with a heavy body, long neck, large head and long, straight bill. The upper mandible is flat with a medium ridge, hooked at tip; the lower is loosely articulated and flexible with a suspended, extensible gular pouch. The wings are long and broad; the tail, short and rounded. Except for the Brown Pelican, the plumage is mainly white with areas of grey, brown and black. The face, throat and orbital area are bare. At courtship the American White Pelican develops a horn-like growth on the bill; the Great White Pelican has a swollen forehead, yellow in the male, orange-red in the female. All species develop startling secondary sex characters in the colours of the head, face and pouch. The sexes are similar, the male usually being larger.

Habitat. All inhabit inland fresh and brackish lakes and coastal waters except Brown Pelicans which are restricted to coastal marine habitats.

Distribution. Pelicans are pantropical and subtropical. In the New World, the Brown Pelican occurs along the Pacific coast from Washington to Chile and Galapagos and along the Atlantic from North Carolina to the Gulf of Mexico and Caribbean to Guiana. The American White Pelican is found from northern Alberta and Manitoba south to coastal Mexico and Guatemala east to Florida. In the Old World, Great White Pelicans range from Africa and south-east Europe to south-east China and the Malay Peninsula. The Dalmatian Pelican occurs from south-east Europe to Mongolia and northern China south to Iran and northern India. The Pink-backed Pelican occurs in Africa (south of about 20°N), Madagascar and south-west Arabia. The Grey Pelican inhabits India, southern China, and the Philippines south to the Malay Peninsula and Indonesia. The Australian Pelican occurs throughout Australia in suitable habitats, and in Tasmania and New Guinea.


White Pelican *Pelecanus onocrotalus*. (*J.B.*).

Populations. Colony size varies from a few individuals to many thousand pairs. Generally pelicans have declined markedly in range and numbers due to pesticides, drainage, and sensitivity to disturbance.

Movements. Pelicans fly in V-formation, in lines or single file, often travelling one behind the other with the leader beating wings or gliding, the rest doing likewise. Pelicans also circle high in thermals and soar for considerable distances. Certain pelican populations undergo post-breeding dispersal, with some travelling long distances.

Food. The diet is fish and sometimes crustaceans. Most species are surface-feeders, catching fish with the pouch. When the bird puts its bill into the water, the lower mandible expands into a broad scoop. The pelican traps the fish in the pouch under water, raises its head to drain water from the pouch, then swallows the fish whole. Sometimes pelicans transport fish in a partially digested state.

The Pink-backed and Grey Pelicans usually swim singly or in small groups and, upon sighting prey, dart out their head and neck to catch fish. The larger species often use a herding technique when groups of 5 to several hundred swim forward, often in U-formation with the open end directed forward towards the beach or shallow water. As the group moves along, several partly raise their wings and simultaneously plunge their heads into the water. Each successful bird raises its bill upward and swallows fish. The Brown Pelican dives to catch fish under water.

Behaviour. Pelicans are gregarious all year in groups of a few to several thousand individuals. Their non-breeding behaviour, as typified by the Brown Pelican, includes wing- and body-shake; tail-wag following landing in water or sitting on nest; bill-toss after preening; wing-flap for balance, comfort movement, or reaction to disturbance; wing-and-leg-stretching; glottis-exposure and bill-throw for stretching gular pouch and tissues of throat and upper breast; scratching head, neck, and pouch; bill-plunge to moisten gular pouch and to drink; head-rub to maintain head and neck feathers; preening; bathing; walking; swimming; gular flutter and spreading wings in response to temperature changes; and sleeping.

Pelicans appear to arrive at the nesting area unmated. In tree-nesting species the male occupies a potential nest site where he sways the head and bill through a figure-8 (head swaying); arches neck away from body and points bill downward (bowing); turns head from side to side (head turning); raises bill toward horizontal position, stretches gular pouch taut, spreads wings and sometimes opens bill (upright); and throws bill over back, thrashes wings and claps mandibles (bill-clapping, Pink-backed Pelican). The female initially selects the male, and also performs the above displays. No obvious behaviour precedes copulation. In ground-nesting species the displays are similar; in addition, males and females may swim, walk or fly in groups or walk along shore with head held high, sometimes with wings partly spread (strutting walk); males may gather in groups where they raise bills skyward (upright or head-up), make 'mooing' sounds, then thrust bills toward centre of group (bowing). The female selects the nest site.

Voice. Pelicans are usually silent except at breeding colonies. There some produce only an expulsion of air from the lungs during bowing and upright displays, while others produce *moo, ha-oogh* and deep grunts. Young make screaming and wailing sounds when soliciting food.

Breeding. Pelicans are colonial breeders, nesting in trees or on ground free of mammalian predators. Tree nests are large structures of dry sticks, sometimes 30 m above ground. Ground nests are small depressions, sometimes with sticks, leaves, reeds and pebbles. The male collects the nest material, the female builds the nest. In the tropics the nesting season may extend over several months, with some colonies peaking in rains, others in dry season. Usually 2–3 eggs are laid; they are large and elongated with a chalky coating. Incubation lasts 30–37 days, begins with the first egg, and is shared by both parents.

The newly hatched young are pink and naked, turn black or grey within 4–14 days, and thereafter develop a coat of white, grey or blackish down. After about 3 weeks, the young of ground-nesting species collect in crèches (pods). The young are cared for and fed by both parents. Small young are fed on partially regurgitated food; from about one week on, the young bird puts its head into the parent's pouch and feeds itself. Young pelicans take 70–80 days to reach the flying stage.

See photo FLIGHT. E.K.U.

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Lamba, B.S. 1963. Nidification of some common Indian birds, no. 7. The Spottedbilled or Grey Pelican (*Pelecanus philippensis* Gmelin). Pavo 1: 110–119.

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PELLET: a compact mass composed of those undigested portions of a bird's food that have been retained in the stomach by a mechanical barrier for a period before being regurgitated and ejected through the mouth, rather than evacuated as faeces; sometimes described as 'castings'. They vary considerably from species to species with respect to size, colour, shape, and the proportion of prey fragments that can be identified, but they form an important research tool for ornithologists when examining an individual bird's feeding tastes and variations in diet with season, year, region and habitat.

The physiology and mechanics of pellet formation have been examined using radio-active tags but there is scope for further studies. Pellets are composed of materials of relatively low nutritional value, while those produced by starved birds in captive conditions show a greater degree of digestion than is normal in the wild. Pellet ejection may be immediate and apparently 'effortless' or may take as long as an hour with apparent 'nausea'. The process often consists of several upward stretches of the head and neck—convulsive movements—followed by a lowering and, especially in passerines, shaking of the head, with the pellet expelled up to 1 m or more.

Pellets are most commonly associated with birds of prey (and notably owls) because their ability to digest bone is poor while the skeletal record in their pellets is good so that the diet may be accurately quantified. Pellet production has been widely observed in birds, covering some 330 species and more than 60 families (International Bird Pellet Study Group) including unlikely groups such as jays (Corvidae), flycatchers (Muscicapidae) and honeyeaters (Meliphagidae). Pellet ejection has also been recorded in certain mammals, reptiles and amphibians.

Most pellets produced by large birds comprise a central core of hard materials such as bones, beaks, claws, scales, teeth and chitin, enveloped by softer substances like fur, feathers and, less often, vegetable matter. Lengthy hard food fragments such as bird beaks, legs, and mammal long-bones tend to be aligned with the longitudinal axis, the majority of pellets being elongate and oval in shape, fewer rounded or segmented.

The contents of pellets are naturally determined first by the spectrum of food eaten; second, by the digestive ability of the species concerned. Owls usually swallow food items entire and their pellets contain the great majority of all bony elements and good evidence of most invertebrates eaten. Diurnal raptors are not so helpful to the analyst—they tear flesh and bone, digest much bone, frequently only partially consume a prey item, so that the pellet record is incomplete. Herons (Ardeidae) regurgitate fur castings with little or no bony evidence of fish, amphibian or mammalian foods. The pellets of other birds may be dominated by single items such as corn husks (Rook *Corvus frugilegus*), wax (Honey Buzzard *Pernis apivorus*), fish bones (Kingfisher *Alcedo atthis*), sand (Dipper *Cinclus cinclus*), chitinous insect hard-parts (Spotted Flycatcher *Muscicapa striata*), crustacean and mollusc fragments (some waders—Scolopacidae).

Pellets often also contain the unexpected. Scavenging gulls (Laridae) are notorious for the range of bizarre binding materials like cellophane, paper, plastic and rubber incorporated. Pellets can be important sources for the recovery of bird rings, especially those cast by regular small-bird feeders like Kestrel *Falco tinnunculus*, Short-eared Owl *Asio flammeus*, and Long-eared Owl *A. otus*. Other predators like the Barn Owl *Tyto alba* are very effective aerial 'samplers' of small mammal populations, indicating the presence of scarce or rare species and allowing large quantities of mammal bones to be collected far quicker than by normal trapping techniques.

The ease with which pellets can be collected varies greatly from species to species. For most passerines one needs to witness the characteristic 'retching' behaviour before searching. Regular visits to the loafing sites of homogeneous groups like gulls and waders can prove productive. Regular roosting sites and occupied nests are otherwise the best sources of material, the last resort being an examination of the stomach contents of dead birds.

Fresh pellets are usually damp and soft in texture with a surface mucous layer. This hardens quickly to produce a glossy varnished appearance (Barn Owl). Moisture may comprise 60% of the total initial pellet weight which is rapidly lost by evaporation. The rate at which pellets decompose depends on the species of bird, season, location and the micro-fauna and flora. Barn Owl pellets regurgitated in the protected environs of a dry barn may remain intact for many months, sometimes even years, while Tawny Owl *Strix aluco* pellets cast in damp woodland vegetation may be rain-leached or ice-shattered in a few days. Pellets composed of vegetable matter such as husks and seeds or fragments of insects, crustacea, or molluscs, are prone to an early breakdown.

The most important decomposers of fur and feather castings are certain tineid moths, trogid beetles, mites and saprophytic fungi. The insects especially feed in their larval form on the fur and feather matrix, and pellets may soon crumble into small piles of bones which are easily scattered or buried. A productive exercise is to scrape away earth at traditional nesting places or beneath pellet 'ejection posts' to reveal an historical layer of buried bones. 'Fossilized' pellets have been found during archaeological excavations and helped throw light on the past distribution of small mammals.

Pellets can be dissected in a dry or wet state, though most analysts prefer first to soak the material in a shallow tray of warm water before

Marsh Sandpiper *Tringa stagnatilis* bringing up a pellet. (*Photo: J.F. Reynolds*).

separating the contents with needles or forceps. A pocket lens or low-power microscope is necessary to identify the prey fragments with the aid of a reference key.

For large quantities of pellets a centrifuge may profitably be used to separate the hard and soft elements. Pellets are best preserved dry and entire by an early spray with a strong insecticide followed by several coats of a quick-drying polyurethane. The dissected contents may be stored in glass files or mounted on stiff cardboard. Pellets are excellent ecological tools for the educationalist wishing to demonstrate the principles of food preferences, food chains, and energetics. D.E.G.

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PELLORNEINI: see BABBLER.

PELVIC GIRDLE: see SKELETON, POST-CRANIAL.

PEN: special term for a female SWAN.

PENDULINE TIT: substantive name of *Remiz pendulinus* (Passeriformes, suborder Oscines); in the plural general term for the family Remizidae, formerly included in the Paridae (see TIT). There are 10 species in 4 genera.

Characteristics. The penduline tits are active birds from 8–14 cm long. They share many characteristics with the true tits, but have finer, more pointed bills and are even more acrobatic, being able to climb upside down along the underside of branches. The plumage of *Remiz* is basically pale buff, chestnut and black, and shows considerable variation within populations and between races. The kapok tits *Anthoscopus* are mostly brown and yellow, and the Verdin *Auriparus flaviceps* is yellow and grey with a rusty patch on the carpal area.

Habitat. Most species are found in open, scrubby areas where they are resident throughout the year, although some are nomadic outside the breeding season.

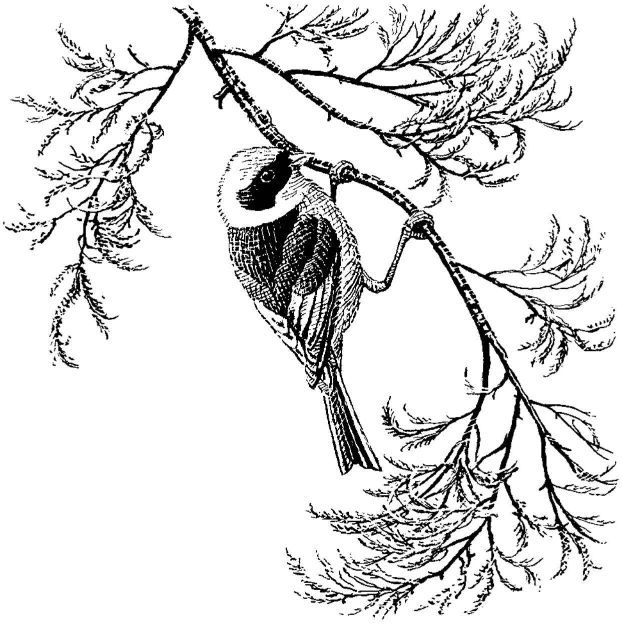
Distribution and systematics. *Remiz* (monotypic) is discontinuously distributed across the Palearctic from the Atlantic to the Pacific; the kapok tits (*Anthoscopus*, 7 species) are found in dry bush habitats over most of Africa south of the Sahara. In North America the Verdin is restricted to the semi-deserts of the south-western United States and northern Mexico. The Fire-capped Tit *Cephalopyrus flammiceps* is found in the evergreen forests of the Himalaya. Although structurally very similar to the other Remizidae and using the same highly developed acrobatic foraging and food-handling techniques (Löhrl 1967), its main affinities may lie with the true tits.

Food. All species mainly feed on invertebrate prey taken from the outer twigs and branches of trees and bushes, supplemented with seeds and fruit.

Behaviour. Most species are generally found in flocks, but the Verdins are solitary outside the breeding season, and it has been suggested that they may have closer links with the Bananaquit *Coereba flaveola* than with the Remizidae (Taylor 1970).

Voice. Songs are generally poorly developed but the species which flock have sharp, monosyllabic contact calls.

Breeding. The 2 widely distributed Old World genera, *Remiz* and *Anthoscopus*, build similar, pendulous domed nests of vegetable down and breed as groups rather than distinct pairs. *Remiz* nests are suspended from twigs and generally about 5 m above water. Nest-building is started by the male weaving a foundation loop of grasses and roots on which the felted nest is built over a period of weeks. The main material used is pappus from willow *Salix*, poplar *Populus*, reed-mace *Typha* or willow-herb *Epilobium*. The 5–10 white eggs, incubated by the female, hatch after about 12 days and the young fledge 16–18 days later. *Anthoscopus* nests have a prominent false entrance and dummy chamber with the real entrance capable of being closed by the birds. Vegetable down is generally the main nesting material but animal hair may also be used. The clutch consists of 3–6 white eggs, a few less than *Remiz*, and the hatching and fledging periods are a little longer. In both genera the breeding groups may roost together in the nest, and may have co-operative breeding. The Verdin does not have helpers at the nest, and only one of the 3 races uses vegetable down; the other 2 weave their nests from thorny twigs. All Verdins start nest-building from a platform lodged in the outer part of a bush and not from a hanging loop of pliable material. From 3–6 blue-green speckled eggs are laid and the young fledge some 3 weeks after hatching. The Fire-capped Tit lays a clutch of 3 or 4 pale blue-green eggs in a lined hole in a tree. C.J.M.



Penduline Tit *Remiz pendulinus*. (*D.W.*).

Löhrl, H. 1967. Zur verwandtschaftlichen Stellung von *Cephalopyrus flammiceps* auf Grund des Verhaltens. Bonn Zool. Beitr. 18: 127–138.

Taylor, W.K. 1970. Some taxonomic comments on the genus *Auriparus*. Auk 87: 363–365.

PENGUIN: substantive name of all species of Spheniscidae, sole family of the order Sphenisciformes. Penguins are flightless sea birds of the Southern Hemisphere highly adapted for marine life. They range in weight and stature from birds of about 1 kg and 40 cm body length to 30 kg and 115 cm.

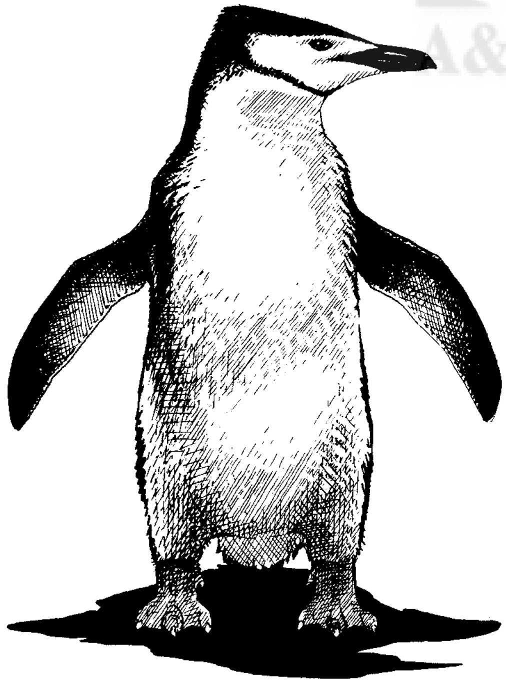
Characteristics. Despite their variation in size, and with breeding habitats ranging from the bare lava shores of equatorial islands through cool temperate forests, sub-Antarctic tussock grassland and beaches to Antarctic sea ice, penguins are remarkably similar in structure and plumage. They are all chiefly blue-grey or blue-black above and mainly white below; specific distinguishing marks are chiefly on the head and upper breast, visible while swimming on the surface. The main chick plumages are grey or brown uniformly or with one of these colours dorsally and white ventrally. Juvenile plumage is usually very similar to, but distinguishable from, that of adults. Most species are slightly sexually dimorphic; penguins of the genus *Eudyptes* notably so.

They lack defined feather tracts (unlike most birds; see PTERYLOSIS) and short specialized feathers closely cover the body surface. Their bodies are highly streamlined, the wings reduced to strong, narrow, stiff flippers, with which they swim rapidly. The feet and tarsi are short, the legs set well back on the body, being used, with the tail, as rudders. On land penguins frequently rest on the short tarsometatarsus (heel) with the stout rectrices forming a prop. The short legs induce a waddling gait but on ice penguins can move rapidly by tobogganning. Penguins have comparatively solid bones and they generally weigh only a little less than the water they displace, reducing the energy required to dive. The duration and depth of dives varies greatly but the Emperor Penguin *Aptenodytes forsteri* can submerge for 18 min and reach at least 265 m, while even small species may stay down for 6 min and reach nearly 100 m; typical values, however, are very much less than these. Swimming speeds probably range from 2–3 knots up to perhaps 15–20 knots in short bursts. Swimming often involves porpoising, whereby the bird breaks the surface with its momentum carrying it through the air for a metre or so before re-entering the water. This may facilitate breathing while travelling fast and may also confuse potential predators. The basic physical adaptations of penguins are thus concerned with swimming efficiently and also with thermal insulation. In addition to the dense waterproof feather coat, there is a well-defined fat layer and a highly developed vascular counter-current heat exchange system in the flippers and legs. All these are best developed in species of high latitude but are found even in temperate and tropical penguins which live in regions of cool water currents. When on land, however, these adaptations may lead to problems of overheating. It is significant that the species of warmer latitudes have relatively larger flippers and areas of bare facial skin as adaptations to dissipate excess heat. In addition they live in burrows to reduce direct insolation.

The fossil record of penguins begins in the late Eocene (45 million years BP) and about 32 species are currently recognized. Most were between 50 cm and 1 m tall (much as living species) but 2 or 3 species were probably about 150–160 cm tall and may have weighed 135 kg. Their distribution was similar to that of living species, with most specimens coming from (in order of importance) New Zealand, Patagonia, Antarctic Peninsula, South Australia and South Africa. The fossil record provides no direct indication of the origins of penguins (though they presumably passed through a stage combining flight and underwater swimming like the auks of the northern hemisphere which are their nearest ecological equivalent) but one firm line of evidence suggests a very distant relationship to the Procellariiformes.

The 16–18 living species (depending on whether the Royal Penguin *Eudyptes (chrysolophus) schlegeli* and the White-flippered Penguin *Eudyptula (minor) albosignata* are regarded as full species or not) are divided into 6 genera. Most species are currently found between 45°S and 60°S, with the greatest species diversity in the New Zealand area and the Falkland Islands; the main numerical concentrations, however, are around the coasts of Antarctica and on the sub-Antarctic islands. The biology and adaptations of 4 of the 6 genera are reviewed later; only the general patterns are summarized below.

Distribution. The genus *Aptenodytes* comprises the 2 largest penguins, Emperor *A. forsteri* and King *A. patagonicus*; they are completely allopatric, the former breeding on the sea ice around the Antarctic Continent, the latter breeding at most sub-Antarctic and cold temperate islands. The 3 species of the genus *Pygoscelis* include 2 circumpolar ones, Adélie *P. adeliae* around the Antarctic Continent and Gentoo *P. papua* at the sub-Antarctic islands. These 2 species overlap in the Antarctic Peninsula area where the third species, Chinstrap *P. antarctica*, occurs in considerable numbers, principally between the centres of abundance of the other 2.



Chinstrap Penguin *Pygoscelis antarctica*. (*B.P.*).

The Yellow-eyed Penguin *Megadyptes antipodes* is ecologically similar to the Gentoo and essentially replaces it at the New Zealand sub-Antarctic islands (not Macquarie Island where Gentoo occurs) and South Island mainland.

Of the crested penguins, 3, the Fiordland *Eudyptes pachyrhynchus*, Snares Crested *E. robustus* and Erect-crested *E. sclateri*, have allopatric breeding ranges and are confined to the same area as *Megadyptes* but the other 2 species, the Macaroni *E. chrysolophus* and Rockhopper *E. chrysocome*, have wide circumpolar distributions occurring together at several sub-Antarctic islands.

The 4 species of the genus *Spheniscus* span the greatest longitudinal range with the Galapágos *S. mendiculus* at the Equator, the Humboldt *S. humboldti* from equatorial Peru to central Chile (entirely within the cool Peruvian current), and the Magellanic *S. magellanicus* in southern South America and its off-lying islands, including the Falklands. The only African penguin, the Jackass *S. demersus*, is confined to the coast of South and South-west Africa, influenced by the cooler waters of the Benguela and Agulhas currents. The genus *Eudyptula*, ecologically similar to *Spheniscus*, has a single species, the Little Blue *E. minor*, the smallest of the family, throughout New Zealand and much of the south coast of Australia and a closely related species or subspecies, the White-flippered *E. albosignata*, on the east coast of New Zealand's South Island.

Movements. Winter distributions and movements are imprecisely known. The tropical and warm temperate species are sedentary. Most eudyptid species and southern populations of Gentoo and Magellanic Penguins disperse widely (and generally northwards) in winter but northern populations are chiefly resident. Antarctic species move at least to the pack ice edge in winter. Juveniles disperse widely after fledging and there are many records far from breeding sites.

Food. Crustaceans, fish and squid are the main prey of penguins. Fish are important in the diet of inshore feeding species, e.g. *Spheniscus* species, Little Blue and Gentoo Penguins and also of the deeper diving King and Emperor Penguins. Squid perhaps predominate in the food of the King Penguin and seem fairly frequently taken by Emperor and Rockhopper Penguins and some spheniscids. Euphausiid crustaceans (krill) are the principal prey of perhaps all pygoscelid and most eudyptid species and are certainly taken by all Antarctic penguins. When feeding chicks, individuals of most species are at sea exclusively or mainly during daylight hours but by diving they could follow any diel migration of their prey. The Little Blue Penguin is anomalous in not normally feeding its chicks until well after nightfall. As the smallest species it presumably has the shallowest diving capacity and may therefore be more dependent on crepuscular feeding, when a greater proportion of prey are near the surface. It may also be avoiding diurnal predators. Penguins may be assisted in prey detection by echolocation, using sonar based on cavitation clicks produced by their swimming movement.

Behaviour. Most penguins are highly social, both on land and at sea, and often breed in vast colonies, only defending the small area around the nest. Although all species have complex courtship and mate recognition behaviour, social behaviours are perhaps most developed in the densely colonial pygoscelid and eudyptid penguins. Of the latter, those species that breed in dense vegetation show less intraspecific interaction, presumably because, like *Megadyptes* also, their nests are farther apart. Despite living in burrows, spheniscid penguins, which usually breed in dense colonies, have fairly elaborate visual and vocal displays; *Eudyptula*, in which burrows are usually well dispersed, less so. Emperor Penguins, because of the physiological need to huddle when incubating, lack fixed territories and only defend their immediate living space (when not huddling). Individual recognition, whether of mates or offspring, is based mostly on calls but in burrowing species, and in others where chicks stay close to the breeding site after the brooding period ceases, nest site location is an important, if not a vital preliminary.

Breeding. Emperor Penguins breed in winter. King Penguin chicks overwinter at the breeding colony, but are rarely fed during this period and grow mainly during the previous and subsequent summers. Otherwise Antarctic and most sub-Antarctic and cold temperate penguins breed in spring and summer and their timing is highly synchronized within and between colonies. The Gentoo Penguin is least well synchronized and at Marion Island it lays in winter (June); this may reduce competition for food with the large number of eudyptid penguins there. The more temperate eudyptid species have a longer breeding season and its timing is more variable. In *Spheniscus* (except *S. magellanicus*) there are usually two main peaks of breeding but laying occurs in all months of the year. This is also true of most *Eudyptula* populations and in South Australia some pairs are able to raise broods successfully twice a year. Penguins usually mate with the partners of previous years: in a colony of Yellow-eyed Penguins 61% of pairings lasted 2 to 6 years, 12% 7 to 13 years and the overall divorce rate was 14% per annum; in a study of the Little Blue Penguin one pairing lasted 11 years and the divorce rate was 18% per annum. In a major Adélie Penguin study, however, no pairing lasted 6 years and the divorce rate was over 50%.

Royal Penguins breed first when at least 5 years old; Emperor, King, Gentoo and Adélie Penguins when at least 3 (♀) or 4 (♂) and Little Blue, Yellow-eyed and Jackass Penguins when at least 2 years old.

Only *Aptenodytes* penguins lay a single egg, the remainder normally laying 2 eggs, occasionally one (inexperienced birds where this is known) or 3. In the Yellow-eyed Penguin (and probably generally) age affected fertility so that hatching success in the study colony was 32%, 92% and 77% of eggs incubated by birds of age 2, 6 and 14–19 respectively. In eudyptids the first egg of the clutch is very much smaller than the second; only in Rockhopper and Fiordland Penguins do both eggs hatch and only one chick is ever reared. In other penguins hatching is also staggered and this can promote brood reduction, particularly in warmer water species, but even so 2 chicks are not infrequently reared.

All penguins have the capacity for storing substantial fat reserves (e.g. before the moult fast) but only the Emperor, King, Adélie and eudyptid penguins undertake long fasts in the courtship, incubation and brooding periods. During fasts lasting 110–115 days for male Emperor Penguins and 35 days for Adélie and eudyptid penguins up to 45% of initial body weight may be lost. By contrast Gentoo, Yellow-eyed, Little Blue and spheniscid penguins usually change incubation daily although in some species the female may incubate for more of each day. After the brooding period ceases the frequency with which chicks are fed increases. Intervals between meals are about 3 days for King and Emperor Penguin, about one day for Adélie and most eudyptids but in Gentoo, *Eudyptula* and *Spheniscus* both parents bring food each day. The rate of chick growth probably reflects the size of meals and the frequency with which they are delivered. This is presumably determined by food distribution and availability and it has also been suggested that intra-specific competition for food may affect both breeding success and the age (or level of experience) at which first breeding attempts are made. Reduction of interspecific competition between penguins is thought to be achieved by differences in prey type, foraging range and timing of breeding season. Chicks grow rapidly (though initially rather slowly in the Emperor Penguin), particularly in Antarctic species and the Macaroni Penguin among sub-Antarctic species. After 2 to 3 weeks (6 weeks in *Aptenodytes*) the chicks of species breeding in open areas form large aggregations (Adélie, Gentoo, *Aptenodytes*) or small ones involving a few chicks from adjacent nests (Chinstrap, Jackass, *Eudyptes* spp.).

Moult. In most species, once chicks are independent, the parents fatten quickly for a moult fast of 2–6 weeks depending on species. The daily energy cost of moult is about twice that of incubation. Jackass and Galapágos Penguins show a less well defined moult period; moult occurs at any time between breeding attempts. In other species immature birds usually complete moult before breeding birds start and at least in eudyptid penguins the timing of moult becomes later with age until the first breeding attempt is made.

Populations. Compared with other seabirds, annual survival of adult penguins is relatively low, being at least 69% for Adélie, 86% for Royal, 87% for Yellow-eyed and 86% for Little Blue Penguin, but 95% for Emperor Penguin. Longevity may well be inversely related to breeding success (including juvenile survival) which is high in most Antarctic species except Emperor Penguin, where only 19% of fledglings survive their first year of life. Some penguin populations in the Antarctic Peninsula area have increased substantially in numbers, e.g. Chinstrap Penguin has increased fivefold in 30 years at some established sites, while Adélie Penguin has doubled in the same period. This is attributed to greater availability of krill due to the drastic reduction in stocks of Antarctic krill-eating whales. In contrast Jackass and Humboldt Penguins have decreased markedly, chiefly because of human activities like egg and guano collection and commercial fishing. Yellow-eyed Penguins and some Adélie Penguin populations have declined due to increased human interference. J.P.C.

Aptenodytes. This genus comprises the 2 largest living penguins. The Emperor Penguin stands well over 1 m tall and weighs 20–40 kg; the King Penguin nearly 1 m tall but weights only 10–20 kg. Their plumage is very similar, blue-grey above, white (King) or yellowish (Emperor) below with conspicuous golden or bright yellow auricular patches and orange or violet-blue mandibular plates.

Both species have a circumpolar distribution. The Emperor Penguin has the most southerly distribution of any penguin (all colonies being south of 65°S), and as it breeds in winter, faces some of the most extreme climatic conditions for breeding of any bird. The low mean winter temperature (−10 to −20°C), high winds (mean 40 km h^{-1} but reaching 150–200 km h^{-1} at some colonies) and blown spindrift snow combine to produce an environment where heat loss can be critical. There are about 26 known colonies, mainly on the coasts of Enderby, Wilkes and Victoria Land; all but two are on fast sea-ice and most are backed by an ice-cliff providing shelter from wind. They range in size from Coulman Island with *c.* 25,000 pairs to the Dion Islands with only 500; the world breeding population is estimated at 200,000 pairs.

In contrast King Penguins lay in summer (but take a year to raise a chick) on flat or gently sloping ground at sub-Antarctic islands. The world breeding population is about one million pairs with the largest concentrations at the Indian Ocean sub-Antarctic islands (Prince Edward Islands, Crozet Islands) but they breed as far south as South Georgia and the recently re-colonized Heard Island.

Data on pelagic movements and distribution outside the breeding season are lacking. Emperor Penguins seem rarely to move outside the Antarctic Circle but stray birds (mainly immature) have reached Tierra del Fuego, Falkland Islands, southern New Zealand and many sub-Antarctic islands. King Penguins ringed at Iles Crozet have been retrapped at Macquarie and Marion Islands.

Both species have been recorded as eating squid, fish and crustaceans, but it is probable that squid and fish form the bulk of Emperor Penguin diet in the breeding season and of King Penguins at least in autumn and spring.

Both *Aptenodytes* species raise large chicks which become independent by the Antarctic mid-summer when food resources are at their most abundant. They have tackled this problem in quite different ways; the King Penguin by taking over a year for a successful breeding attempt and the Emperor Penguin by breeding in the cold, dark Antarctic winter. The latter is possible only with a remarkable conjunction of physiological and behavioural adaptations.

An Emperor Penguin's body size and shape combine to provide a relatively low surface to volume ratio (important for reducing heat loss) and in addition its appendages (flipper, bill) are 25% smaller in proportion than in any other penguin. Heat loss is further reduced by extreme proliferation of the vascular counter-current heat-exchange system and excellent insulation is afforded by the very long double-layered, high density feathers which even extend to cover the tibio-tarsi. All these combine to establish a lower ambient critical temperature (below which metabolic rate must be increased to maintain body temperature at a constant level) of −10°C with wind speed of up to 18 km h^{-1}.

Even though the size of the Emperor Penguin permits it to store proportionately large fat reserves, these would be insufficient to cope with the demands of long fasts in prevailing winter conditions. However a 25–50% reduction in individual heat loss is achieved by adults and chicks huddling in large groups (up to 5,000 birds at 10 per m^2) and reducing activity to a minimum. This behavioural adaptation is fundamental in permitting Emperor Penguins to breed during the Antarctic winter. Such social behaviour during breeding is unique among the otherwise highly territorial males of the family and is feasible only because of their ability to move with the egg on their feet and cover it (and the young chick) with the pouch-like fold of abdominal skin. Although King Penguins incubate in a similar fashion, they breed with constant inter-individual distance and also lack such extreme physiological specializations, presumably because temperature and wind chill effects rarely exceed their lower critical temperature of −5°C. Chicks, however, frequently form dense huddles in winter.

In the Emperor Penguin, in addition to sex-specific differences, there is a very clear individual variation in calls which, in a species lacking any fixed nest site or territory, is the basis for mate and parent-offspring recognition. In the King Penguin, which has a relatively fixed incubation site, although sex-specific differences are retained, individual variation of calls is much less marked.

For Emperor Penguins the breeding season commences with courtship and copulation in March-April, following 2 months at sea laying down substantial fat reserves. Females leave after laying in mid May, having lost 25% of body weight in the 6 week fast while ashore. Only males incubate (for 62–64 days) and also feed the chick for a few days (on an oesophageal secretion comprising 60% protein and 28% lipid) if the return of the female is delayed. During their 110–115 day fast males lose up to 45% of their initial body weight. The female broods the chick for 40 days and thereafter both parents rear the chick through the winter, the chicks themselves forming tight huddles. While losses at the egg stage are fairly consistent (4–16%) between years, chick losses are more variable (usually 4–30% but exceptionally up to 90%) and reflect the variation in winter conditions. Chicks depart in December at only 60% of adult body weight, the lowest figure for any penguin, presumably because the adults need the remaining time to moult and return to breeding condition by the end of the summer. Only 19% of fledglings survive their first year of life. However, Emperor Penguins may breed first at 3 years of age (although many do not do so until age 6) and mean annual survival from age 2 is 95%. Life expectancy from fledging is about 20 years.

King Penguins start laying in late November and continue until mid April although there are pronounced peaks at the beginning and towards the end of this period. Eggs hatch in 55 days and incubation duties are shared by the parents in 5-day shifts after an initial 14-day shift by the male. Early breeders raise their chick to 80% of adult weight by June and feed it sporadically (fasts of 2 months or so with a weight loss of about 40%) until September when regular feeding resumes until the chicks depart in November-December. The adults then moult and usually lay again in February-March. This time much smaller chicks overwinter (and many die) and finally fledge in January-February. Parents with this timetable cannot breed again until the following summer. After a breeding failure, however, many (but probably not all) birds postpone moult until the following September-October when it thus immediately precedes the next breeding attempt. This variety of breeding and moulting schedules ensures that in any colony at most times there are adults, eggs and chicks at many stages of moult, incubation and growth. The above account applies principally to South Georgia; at Iles Crozet it appears that most adults when successful breed only biennially. J.P.

Pygoscelis. A genus, of 3 species, with a circumpolar distribution in the Antarctic and sub-Antarctic. The species are *c.* 50–60 cm long and weigh between 4 and 8 kg. The Adélie Penguin breeds at numerous sites on Antarctica's coast and associated islands. Colonies range in size from less than 100 to at least 500,000 pairs and it is perhaps the most abundant of any penguin species. With the Emperor Penguin, it is the most southerly breeding penguin. The Chinstrap Penguin occurs in the northern Antarctic, principally in the region of the Scotia Sea and Antarctic Peninsula north of 65°S. The Gentoo Penguin has the most northerly distribution of the three. It breeds at a few Antarctic sites but mostly on sub-Antarctic islands near the Antarctic Convergence, for instance Crozet, Kerguelen, Marion, Prince Edward, South Georgia and Macquarie Islands. It is particularly abundant in the Falkland Islands.

Knowledge of the pelagic ecology of these species is virtually confined to the summer breeding period. In winter most populations of Adélie and Chinstrap Penguins must move north near to the limit of pack ice; their subsequent dispersion is unknown. The northern populations of the Gentoo, however, are relatively sedentary.

At all seasons the Gentoo Penguin is notably less pelagic than the others and the higher incidence of fish in its diet probably reflects this. Although some Adélie Penguin populations take many larval fish, euphausiids (particularly *Euphausia crystallorophias* around the periphery of the Antarctic continent and *E. superba* elsewhere) seem the most important prey for all 3 species and differences in foraging range and possibily size of prey eaten seem significant aspects of interspecific differences in feeding ecology.

More is known of the social behaviour of Adélie Penguins but most of their displays have somewhat similar counterparts in the other 2 species. Generally Chinstraps seem more aggressive and Gentoos more timid. In the Adélie Penguin breeding displays are most prevalent among young birds or older non-breeders; after egg laying breeders display rather little. The displays are affected by two important factors. First, these penguins are highly gregarious at sea and when breeding on land they maintain an almost inviolate individual distance and vigorously defend the space within pecking range of their nest. Second, partners associate for relatively few days in a breeding season shortened by the constraints of rigorous climate and high latitudes. There is thus a particular need for straightforward yet accurate communication. Within these constraints the repertoire of basic messages common to all higher vertebrates is present, with the possible exception of play. Individual birds vary greatly in aggression and this may relate partly to age. Some of the younger non-breeders who are physiologically mature enough to breed fail to do so until their social behaviour matures as well.

The breeding biology and behaviour of Adélie Penguins has been studied intensively. That of the other 2 pygoscelids is less well known but is probably rather similar, allowing for their more northern distributions and less intensive environmental constraints. Nesting is limited to snow- and ice-free areas and, because these are relatively rare in the Antarctic, there is much overlap in the type of terrain that the 3 species choose. Adélies seem to be the most selective, tending to build nests on exposed ridge tops. This may reflect the need in higher latitudes to avoid areas where drifting snow would cover nests or where melt water could inundate them. Chinstraps often prefer slopes, whereas Gentoos more often choose flatter areas closer to the beach, particularly at sub-Antarctic islands where drifting snow may be less of a problem.

Adélie Penguins arrive at their colonies a few weeks earlier in the spring than their relatives: September and early October in the Scotia Sea region, but late October in the Ross Sea which is much farther south. Males on average arrive a few days earlier than females. Unusually extensive pack-ice delays the arrival even of Adélies, since they walk over the ice much less rapidly than they swim.

Adélie Penguins fast throughout the territory establishment, courtship and egg-laying periods, thus reducing the number of times they have to walk between colonies and accessible feeding areas. Males remain for an additional 2 weeks to incubate eggs while females replenish their fat reserves by feeding at sea. Females incubate for about 10 days, then males for 5 or more days, and, at about the time the female next returns (about 35 days after the first egg was laid) the eggs hatch. With Chinstrap Penguins, which begin to nest after the pack-ice has become more broken up and has diminished in extent, the periods of fasting are shorter, and thus nest-reliefs more frequent, Gentoo Penguins have a daily change-over. The normal clutch for all 3 species consists of 2 eggs. A third egg will be laid only if the first is lost before the second is laid. Full incubation does not begin with the first egg; thus, although 2–4 days occur between laying of the eggs, the chicks hatch about 1–2 days apart.

If the pack-ice is more persistent than usual the returns of feeding Adélie Penguins are delayed, resulting in increased numbers of nest desertions as the fat reserves of incubating birds run low. This happens most often when the male is due for relief by the female at the end of his 5-week fast. The accelerating rate by which the ice disappears means that, even on the Antarctic Continent by early summer and the time eggs hatch, feeding trips take only 3 to 4 days and a week later are reduced to one to 2 days. The more frequent nest reliefs also correspond to the period of most rapid growth in the chicks. For the first 3 or 4 weeks one parent continually broods the chicks, but chick requirements become too great for one parent to sustain and both must forage simultaneously. Chicks then group together in crèches as a means to reduce predation from skuas *Catharacta* spp. At 7–8 weeks of age the chicks leave the colony of their own accord and go to sea. In most seasons each breeding pair averages less than one chick fledged. The fledging period is only slightly longer in the Chinstrap Penguin but is at least 12 weeks in the Gentoo Penguin whose actively swimming chicks are often still fed by their parents.

Age, and to some extent breeding experience, affect the breeding biology of Adélie Penguins. Very few one-year-olds visit the colony. Many 2-year-olds do so for a few days during the period of chick hatching, but most birds make their first visit as 3 and 4-year-olds and a few not until 5 years. With increasing age, up to about 7 including both breeders and non-breeders, birds arrive earlier in the season, make more visits and stay longer. Some females can first breed at 3 years of age, males at 4, but most females and males first breed at 4–5 and 5–6 years respectively. Most females have bred at least once by 5, but males have not all bred until 8. A year of previous breeding experience increases a bird's chances of breeding successfully. Birds that delay their first breeding to later years are often inept, breeding unsuccessfully or failing to breed more often than not. Most breeders are 5–10 years of age. Breeding is hazardous and only a few birds live as long as 18 years; the oldest birds even so tend to be those that first bred at a late age and to be non-breeders in several seasons thereafter. The high mortality among breeders (in which leopard seal *Hydrurga leptonyx* predation may be important) is apparently offset by high breeding success due to reliable and abundant food sources. D.G.A.

Eudyptes. A genus of medium sized (weight 2.6–6 kg), heavy-billed penguins differing from other members of the family in being highly sexually dimorphic, in having prominent yellow or orange crests on their heads, and in laying clutches of 2 eggs of very dissimilar size from which only a single chick is reared. There are 5 species (6 if the Royal Penguin *E. schlegeli* is considered a full species rather than a sub-species of the Macaroni *E. chrysolophus*) falling into 2 distinct groups: the large Royal and Macaroni Penguins (sometimes classified in the genus *Catarrhactes*) which have loose dull orange crests arising from the centre of the forehead and 14 rectrices, and the rest which are smaller, with more compact and lustrous yellow crests arising from superciliary stripes on either side of the head, and 16 rectrices.

All 5 species occur in the Australasian region and 3 are confined to New Zealand seas. The other 2 species, Rockhopper and Macaroni/Royal have a circumpolar breeding distribution at sub-Antarctic islands although the Rockhopper Penguin occurs further north (to Tristan da Cunha) and the Macaroni further south (to the South Shetland Islands).

Most species nest colonially in the open either on the coast or inland up to about 300 m. The exception is the Fiordland Penguin, which nests in dense, wet forest north of the Subtropical Convergence on the west coast of the South Island of New Zealand. In this forest environment it experiences considerably less extreme temperature and exposure compared with nesting in the open.

The more widespread species are very numerous and one world estimate for the Rockhopper Penguin was 4¾ million pairs. Some 2 million Royal Penguins nest at Macquarie Island and about 5 million pairs of Macaroni Penguins breed at South Georgia. Least abundant is the Snares Crested Penguin, estimated to have not more than about 50,000 birds at its sole breeding place on the Snares Island, south of New Zealand.

After moulting the non-breeding season is spent at sea. Some birds wander far, e.g. an Erect-crested Penguin from New Zealand to the Falkland Islands and a Rockhopper of the northern race to the Chatham Islands, New Zealand.

All species probably eat krill and *Euphausia superba* forms 80% by weight of the diet of Macaroni Penguins at South Georgia. It is possible that the difference in bill size of males and females may result in prey of different sizes being taken. Fish and squid make up the remainder of the diet and are of greater importance to the Rockhopper Penguin. In most species the chick is fed daily, on average, indicating that that the parents are able to forage extensively in continental shelf and slope waters.

All species are highly colonial on land and social at sea, only the Fiordland Penguin nesting in a rather dispersed pattern, but this is probably a consequence of the use of a forest habitat and there is nonetheless much vocal interaction among nearby nesting pairs. Crested penguins show a marked philopatry: young birds returning as yearlings usually to that part of the colony where they were born and breeding birds return to the same nest and partner during successive years, although some divorce does occur. A complex system of displays and vocalizations is used, including nearly 20 distinct displays.

Breeding takes place in the southern summer except for the Fiordland Penguin which lays in late winter. Maturity is delayed and each successive age group comes ashore earlier and stays longer. Few Royal Penguins less than 6 years old attempt to breed, success appearing to depend upon the parents' age and weight on arrival, and few birds less than 10 years old regularly rear young successfully. The breeding cycles all involve long fasts at the nests before laying (male arriving before female), followed by 10–15 day incubation stints when the on-duty bird again fasts. In all but the Fiordland Penguin the female incubates first, having been ashore for less time than the male. Hatching occurs after 31–37 days and with all the species the male then remains to guard the chick, not feeding it, but fasting for 2–3 weeks. The female alone brings food to the chick during this guard stage. The chick then enters a small crèche and the male leaves for the sea. Thereafter the chick is fed by both sexes, but still mainly by the female, for a total of about 60–75 days depending on species. The parents then depart to sea for between 14 days (Macaroni) and 70 days (Snares Crested), laying down fat reserves nearly equivalent to their original body weight, before a moult fast at the breeding colony lasting *c.* 25 days. All birds then go to sea, some having reached their minimum weight during the season.

Unique to this genus is the laying of first a small and then a large egg. For example, the second eggs of the Rockhopper, Snares Crested and Macaroni Penguins are 46%, 29% and 71% larger respectively than the first eggs of those species. Both eggs are viable but only one chick is reared. In contrast, the difference in egg size is only 17% with the Fiordland Penguin and in this species twins are often reared for a few days. Thereafter, as with the other species, the smaller chick dies; usually, but not always, the chick hatched from the smaller egg. Such a system may exist to cope with the high egg loss consequent on the considerable amount of fighting between neighbours, which in turn results from sexual selection favouring aggressive males. That the eggs are of different sizes ensures that if both hatch—as quite often occurs in the less concentrated colonies of the Fiordland Penguin (where fighting is correspondingly reduced) only one chick survives for long. If the eggs were of similar sizes then many similar sized twins might survive to the guard stage only for both to die when their food needs exceeded their parents' abilities to supply it. J.W.

Spheniscus. A genus of 4 medium sized (*c.* 3 kg weight) species of essentially low latitudes: the Galapágos Penguin breeding on two islands of this archipelago at the Equator, the Humboldt Penguin in Peru and Chile from 6°S to 34°S, the Magellanic Penguin breeding north to 32°30′S in western and 48°S in eastern South America and the Jackass Penguin breeding from southern Africa (35°S) north to 16°30′S on the west coast and 26°S on the east coast. They are basically sedentary species but southern populations of the Magellanic Penguin migrate northwards after breeding. This account is taken mainly from recent studies of the Jackass Penguin and the Galapágos Penguin.

All *Spheniscus* species breed in burrows dug with the feet in sand or under rocks and bushes but densely packed surface colonies of Jackass Penguins also occur. They are inshore feeders, restricted to continental shelf areas and their diet is mainly fish, often anchovy *Engraulis* sp. and pilchards *Sardinops* sp., though squid are also taken, at least by Jackass Penguins. At sea, Jackass Penguins forage in small groups and dive synchronously, often after a head-bobbing signal.

Diving depths or actual foraging techniques are unknown but deep dives are unlikely since they feed mainly on surface-shoaling fish. Two species, the Jackass and the Humboldt, occur in high productive upwelling systems that support large fishing industries. Populations of these 2 species have decreased alarmingly, initially due to egg removal and guano collection, subsequently due to competition for food; the fishing industries of the west coasts of South America and South Africa both 'prey' on the same species of fish as do the penguins. The survival of these 2 species is inextricably linked to the presence of the anchovy and pilchard and therefore to a compromise between exploitation and conservation.

The breeding displays of the Jackass Penguin resemble those of other non-*Aptenodytes* penguins. Adaptation for hole-nesting appears to have resulted in particularly loud raucous vocalizations. *Spheniscus* penguins engage in 'ecstatic displays' and 'mutual ecstatic displays' as do most penguin species. 'Beak-slapping', an aggressive display, occurs in Jackass and Galapágos Penguins and may be restricted to the genus; during 'beak-slapping' 2 birds (often mates) face each other and shake their heads rapidly so that the beaks slap together.

The Magellanic Penguin, with the most southerly distribution, has the most restricted breeding season and moult follows chick fledging. By contrast Jackass Penguins may breed in all months but 2 peaks a year are usually noticeable, the first following the annual summer moult. Galapágos Penguins may breed and moult twice a year (but sometimes not at all); again breeding follows moulting, an unusual pattern in birds.

Clutch size is one or (usually) 2 and 2 young may be reared. There is little difference in size between first and second laid eggs. Asynchronous laying and hatching leads to brood reduction by starvation of the younger sibling if the food supply is inadequate.

Being inshore feeders, *Spheniscus* penguins have no breeding fast; changeover at the nest is usually daily; prolonged incubation bouts of several days normally result in desertion. Jackass Penguin chicks may be fed several times a day, typically in the late afternoon or evening. When older, they are often left alone during the day and may form small crèches (usually not more than 5 chicks), and are then fed daily by both parents.

The chick-rearing period in the Jackass Penguin varies by as much as 40 days. The younger chick often stays at the nest for as long as 2 weeks after its elder sibling has left. During this period it is able to 'catch up' and even exceed its sibling's weight. Breeding success in Jackass Penguins varies with nest habitat and has been reduced historically by removal of the GUANO 'cap' in which birds once burrowed; surface nests are less successful, due mainly to enhanced predation. A similar trend has apparently occurred in the Humboldt Penguin. The Galapágos and probably the Humboldt Penguin's breeding season and success is related to the occurrence of warm water influxes (El Niño) and a decrease in upwelling. Similar changes in the degree of upwelling may affect the Jackass Penguin in parts of its range.

Jackass Penguins fledge at approximately ⅔ the weight of adults and undergo a juvenile dispersal to warmer waters, returning to moult into adult plumage at about one year of age—though this varies by many months. Breeding does not take place in the first year of adulthood, and not always in the second.

See photos COLONIALITY; CRÈCHE; EGG; MOULT; PARENTAL CARE.

J.C.

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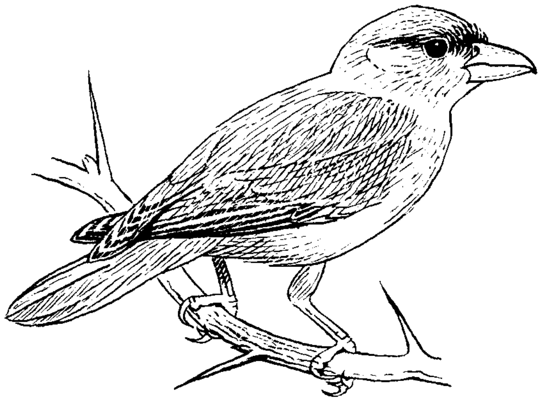
PENIS: male copulatory organ, present in a few kinds of birds (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

PENNA: alternatively 'pennaceous feather', one in which the barbs form a coherent vane (see FEATHER; and compare PLUMA).

PEPPER-SHRIKE: substantive name of the 2 species of the subfamily Cyclarhinae of the Vireonidae (Passeriformes, suborder Oscines); in the plural, general term for the subfamily. This is a Neotropical group usually placed among (as here) or close to the vireos. Pepper-shrikes are heavily built birds, 15–18 cm long, with large heads and powerful bills strongly hooked at the tip. The wings are short and the flight is weak; the plumage is loose in texture. The better-known species, the Rufous-browed Pepper-shrike *Cyclarhis gujanensis*, has a wide range from southern Mexico south to Uruguay; the other, *C. nigrirostris*, is confined to Colombia and Ecuador.

The Rufous-browed Pepper-shrike is greenish above, with a red-brown steak through the eye, grey crown, and yellow breast. It is a bird of open woodland, cultivation, and second growth; it lives in pairs and is sedentary. The food consists mainly of insects and other invertebrates, which the birds search for among the foliage of the middle levels and tops of trees. Pepper-shrikes hold down large prey with the foot and pull it to pieces with the bill, which is also well adapted for tearing open cocoons adhering to leaves and bark. The commonest call is a melodious but monotonous phrase of set pattern, like that of an Old World oriole (Oriolidae); this is uttered repeatedly from leafy cover where the bird itself is often difficult to see. The alarm calls are loud and extremely harsh.



Rufous-browed Pepper-shrike *Cyclarhis gujanensis*. (*P.J.K.B.*).

The nest is a semi-pendent hammock slung, like that of a vireo, from a fork of a tree or tall bush. The eggs, 2 or 3 in number, are pale cream or pinkish, spotted and blotched with brown. The part played by male and female in incubation is uncertain, but both sexes feed the young.

D.W.S.(1)

PERCHING: loosely, the act of standing (sometimes sitting) on some more or less elevated object, especially one providing only exiguous space; more particularly, doing this while gripping the perch with the feet. The Passeriformes are sometimes referred to as the 'perching birds' because their toes, and the flexor tendons actuating these, are notably adapted to gripping a small branch or similar object, e.g. taut wire (see LEG). Many other birds, however, are well able to perch, although lacking the particular specialization of foot structure. Others again can only stand on an object flatfooted, as they do on the ground, and have therefore limited powers of perching; some, of course, make no use of any kind of narrow perch, if indeed they stand in elevated positions at all. A few birds, e.g. nightjars, commonly perch along the axis of a branch instead of transversely. Distinct from perching is clinging to the roughnesses of a vertical or overhanging surface; to this action some birds are particularly adapted, e.g. swifts—which are unable to perch in the ordinary sense—woodpeckers and nuthatches among others. The hanging parrots or 'bat parrots' *Loriculus* spp. have the habit of hanging head downwards, by their feet, from branches.

See photo overleaf.

PERCHING BIRDS: see PASSERIFORMES.

PERDIZ: name used in Latin America for *Rynchotus* spp. (see TINAMOU).

PEREGRINE: *Falco peregrinus* (see FALCON).

PERICARDIUM: see HEART.

PERIODICALS, ORNITHOLOGICAL: see under ORNITHOLOGY.

PERIODICITY: see PHOTOPERIODISM; RHYTHMS AND TIME MEASUREMENT.

PERIOSTEUM: see SKELETON, POST-CRANIAL.

PERIOTIC: a paired bone of the SKULL.

PERITONEUM: membranous lining of the abdominal cavity and reflected over the outer surfaces of organs lying therein.

PERNINAE: see HAWK.

PERVIOUS: as applied to nostrils, see NARIS.

PESSULUS: see SYRINX.

Sandwich Terns *Sterna sandvicensis* perching on log. (*Photo: J.B. & S. Bottomley*). See PERCHING on previous page.

PESTICIDE: a chemical agent used by man to control living organisms which are inimical or believed to be inimical to his interests. The term covers herbicides, fungicides, insecticides, rodenticides, chemosterilants and growth retardants. The term is sometimes used in a more restricted sense as a synonym for insecticide. Most pesticides are synthetic organic substances, but some are inorganic or naturally occurring organic ones. See TOXIC CHEMICALS.

PESTS, BIRDS AS: wherever man has established settlements he has found that some of his resources are shared by birds. With most bird species this is acceptable but a few conflict with man's interests. The result of this conflict is some kind of damage, where the term 'damage' infers a direct loss, ultimately in terms of money, or causes expenditure to counteract the problem. In some instances, however, this definition cannot be strictly applied. A farmer who sees his fields apparently devastated is not prepared to wait until harvest time to see whether his yield is in fact reduced. In other words, if a farmer thinks that birds are causing damage, he will take steps to prevent it whether or not a real loss is incurred. Even where damage does occur, it is often very difficult to estimate the financial losses. The equation is rendered even more difficult by the capacity of some of the pest species to confer potential benefit by their consumption of insect pests. Estimates of damage that are available for some species in some situations indicate that losses can be considerable (Jackson and Jackson 1977) and in developing countries severe damage may result in loss of human life. Damage to crops is usually local, however, and although individual farmers can lose a high proportion of their yields, expressed in national terms birds generally consume only a small proportion of total production.

Kinds of damage. Bird problems fall in several areas: agriculture (including horticulture and fisheries), forestry, urban and aviation are those which attract most attention.

Damage to agricultural crops occurs mainly at sowing/germination and at ripening, the seeds being the target food; but the foliage is also grazed by some birds, notably pigeons and sometimes by larks, pheasants and geese. The seeds of cultivated crops such as maize, barley, wheat, sorghum, millet and rice are eaten by a wide variety of birds, especially certain sparrows, weavers, starlings, parakeets and New World blackbirds (Icteridae). Damage to sown and germinating seeds is, owing to the compensatory capabilities of the plants, generally less serious than damage to ripening crops. Following recent changes in animal husbandry, where cereal grains are fed to cattle in the open, post-harvest losses due to starlings and New World blackbirds have become serious in some countries. These birds, together with some crows, can also be responsible for losses of pelleted animal foods where these are presented in the open.

Many fruiting plants have evolved dispersal mechanisms involving birds and mammals, and cultivated fruits inevitably suffer the attentions of starlings, thrushes, finches, parrots and many others. The decline of the cherry industry in some areas of Europe is blamed partly on predation by Starlings *Sturnus vulgaris*. Olives in North Africa and grapes in Europe, North America, parts of Africa and elsewhere also suffer severe bird damage, and a wide variety of other fruits is attacked. Fruit blossoms may also be eaten (though some species that attack flowers may be important pollinators e.g. sunbirds Nectariniidae), and Bullfinches *Pyrrhula pyrrhula* can cause extensive damage by eating the buds of certain cultivars of apples, pears, plums and blackcurrants.

Claims that seabirds can compete with commercial marine fisheries seem to be unfounded, declines being attributed largely to the industry itself. At fish farms, bird predation is of great concern to the owner since financial losses can be high. Herons, gulls, Ospreys *Pandion haliaetus* and others take fish while Mute Swans *Cygnus olor* have been blamed for taking fish eggs.

Damage in forestry is due mainly to large concentrations of birds such as European Starlings and American Red-winged Blackbirds *Agelaius phoeniceus* roosting in young plantations. The weight of birds can break off branches, possibly leading to subsequent mis-shapen growth of the trees, and trees may even be killed by the large deposits of guano.

While birds are generally welcome around human habitations, some cultures regard them, or at least some species, as harbingers of ill omen. In some places the breeding and roosting of birds in or on buildings can necessitate expensive cleaning or repair or can cause public health problems. The guano stains beneath House Martin *Delichon urbica* nests constitute a relatively minor problem but the nesting of some species can cause structural damage. The construction of bulky nests in roof spaces by various starlings and by Jackdaws *Corvus monedula* can lead to subsequent dangers of damp, while in aircraft hangars nest material and faecal droppings can result in expensive and dangerous problems when they fall into the air intakes of jet engines; occasionally, nests are even built inside aircraft. Woodpeckers have been recorded drilling holes in wooden roofs, telegraph poles and even, in Israel, irrigation pipes. Where thatching is a common roofing material, nest-building in the thatch by birds such as sparrows (*Passer*) and Indian Mynahs *Acridotheres tristis* can destroy insulative and water-proofing properties of the roof. Recent inland foraging of various gulls is being accompanied by their breeding on buildings, leading to problems of fouling and unacceptable noise, especially in early morning. Roosting by gulls on buildings has also resulted in damage to roof materials, especially where expanded polystyrene insulation is used. Fouling by roosting Starlings and Feral Pigeons *Columba livia* in cities results in degradation of masonry, dangerously slippery roads and pavements, and possible dangers of disease. In North

America, the main problem associated with roosts of icterids and starlings near conurbations lies in the guano providing a growth medium for *Histoplasma capsulatum*, the causative agent of endemic histoplasmosis in humans. Some pigeon populations have a high incidence of avian tuberculosis *Mycobacterium avium* and the roosting of gulls on reservoirs increases their potential to transmit salmonellae to man. Psittacosis (a form of ornithosis) can be contracted as a result of close contact with birds, especially parrots and their allies. Wild birds are sometimes claimed to act as vectors of diseases of domestic stock e.g. foot and mouth disease and transmissible gastroenteritis of pigs, but conclusive evidence of the involvement of birds is often lacking.

Collisions between birds and aircraft—'bird strikes'—range from relatively minor to catastrophic. Slight structural damage can be expensive to repair but the ingestion of birds by jet engines, leading to engine failure, can result in loss of the aeroplane, sometimes with loss of life. Most bird strikes occur near airfields when aircraft fly low, in the airspace most frequently occupied by birds; it is at take-off and landing that sudden loss of power can be most serious. The species most frequently involved are those, like certain gulls, corvids, plovers (Charadriidae) and starlings, that inhabit open grassy areas.

Damage prevention. The two basic approaches are to reduce the population of bird pests by killing them or to make the resource being damaged, or from which damage occurs, less attractive to the birds.

Attempts to reduce populations form the basic philosophy of damage reduction of many farmers. Most bird pests are, however, extremely numerous and successful. They have a high annual mortality and population turnover and their 'natural' mortality must be exceeded to achieve effective population reduction. Traditional methods of killing, e.g. by shooting or trapping, fail to achieve the desired level of mortality and even agents of mass destruction using poisons, flame-throwers, explosives (see QUELEA CONTROL; Tahon 1980), stupefying chemicals or surfactants (feather wetting agents—Lefebvre and Seubert 1970) have not reduced general population levels. Mass destruction can provide sufficient reduction to permit alleviation of local damage in some instances (e.g. Quelea and European Starling). In the United States, urban roosting icterids and starlings are killed rather than dispersed to prevent the establishment of new roosts whose guano deposits might act as foci of infection of histoplasmosis. In the western world the growing protectionist lobby is forcing a more critical approach to mass killing of birds and to the techniques that may be employed, and damage prevention measures that do not involve killing will inevitably play a greater role in future.

One approach to damage is to let it continue and offer compensation to the farmer. This is done in Canada where the damaging birds are wildfowl, themselves a valuable sporting resource (Boyd 1980). There are obvious difficulties in deciding the level of compensation and who should meet the cost. Another approach, involving similar financial problems, is to provide alternative attractive food for the bird pests, on the farm or in refuges (Owen 1980).

More commonly used approaches involve rendering the place where damage occurs less attractive. This can be done in several ways but most techniques rely on the presence of an alternative resource to which the birds may be driven. This is especially true of attempts to drive birds away from vulnerable areas (see SCARING and REPELLENTS, CHEMICAL) rather than of physical modifications to the crop or habitat. The ultimate form of physical modification is to exclude birds totally from a vulnerable resource. Cages to exclude birds are commonly used over fruit in domestic gardens but this form of protection is less frequently adopted in commercial horticulture. Disposable plastic netting is now draped over large areas of vineyards in Europe, while more permanent forms of netting are sometimes used over cherry orchards in Britain and New Zealand: the development of dwarf forms of cherry tree will make this form of bird protection easier in the future. A similar approach has been applied where cattle are fed indoors: a mixture of plastic and wire netting and strips of heavy duty PVC is used to cover entrances to buildings through which birds might otherwise have access (Feare and Swannack 1978).

Less complete protection can be afforded by other forms of habitat modification. Good and Johnson (1976) were able to manipulate the positions occupied by Brown-headed Cowbirds *Molothrus ater* in their roosts by thinning the roosting trees, and Brough and Bridgman (1980) showed that the bird populations of airfields could be reduced by allowing the grass to grow tall. A degree of crop protection may also be achieved by growing cultivars that are less susceptible to attack by birds in areas where damage is anticipated. For example, Bullfinches eat certain cultivars of fruit buds in preference to others and some cereal crops have long-awned cultivars that possess some resistance to bird attack (see QUELEA CONTROL). The mechanism of the Bullfinch's selection is not known but, as with scaring devices and chemical repellents, the efficiency of these 'bird resistant' forms is likely to diminish when acceptable alternative foods are absent. C.J.F.

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PETREL: whole or part of the substantive name of many species in 3 of the 4 families of the order Procellariiformes (Tubinares); in the plural a general term together with 'tubenoses' for the order. It comprises the families Diomedeidae (albatrosses), Procellariidae (fulmars and shearwaters), Hydrobatidae (storm-petrels) and Pelecanoididae (diving-petrels); in the past some authors have treated the Hydrobatidae as a subfamily of the Procellariidae, but they differ in their serum proteins among other characters. The order forms a group of totally marine species which share a number of distinctive characteristics.

Characteristics. The Procellariiformes are distinguished by deeply-grooved, markedly hooked bills. Their long tubular nostrils are associated with a marked development of the olfactory part of the brain. They all have a distinctive musky smell, and it appears that the whole order is adapted to locate either their feeding-area, food, each other or their breeding-places by smell. Most or all species collect and store in their stomachs large quantities of oil from the energy-rich food-stores laid down by marine organisms. This oil is used as food for their young, and is also spat out as a defence against predators. They are very helpless on land, most species being clumsy and walking only with difficulty. The larger ones bite viciously.

The tubenoses appear to be a very ancient group, perhaps of southern origin, although several modern genera are already present in northern deposits dating at least as far back as the Miocene. They appear to be most closely related to another southern order, the penguins (Sphenisciformes), the petrels having developed as aerial seabirds while the penguins developed as aquatic ones. The two between them show the most advanced adaptation for a marine environment now found among birds. There are some 23 genera and 80 to 100 species distributed throughout the oceans; one family, the Pelecanoididae, and about half the genera and species are still restricted to the Southern Hemisphere with progressively fewer species in the North Pacific, North Atlantic, Indian Ocean and Mediterranean.

Tubenoses all have very similar life histories adapted to the relatively stable, secure, uniform marine environment with its exposure to the weather. They have a long period of immaturity, a long breeding cycle and low reproductive rate adapted for slow formation of the egg and growth of the embryo and chick while the parents travel widely in search of food. They have a long expectation of life in an environment relatively free from predators. They show more variation in other characters adapted for the exploitation of different aspects of the marine environment, notably either from the air or by diving under water, and for the avoidance of interspecific reactions, including size, structure, markings, patterns of distribution and migrations, and timing of breeding seasons and moult.

The albatrosses (70–140 cm in length) are among the largest and the storm-petrels (12–25 cm in length) the smallest seabirds. Within several of the larger groups closely related species of different sizes, habits and appearance are found in the same area. In some cases, such as the albatrosses, prions *Pachyptila* and gadfly petrels *Pterodroma* and *Bulweria*, they are all very similar in structure; in others, such as the fulmars, shearwaters and storm-petrels they show a marked variation in structure adapted for different types of flight or methods of feeding. Many species show a simple counter-shaded colour pattern, dark above and light below, sometimes with contrasting markings on the head, wing-coverts, tail-coverts or flight-feathers; but pale, mottled, or uniformly dark variations are common even among closely related forms. Many species are markedly polymorphic and most show traces of polymorphism. The species nesting in high latitudes tend to be white all over, or grey or pale brown above and white below, with yellow, pink, green or blue and black bare parts; those breeding in warmer climates tend to be brown or black above with less or no white below and red and black or entirely black bare parts. Some groups of closely related species or races show great geographical variation in conformity with this trend.

The peripheral markings often provide interspecific recognition characters, including the brightly coloured bills and complex wing-markings of the larger species which display by day, and the white faces of many gadfly-petrels and some shearwaters, and the white rumps of many storm-petrels, which display by night. Closely related species which occur at the same breeding places often show contrasting markings or occur in different colour phases, and races of the same species may show differences in appearance which can be related to the occurrence of species with which they might come into conflict. In general, representative species tend to be smaller, but races of species larger, in lower latitudes, but there is much variation, which can often also be related to the local competitive situation. Some well-defined larger superspecies may have closely related smaller 'shadow species' breeding in the same area at another season, as in the case of the Manx and Little Shearwater *Puffinus puffinus* and *P. assimilis* and the Hawaiian and Bonin Petrels *Pterodroma phaeopygia* and *P. hypoleuca* and their allies.

Marked variation in appearance with age and sex is only found in the largest species, the albatrosses and giant petrels, in which the young birds tend to be dark while male Wandering Albatrosses *Diomedea exulans* become whiter than the females. Young birds may also show more marked pale feather-edges above in some other species, including the small Hydrobatidae, and at first have soft, undeveloped bills. Their appearance contrasts markedly with that of the senile individuals which are not uncommon in these long-lived species, with more rugged bills, scaly legs, worn or missing claws, and dishevelled plumage. Males tend to be larger than females in most groups, but may be smaller in the Hydrobatidae; marked variation in the amount of sexual dimorphism may occur even among races of the same species. Dwarf individuals sometimes occur, possibly birds which were fed inadequately as chicks; one such runt examined had aspergillosis.

Habitat. All species are totally marine, feeding alone or in groups dispersed over the open ocean according to the distribution of their food, more birds and larger flocks occurring in the areas of upwelling and marine turbulence associated with plankton production along the lee shores of the continents and around the convergences between water masses at sea.

Distribution and movements. Most species appear to be more or less closely restricted to distinct circumpolar zones of surface water at sea. Some are comparatively sedentary or disperse throughout the habitat outside the breeding season, and others perform more or less complex migrations between good feeding areas in different zones in the same or opposite hemispheres. Some populations appear to perform circular movements, either around the world in the circumpolar belts of winds in the higher latitudes of the Southern Hemisphere, or around the anticyclones stationary in the middle latitudes of other oceans, so that they are assisted by following winds throughout their migrations. These travellers may often be largely young birds, while the adults make more direct movements. The movements of closely related species often appear to have a complementary pattern, so that their distribution forms a mozaic, as for example in the large shearwaters and gadfly petrels.

In general, the species occurring in high latitudes of either hemisphere usually appear either to be sedentary or to move into lower latitudes in the winter. The species occurring in middle latitudes may either be sedentary, or move into the tropics or the comparable latitudes of the opposite hemisphere in the winter; and the tropics are occupied either by residents, or by wintering populations of birds breeding in the higher latitudes of both hemispheres and which replace each other at different seasons. Most species breed in the highest latitudes of their range in the local summer, but some in the lowest latitudes in the winter, possibly either because there are no suitable breeding places in higher latitudes, or because there are too many competitors there, or because they originated in the other hemisphere. Where a number of similar species feed or breed in the same area they are thus often found to avoid competition for food or conflicts at the nest-sites by occurring at different seasons.

Populations. The welfare of many species has been affected in recent centuries by human activity. Some have been reduced by past exploitation for food, feathers, or fish bait, but few are known to be killed directly by man now except where their chicks are harvested on a limited scale in Australasia and at Tristan da Cunha, and where they are lost accidentally in fish-nets in northern seas. Many populations have also been seriously reduced by the loss of habitat and predation due to imported mammals such as rats, cats, rabbits, goats, hogs, and mongooses at island breeding sites. A number of species including the Short-tailed Albatross *Diomedea albatrus*, 2 shearwaters, and 5 gadfly petrels were 'lost' for long periods of years and found to be reduced to small vulnerable populations when they were rediscovered. So far only one species is definitely thought to have been exterminated, the Guadelupe Storm-petrel *Oceanodroma macrodactyla*, which was lost in the early decades of the 20th century from an island off Lower California invaded by cats. On the other hand, many species including albatrosses, large shearwaters, and the Northern Fulmar *Fulmarus glacialis*, which is spreading all round the temperate North Atlantic, have profited greatly by feeding on the offal discarded by fishing boats.

Food. The natural food of tubenoses consists of the larger zooplankton, cephalopods, fish and sometimes other birds. Many species now follow ships for refuse or food turned up in the wake, and some avoid them. The different groups specialize in catching different foods under different conditions at different distances from the shore, so there is a considerable series of representative forms exploiting different zones of surface water in different oceans.

Behaviour. All species normally keep well away from land when not engaged in breeding activities, but may come inshore when the visibility deteriorates and sometimes appear inland in large 'wrecks' after gales. Usually there appears to be some underlying factor such as the failure of the food supply or disease, since they can ride out most bad weather.

Birds normally come ashore only to breed, though the more sedentary species may visit the breeding stations at intervals for much of the year.

Adults start to re-establish their territories and renovate their nest sites weeks or months before laying. They then usually depart again for a 'honeymoon' lasting days or weeks during which time they appear to feed separately before the female returns to lay and the male to take the first spell of incubation.

Voice. There are complex vocal displays at the breeding sites, the larger species also rattling their bills, behaviour carried out both in the air overhead and at the nest. Repertoires include a variety of wailing, moaning, screaming, cackling and squalling noises, often with a weird effect at night so that the birds have been mistaken for evil spirits. At sea they are usually shy, quiet and undemonstrative except when fighting over food.

Breeding. Nesting is usually social, sometimes in vast, dense colonies running into hundreds of thousands of pairs, though others are more widely scattered. Most nest on oceanic and offshore islands, but some species may use mainland cliffs and headlands, mountain tops and deserts, and even buildings, if they are undisturbed. The smaller species usually nest in a chamber at the end of a long burrow which they dig for themselves, but sometimes in holes among rocks or concealed in vegetation, and usually come ashore by night, apparently to avoid aerial predators which appear to be their worst natural enemies. The larger species visit more open nests by day.

Large nests are built on the ground by the southern albatrosses and poorer ones by the giant petrels, possibly because they are normally compelled to nest in waterlogged situations. Other species may collect any material which is within reach around the nest. They normally lay one comparatively large white egg with a coarse shell and sometimes fine reddish spots, but never well developed markings. The female has a distended cloaca for weeks afterwards (the only indication of her sex for many species). Two eggs have been recorded, probably often the work of 2 females or replacement after an egg is lost, but this appears to be very rare. The incubation period is long, nearly 6 weeks in the smallest storm-petrels, 2 months or more in the larger species, and the chick is hatched blind, but covered in long, thick down. While incubating the egg and brooding the chick, the parents relieve each other at intervals of days. The chick is soon left alone and only visited to be fed at equally long intervals. Both parents feed the chick by regurgitation with a mixture of half digested food and oil which is derived from it, and if well fed the chick soon becomes very fat. The frequency of feeding is liable to vary greatly with the weather and possibly the experience of the parents, and sometimes individual chicks or even whole colonies may starve. The successful chicks eventually become much heavier than their parents, though the weight falls again as the feathers grow, and at fledging they usually weigh much the same as the adults. It has been suggested that the parents eventually abandon the chick before it fledges, but in some species at least it may be fed irregularly until it leaves, and some parents may even continue to return to the nest afterwards. Some weakly and backward young, possibly the offspring of dead or incompetent (immature or senile) birds, may certainly be abandoned in the nest, especially in migratory species, but may do well if they are then given supplementary feeds.

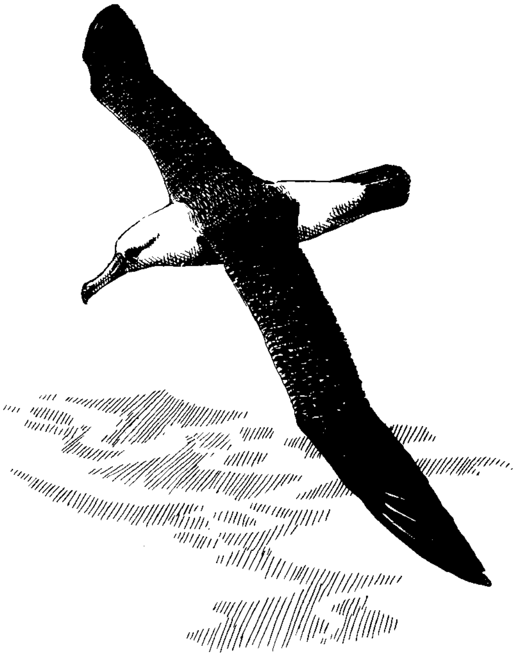
The fledging period is very long, some 2 months in the storm-petrels, 3–5 in the medium sized species, 9–12 in the largest albatrosses. The young sit quietly in the nest at first, but start to move about and exercise themselves by flapping their wings as the time to leave approaches. Most chicks eventually appear to fly directly from the nest, especially if it is situated inland. They are liable to make abortive flights and land in unsuitable places or come to village lights at night at first, and weakly young may swim out to sea if they can reach the water. Strong young fly well on fledging and probably never see the nest or their parents again; some transequatorial migrants immediately set out on long migrations, which must include a further period of starvation as they cross the tropics, and wrecks are particularly liable to occur at this time. Ringed birds have been recovered in the opposite hemisphere within days of the probable date of fledging.

Young birds fend for themselves on leaving the nest and spend their early years at sea, sometimes congregating in 'nurseries' where there is a good food supply. Later, they start to return to land for increasing periods in the breeding season, and also leave to start the annual moult early. During this time they often appear to wander and prospect new sites, though most eventually return to their natal colony. They then spend more years displaying and excavating nests before they start to breed, which the smallest storm-petrels may attempt at 2–3 years, but the largest albatrosses not until they are 5–10 years old, with poor success at first. Once they have started to breed, most species attempt it annually, though within the tropics some species may return at shorter intervals, while the largest albatrosses require 2 years for a successful cycle.

Some southern storm-petrels have only one coat of nestling down, but most have two. The juvenile plumage usually appears to be moulted at sea when the birds are about a year old, often in the 'nurseries'. Some of the larger species start a slow body-moult during the breeding season, Snow Petrels *Pagodroma nivea* completing it, but most species delay the moult of the flight-feathers until they have finished breeding for the year. The migrants may then complete it rapidly in some good feeding area in their winter quarters, though the more sedentary species are slower and start to return to the breeding places before it is finished. The power of flight may be impaired for a time when the moult is rapid, notably in some of the large shearwaters, and may be lost entirely by some of the diving petrels which moult the flight feathers simultaneously.

Albatrosses. The family Diomedeidae includes the 14 largest species (length 70–140 cm) in the order, with a vast WING SPAN (2–3 m), long, hooked bills with separate nostrils, short legs on which they can stand well and run to take off, and short, round tails in the 11 members of the genus *Diomedea*, but long, pointed tails in the 2 sooty albatrosses of the genus *Phoebetria*. They achieve continual effortless gliding flight by making use of the updraughts above the waves and the slopes of their breeding islands, and tend to settle on the water when the wind drops. They appear to feed mainly on large cephalopods caught or found disabled at the sea surface, perhaps largely at night, but they can also dive, and take fish and other marine animals. The sooty albatrosses in particular also catch birds, while the other species are among the seabirds which appear to profit most from scavenging around fishing-boats.

Albatrosses nest colonially in the open on remote islands, and one of the largest species, the Royal Albatross *Diomedea epomophora*, colonized Taiaroa Head on the east coast of the South Island of New Zealand when it was protected with a fence. They all have spectacular displays at the nest in which they stand with the wings opened and tail fanned while the head is stretched out and thrown up and the tip of the bill buried in the plumage of the back between the scapulars, to the accompaniment of gurgling and braying sounds. The members of the genus *Phoebetria* which tend to nest on cliffs also carry out aerial displays in pairs accompanied by screams. Two of the great albatrosses, the Wandering *Diomedea exulans* and the Royal, have more complex social displays in which the males (which arrive first at the breeding colony) gather around a female with their vast wings spread, rattling their bills.



Black-browed Albatross *Diomedea melanophris*. (*B.P.*).

It seems likely that there was once a community of primitive albatrosses in the circumpolar Tethys Ocean of the Northern Hemisphere during the Tertiary, since fossil remains of an early form, the English Albatross *Diomedea anglica*, have been found on both sides of the North Atlantic, which is now only visited by stray individuals of the southern species; while the northern species are now confined to the North Pacific. It seems possible that the Galapagos Albatross *Diomedea irrorata*, which occurs over the cold Peruvian Current within the tropics, is the most primitive surviving form, since it has a simple grey coloration with a paler head and bill and builds no nest. Three rather similar species with contrasting markings breed together at the central North Pacific archipelagoes, the Black-footed Albatross *D. nigripes*, which is dark brown with a paler face and base to the tail when adult, the Laysan Albatross *D. immutabilis*, which has a white body with a dark eyebrow, upperwing, back and tip to the tail, and the Short-tailed Albatross *D. albatrus*, now reduced to a population of a few score birds nesting on islands south of Japan; it is dark when young but becomes white with dark wing-tips when adult.

The fact that the northern albatrosses nest in the local winter suggests that the group was originally of southern origin, and they show their greatest development in the Southern Ocean, where there are now 3 distinct groups of species each of which has plumage comparable to one of the northern species, with the addition of distinctive head and wing markings, although they do not appear to be particularly closely related to the northern forms, and differ from them in building nests. The simplest situation and basic pattern of variation is found in the genus *Phoebetria*, which includes 2 small, dark, agile, long-tailed species with dark plumage and a distinctive incomplete white eye-ring, the Sooty Albatross *P. fusca* with a dark brown body and yellow stripe on the lower mandible in the subtropical South Atlantic and Indian Ocean, and the Light-Mantled (Sooty) Albatross *P. palpebrata*, with a paler body and blue stripe on the bill, further south and in the South Pacific.

The 3 great albatrosses are much larger than the other species, with an exceptionally long breeding-cycle, so that eggs laid in one summer give rise to chicks which are fed through the winter to fledge a year later. The Royal Albatross is largely white with dark upperwings and breeds in the New Zealand area, dispersing around the world to South America.

The populations of the Wandering Albatross which breed alongside it are largely dark, like the young Short-tailed Albatross, and never become very white, but the old birds of the populations breeding elsewhere throughout the Southern Ocean become whiter when adult, some of the southern males becoming as white as Royal Albatrosses. A third dark species *D. amsterdamensis* has recently also been found breeding in very small numbers on Amsterdam Island in the southern Indian Ocean.

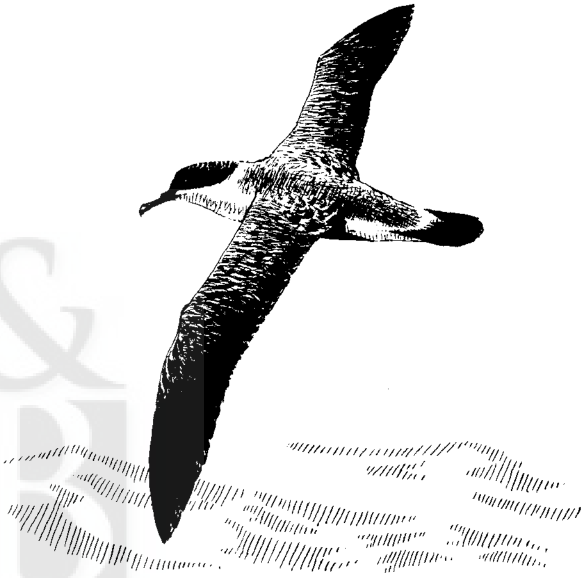
The height of complexity is found with a group of medium-sized species with dark brows, backs and tails similar to those of the Laysan Albatross known as 'mollymawks' from the old sailor's name for fulmars. The most familiar species is the Black-browed Albatross *Diomedea melanophris*, which has a simple black and white plumage pattern and yellow bill when adult. It behaves like the Wandering Albatross, breeding abundantly throughout the subantarctic zone and migrating north in the winter, when it sometimes reaches the northern hemisphere, including Britain, and may become marooned there. In contrast to this, 3 highly-distinct races of Shy Albatross *Diomedea cauta* retain as adults the more or less grey head and bill found in young mollymawks, and behave like the Royal Albatross, breeding around New Zealand and Tasmania and migrating east and west. Finally, 3 allies of the last group, having grey heads and black bills with distinctive yellow stripes, behave like the sooty albatrosses, breeding on oceanic islands in the subtropical South Atlantic and Indian Ocean (Yellow-nosed Albatross *Diomedea chlororhynchos*), subtropical South Pacific (Buller's Albatross *D. bulleri*) and the subantarctic zone of the Southern Ocean (Grey-headed Albatross *D. chrysostoma*) and disperse throughout these zones of surface water.

Fulmarine petrels and shearwaters. The family Procellariidae includes the main body of medium- to large-sized petrels (30–70 cm) totalling some 12 genera and over 50 species. They may be divided into 2 subfamilies, the Fulmarinae, largely aerial species with skulls strengthened by fusion of the lacrhymal bone to facilitate seizure of their food from above the surface (except in the small primitive northern genus *Bulweria*) and the Procellariinae, more aquatic species with longer bills rendered mobile by retention of a separate lacrhymal bone used for seizing fish under water. The Fulmarinae can be subdivided into 3 further specialized groups, the fulmars, prions, and gadfly petrels.

The fulmars include 5 highly distinct species or superspecies of different sizes with a heavy build, short tails and a gliding and flapping flight characteristic of high latitudes. Three monotypic genera are restricted to the Southern Hemisphere, where there are also sibling species of giant petrel *Macronectes* in the subantarctic and subtropical zones of surface water, while there are closely-related species of *Fulmarus* in both the Northern and Southern Hemispheres. The Southern Giant Petrel *Macronectes giganteus* and Northern Fulmar *Fulmarus glacialis* are polymorphic and may be either dark or pale, the Cape Pigeon *Daption capensis* and Antarctic Petrel *Thalassoica antarctica* are chequered brown and white, the pale phase of the Northern Fulmar and its southern representative *Fulmarus glacialoides* are grey and white, and the Snow Petrel *Pagodroma nivea* of the antarctic ice is pure white, and remarkable for the possession of 2 races of very different size. All species have broad bills with distensile gular pouches, and all except the Southern Fulmar have some sort of filtering plates or lamellae in the bill. Most probably they once fed mainly on plankton, though the giant petrels at least have always been scavengers and predators; but they have taken readily to feeding behind fishing-boats. They nest in the open or in shallow niches, visiting the nest by day, and have developed oil-spitting as an effective defence.

The prions *Pachyptila* spp. are a group of some 12 very closely-related species and subspecies of small petrel adapted to feed directly upon the smaller organisms in the surface water by straining it through lamellae fringing the bill. They are all very similar in size and appearance, blue-grey above and white below with darker ear-coverts, 'W' markings on the back, and tips to the tail-feathers, and an erratic, mobile, skimming flight; they differ mainly in the size of the bill and its lamellae. The different forms appear to replace each other ecologically in different zones of surface water, feeding in large flocks along the marine convergences at sea and breeding underground on the subantarctic islands in dense warrens which they visit by night. The Blue Petrel *Halobaena caerulea* is a superficially similar species with a smooth narrow bill and white tips to the tail feathers which appears somewhat intermediate in its structure and behaviour between this group and the next one.

The gadfly petrels *Bulweria* and *Pterodroma* spp. are a group of some 24 rather similar medium-sized petrels with long wings and short, stout, heavily-grooved and markedly-hooked black bills; they live far from land in the centre of the oceans. The smaller species, including the primitive northern genus *Bulweria*, are lightly-built, with fairly long wedge-shaped tails, and a graceful mobile, soaring flight, while the larger members of the genus *Pterodroma* are sturdy, with shorter rounded tails and a forceful flight in great arcs, between which they may tower in the air. They vary greatly in their coloration and many are polymorphic, but in general they tend to be grey or brown above and may have either white faces and underparts or be equally dark below, though in all plumages they tend to show characteristic wing markings. Comparatively little is known about their biology, but some have a remarkable twisted gut apparently adapted to absorb the oil from cephalopods caught largely at night. They have very long breeding cycles. Some of the larger species visit nests in the open by day on remote southern islands, but most nest in burrows which they visit by night, often in forested mountain slopes far inland. Young birds tend to wander great distances, and, in the Pacific, some appear to carry out transequatorial migrations.



Great Shearwater *Puffinus gravis*. (*B.P.*).

The shearwaters are another large group of some 15 species distributed throughout the oceans, though they tend to be commoner near land. They have longer, more slender bills with smaller hooks, and may also be either dark above and light below or uniformly dark, and some are polymorphic. They may be divided into 2 groups with different flight and feeding habits. Some, including the White-chinned Petrel *Procellaria aequinoctialis*, Cory's Shearwater *Calonectris diomedea* and their allies, and the Wedge-tailed and Grey-backed Shearwaters *Puffinus pacificus* and *P. bulleri*, are adapted for an aerial way of life, fishing on the wing in the centre of the ocean, which is associated with the development of long wings, tails and legs. Others such as the Grey Petrel *Procellaria cinerea*, Manx Shearwater *Puffinus puffinus*, and the remaining members of the genus *Puffinus*, are adapted for a more aquatic existence diving on fish-shoals offshore. This is associated with the development of shorter wings, tails and legs with flattened tarsi. One species, the Christmas Island Shearwater *Puffinus nativitatis*, nests more or less in the open on islands in the central Pacific, but they often breed in large, dense colonies of burrows, which they visit by night, near the coasts of offshore islands, though they may also use hills inland. Many species have long and complex migrations between well defined feeding areas in the same or opposite hemispheres.

Storm-petrels. The family Hydrobatidae includes 8 genera and over 20 species of small petrel (12–25 cm) adapted to catch small marine animals at the water surface. They are all more or less dark above with paler wing coverts, and often white rumps, and vary in colour below. They all breed more or less socially in crevices and burrows, usually on islands, though they may use mainland cliffs or travel inland to nest in deserts. Many carry out considerable migrations, the species from opposite hemispheres replacing each other at different seasons as winter

Wilson's Storm-petrel *Oceanites oceanicus*. (*B.P.*).

visitors to the tropics. They may be divided into 2 subfamilies characteristic of different hemispheres, with a wide overlap in range in the intervening area.

The Oceanitinae include some 7 more or less highly differentiated forms characterized by the possession of short, rounded wings, nearly square tails, long tarsi and short toes. They are adapted for a distinct mode of progression, walking or hopping along the surface of the water between the waves, picking organisms from the surface as they go. They occur in 2 colour-phases, dark or white below, all species being polymorphic to some degree. Most are restricted to the Southern Hemisphere, but the White-throated Storm-petrel *Nesofregetta fuliginosa* (= *N. albigularis*) is resident in the tropical Pacific, the White-faced Storm-petrel *Pelagodroma marina* has colonized the North Atlantic, and Wilson's Storm-petrel *Oceanites oceanicus* is a transequatorial migrant which breeds in the antarctic and winters in the northern oceans.

The northern Hydrobatinae include some dozen closely-related species which may be derived from Wilson's Storm-petrel, since they also normally occur in the dark phase but may have white rumps. They show a progressive development of a very different type of flight adapted for calmer northern seas, swooping over the surface like terns, which renders them more vulnerable to wrecks. An early stage of development is shown by the British Storm-petrel *Hydrobates pelagicus* which breeds around the west coast of Europe and winters off South Africa. It reaches its climax in the Pacific, where a minute wedge-tailed species, the Least Storm-petrel *Oceanodroma microsoma*, occurs off California and a swarm of fork-tailed species of the genus *Oceanodroma* of different sizes and colours frequent the areas of upwelling there and off Japan and Peru, some migrating to winter in the tropics.

Diving-petrels. The family Pelecanoididae contains one genus *Pelecanoides* which includes 4 or 5 small aquatic petrels (16–25 cm) belonging to 2 superspecies which may have originated in South America and Australasia, though they have now developed an overlapping distribution in the Southern Ocean. They are known on Tristan da Cunha as 'flying pinamins' or penguins, and are also remarkable for their similarity to the smaller northern auks, especially the Dovekie or Little Auk *Alle alle*, which replaces them in the North Atlantic. They are only easily distinguished by their possession of the characteristic tubular nostrils of the Procellariiformes. The resemblance provides an outstanding example of evolutionary convergence in a similar environment, because not only are the 2 groups extremely similar in size, appearance and proportions, both being black above and white below with short bills, wings and tails; they both have a similar whirring rather than gliding flights and dive straight from the air into the water where they use their wings in pursuit of small marine organisms which they collect in gular pouches. Some alcids behave like the diving-petrels in breeding socially overlooking the sea in holes which they visit by night and where they lay white eggs.

The South American group of diving-petrels possess a pointed arch to the lower jaw and comparatively raised, rounded nostrils. They include the largest species, the Peruvian Diving-petrel or Potoyunco *Pelecanoides garnotii*, which feeds in the cold Humboldt Current and nests on the adjacent guano islands. Further south it is replaced by the medium-sized Magellanic Diving-petrel *P. magellani* in the channels between the mainland and offshore islands and in the Falklands, and by the Small Georgian Diving-petrel *P. georgicus* in the subantarctic islands, including South Georgia, Marion and Prince Edward Islands, the Crozets and Kerguelen, and probably Macquarie and other islands south of New Zealand, where there is a colony in the Foveaux Strait. It feeds upon krill *Euphausia superba* and breeds late in the summer in holes in the sandy upper parts of islands.

The New Zealand group is distinguished by the possession of a rounded arch to the lower jaw and flattened, elongated nostrils, and tend to nest early around the vegetated lower slopes of islands and feed upon copepods. They include an uncertain number of forms, notably the medium-sized Common Diving-petrel *P. urinatrix*, breeding around the Bass Strait in south-east Australia and the main islands of New Zealand, and a number of very similar small populations breeding at the same sites in the subantarctic islands as the Georgian Diving-petrel and also Tristan da Cunha, Gough Island, the Falklands and probably around southern South America, where it occurs alongside the Magellanic Diving-petrel as well. It seems possible that there may be some overlap in the distribution of the large and small forms of Common Diving-petrel, notably in the Chatham Islands, in which case the small form would rank as a distinct species *P. berard*.

Common Diving-petrel *Pelecanoides urinatrix*. (*B.P.*).

See also ANTARCTIC; OCEANIC BIRDS. See photos AGE; DISPLAY; FEEDING HABITS; FLIGHT; NOCTURNAL HABITS. W.R.P.B.

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PEWEE: substantive name (in some cases 'wood-pewee') of *Contopus* ('*Myiochanes*') spp. (see FLYCATCHER (2)).

PEWIT: common alternative name (from the call, and variously spelt) in Britain for the Lapwing *Vanellus vanellus* (see PLOVER (1)); formerly used also for the Black-headed Gull *Larus ridibundus*.

PEZOPHAPIDAE: family of extinct birds. See under COLUMBIFORMES; SOLITAIRE (now in Pezophapidae, previously 'Raphidae', see DODO).

pH: a symbol followed by a value that is a logarithmic expression of the hydrogen ion concentration of a solution, and thus an index of its reaction. The pH of a neutral solution is 7; above 7 alkalinity increases, below 7 acidity increases.

PHAENICOPHAEINAE: see CUCKOO.

PHAETHONTES; PHAETHONTIDAE: suborder and family of PELECANIFORMES; TROPICBIRD.

PHAINOPEPLA: generic name used as common name of *P. nitens* (see SILKY FLYCATCHER).

PHAINOPTILA: generic name often used as common name of *P. melanoxantha* (see SILKY FLYCATCHER).

PHALACROCORACIDAE: see under PELECANIFORMES; CORMORANT.

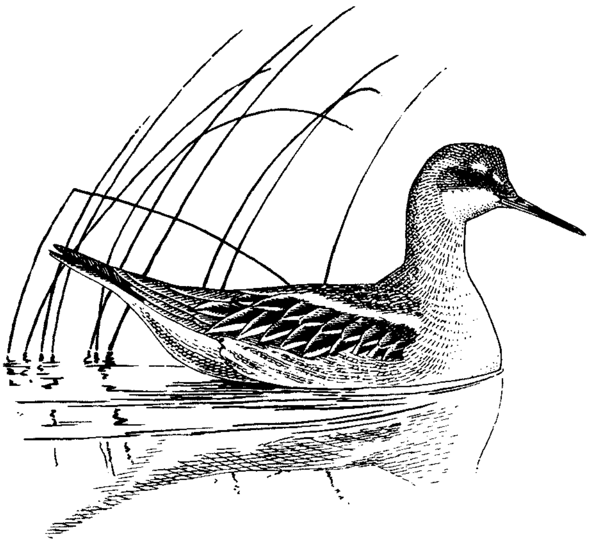
PHALANX: a bony element (plural 'phalanges') of a digit (see LEG; SKELETON, POST-CRANIAL; WING).

PHALAROPE: substantive name (coined by Brisson in 1760) of the 3 species of Phalaropodinae (Charadriiformes, family Scolopacidae). They are small, swimming 'sandpipers', breeding in northern latitudes, with dense breast plumage which provides a raft of air on which they float lightly. There are short webs between the bases of the front toes and all 4 toes are expanded and fringed with contiguous convex scales; the tarsus is laterally compressed. Two of the species become seabirds during the 9 non-breeding months; and it is characteristic of all 3 that the sexual roles are reversed, the female being larger and in nuptial plumage more brightly coloured than the male.

They are assigned to a distinct subfamily because of their aquatic adaptations, and all 3 have mutually diverged so much that they are placed in separate genera by New World taxonomists. They are Wilson's Phalarope *Phalaropus tricolor*, the Grey (or Red) Phalarope *P. fulicarius*, and the Red-necked (or Northern) Phalarope *P. lobatus*; the alternative English names are those in use in the Americas—the 'Grey' being descriptive of most autumn migrants and the 'Red' of the breeding plumage.

Characteristics. Wilson's is slightly the largest (length 23 cm); it has very long legs and a long needle-like bill, and its toes are evenly fringed, whereas those of the other two are lobed, with a waist at each joint. The Grey (length 20 cm) is apparently the most numerous; it has a short bill, unusually broad for a wader. The Red-necked is the smallest and most delicate (length 18 cm), has the most broadly lobed toes and a bill as fine but not as long as that of Wilson's; in spite of its former American name it is a less northern breeder than the Grey. The Grey and Red-necked in all plumages have dark rumps and show a white wing-bar in flight, whereas the rump of Wilson's is white and there is no wing-bar.

All have decorative nuptial plumages, acquired late in spring and, in most individuals, lost before autumn. The various combinations of bay or maroon with white, black, light grey and buff put the females among the most colourful of the Charadrii; the male plumages are more subdued, and cryptic when the bird sits on the nest. They are unremarkable vocalists, often repeating single soft high notes, *tik* and *peep* (also heard at sea); the Grey has additional disyllabic and twittering calls.



Red-necked Phalarope *Phalaropus lobatus*. (*A.H.*).

Distribution and habitat. The Grey and Red-necked are circumpolar breeders, the former mainly in the arctic biome, the latter in the sub-arctic or boreal, but there is some overlap. The Grey is more confined to coastal habitats and often breeds on inshore islands, but both frequent shallow freshwater ponds and lakes; a minority of Red-necks breed far inland. The Red-necked is a rare and rather insecure breeder at several sites on the mainland and islands of Scotland, and until 1971 it bred in western Ireland. The Grey in the British Isles is a sporadic, chiefly autumn, migrant along western coasts, and more rarely elsewhere.

In contrast, Wilson's Phalarope is a temperate-zone breeder confined to the interior of North America, from Alberta (probably to 60°N) to California (37°N) and east to Ontario. It enjoys a warm summer but many of the ponds and marshes it frequents dry up. It is a bird of inland shores and waters at all seasons, wintering in South America.

Movements. The females remain at the breeding colonies only a few weeks, those of the hot-summer species Wilson's being least, and those of the high-arctic Grey most, in a hurry to be off; in all species the majority have left before the peak date of hatching arrives. After the chicks have emerged, the males accompany and brood them; but, only 3–4 weeks after the females have left, the males also aggregate and depart, some of them allegedly deserting small young. Each exodus of adults must relieve the pressure on the food supply, to the benefit of those that stay behind. Finally, after another similar interval, the young themselves are ready to start their long migration.

The adults of all species begin their moult before or soon after they leave their breeding places. Most Greys complete it at sea before going south on migration. They are rarely found in the interior of either Asia or North America, and reach their traditional ocean winter resorts near or beyond the equator virtually undetected en route, no doubt largely by sea. An exception is the 4,000 km fringe of the north-west Atlantic, where large numbers are found in autumn feeding and moulting, from Baffin Bay to Nova Scotia, up to 300 km offshore; south of that they disappear. Some may possibly fly non-stop from arctic Siberia to resorts in the Arabian Sea (> 5,000 km).

The Red-necked, on the contrary, is a conspicuous overland migrant in Asia, funnelling southward in autumn across the steppes, visiting well-known feeding places, and finally crossing the plateau of Afghanistan/West Pakistan and Iran to reach the Indian Ocean. It returns by the same routes in spring (Dementiev *et al* 1969). In Canada, a less massive overland migration is restricted to the prairies and British Columbia. Red-necks also migrate by sea-routes. Being very light birds, both species are subject to occasional 'wrecks' when caught by gales on migration at sea.

At sea both species frequent regions where the mingling of water-masses, or strong offshore winds, lead to turbulence and the appearance of streaks and slicks on the surface, with concentrations of plankton immediately beneath them (Brown 1979; also OCEANIC BIRDS). The 2 species often keep apart, though by no means wholly. The winter resorts in which the Greys predominate are in the enriched waters off Cape Verde and Angola (Africa), and off Chile (20–40°S); the Red-necks are most numerous off the Arabian Peninsula and south of Baluchistan, and over a wide region extending south roughly from Japan to New Guinea, and also off Peru (0–20°S) and Argentina.

Wilson's Phalaropes migrate overland and southward along the Andes to winter chiefly east of the Cordillera, between the mountains and the Atlantic coast, and especially on the pampas of Argentina. Vagrants have been appearing not infrequently in Britain since they were first detected in 1954, chiefly at migration times.

Food. Although in summer phalaropes feed partly ashore, most food is taken at the water surface when they are swimming or wading, and consists largely of insects and small crustacea. All 3 species share the habit of spinning round and round on the water, supposedly to stir up or activate their prey; no doubt the movement is facilitated by having legs amidships, rather than far back like most swimming birds. Sometimes they up-end like ducks, but submerging seems difficult. In the non-breeding season the Grey and Red-necked live at sea in the tropics or further south, feeding on plankton.

Behaviour. All are sociable breeders, usually dispersed in small diffuse groups centred on particular feeding areas or prairie sloughs. In some districts the habitats are extensive, and in suitable parts of south-west Baffin Island and coastal eastern Siberia the Grey Phalarope may be among the commonest birds, reaching 30–200 pairs per km^2 (Kistchinski 1975). Apart from defending the actual nest or mate, the females are non-territorial; they make solitary advertising flights over the colony, and there are also aerial chases, usually with one or several females chasing a male. But Schamel and Tracy (1977) also saw mixed chases and chases of a female by males of the Grey Phalarope, which suggests that the roles change when the males have an unmated surplus. Courtship swimming occurs, and copulation with the female swimming on the water can occur in all species; it apparently always does with the Red-necked, and in most instances with Wilson's, whereas the female Grey is normally on her feet either in shallow water or on land. Incidentally the Red-necked and Grey are so tame as to be easily studied at close range.

Breeding. Single pair-bonds are the norm. The nest is a scrape with a varying amount of lining. The clutch is 4 eggs, less often 3. Nests are commonly well separated though clumping has been recorded in all species. Incubation (18–24 days) is by the male who alone has brood-patches; their development depends on the typically female hormone prolactin, more of which is secreted by male than female phalaropes. Likewise the female's bright plumage is conditioned by testosterone, normally a male hormone. Depending in part on sex-ratios, single females may frequent the immediate nest-area for much of their mate's incubation period, or they may flock with other females remaining in the neighbourhood (indicating a short-lived pair-bond), or the flocks they join may quit the district.

It was long assumed that phalaropes would turn out to be polyandrous, but this has only recently been confirmed, for the Red-necked in Finland and Sweden (Hilden and Vuolanto 1972; Raner 1972), and for the Grey at Barrow, Alaska (Schamel and Tracy 1977). Breeding conditions in the Arctic are notoriously variable, and it appears now that only some females are 'diandrous', and only when there is an excess of males. Graul *et al* (1977) postulate that reversed sex-roles have evolved in various nidifugous birds which breed in ecosystems where feeding is usually so sparse (and the season so short) as to prevent the female from meeting the cost of incubating the eggs as well as producing them; but, if the male can take over the hatching unaided, the population can still remain viable. Once that has been achieved, it will benefit all concerned still more if, in a spring when feeding is better than usual, a female can attract two batchelors in quick succession and lay each of them a set of eggs, so as to give both enough time to rear their families.

See photo COPULATION. V.C.W.-E.

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PHALAROPODINAE: see PHALAROPE.

PHANERIC: term applied to coloration or other characters that are the opposite of cryptic in that their purpose is to be conspicuous (see COLORATION, ADAPTIVE).

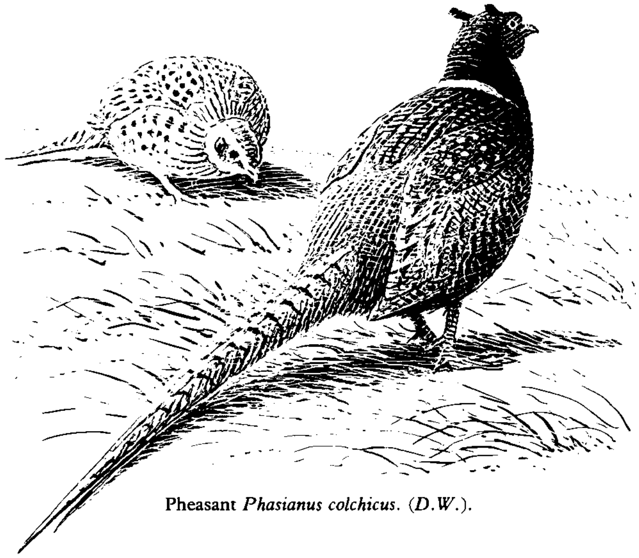
PHARYNX: the cavity of the throat, behind the buccal cavity and leading to the oesophagus and trachea respectively (adjective 'pharyngeal').

PHASE: equivalent of MORPH (see also POLYMORPHISM).

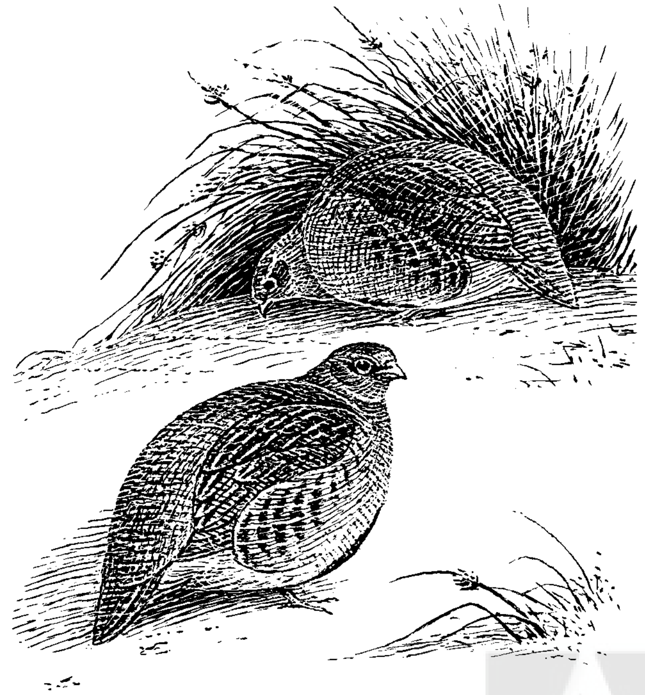
PHASIANIDAE: see under GALLIFORMES; PHEASANT.

PHEASANT: substantive name of many species of Phasianidae (Galliformes, suborder Galli); used without qualification in Britain for *Phasianus colchicus*; in the plural serves as a general term for the family. In the pheasants, called by that name, the males have bright colours or elaborate markings; the duller species, mostly a great deal smaller and with shorter tails, are given such names as 'partridges', 'quail', 'francolin', and 'snowcocks', but are not differentiated by any important characteristics, there being in fact a gradual transition between them. American quail are placed in a separate subfamily or tribe, the Odontophorinae, as distinct from the Phasianinae of the Old World.

Characteristics. The family is one of terrestrial birds which as a rule feed and nest on the ground, but in the majority of cases roost on trees at night. They are heavy birds; their wings are short and rounded, curved and fitting closely to the body, making them capable of a powerful, fast flight, but—except in some migratory quails—one that cannot be sustained for long (see FLIGHT). The legs are strong, with 4 toes (the hallux inserted somewhat higher than the others) armed with heavy claws, and adapted to scratching; the tarsus often shows a spur, or even 2 or more. The bill is short and thick, the upper mandible overhanging the lower. The tail varies from short to very long, the longest tail feathers being



Pheasant *Phasianus colchicus*. (*D.W.*).



Grey Partridge *Perdix perdix*. (*D.W.*).

those of Reeves's Pheasant *Syrmaticus reevesi* and Crested Argus *Rheinartia ocellata* which reach over 1½m in length. The plumage is ample and soft; the sexes are alike in some species, different in others.

Most pheasants are easily kept in captivity and are well known as ornamental birds. The most useful domestic bird, the common fowl, derives from a pheasant, the Red Junglefowl *Gallus gallus*. Other species such as peafowl *Pavo* have been kept in complete or semi-captivity for centuries; but they have not yet changed in size or characteristics, although mutations have occurred, such as the 'Black-shouldered Peafowl', 'Melanistic Pheasant', and the 'Yellow Golden Pheasant'.

A few of the more spectacular pheasants have figured prominently in myths and legends. This is particularly true of the peafowl which are sacred birds in much of India and appear in Buddhist, Hindu and various pagan mythologies including that of the ancient Greeks. The Buddha is sometimes depicted riding on a displaying peacock, and early Christians used the peacock as a symbol of immortality. A peacock competes with the Crested Argus for identification as the model for the Chinese Phoenix, the Fung-whang, while the Golden Pheasant *Chrysolophus pictus* has been suggested as the original of the Phoenix itself (see FABULOUS BIRDS). Concrete examples of such myths are to be found in the famous peacock throne of the Moghul and later the Persian emperors, in the heraldic use of peacocks in medieval Europe, or in the use of peacock feathers to denote rank among Chinese mandarins (the long tail feathers of Reeves's Pheasant, worn on the cap, are used to this day in Chinese opera to signify military characters.)

For convenience the pheasants are divided into 4 main groups:

American quail (18–36 cm). These comprise 36 species in 10 genera, of small rotund birds, distinguished from the Old World members of the family in having a stronger bill, the tip and edges of which are sharp and more or less serrated, and by other important anatomical features. Otherwise they resemble the partridges of the Old World and have similar habits. They are, as a rule, brightly and elaborately marked with brown, buff, yellow, reddish, grey, black and white. The tail varies from short to moderately long. The tarsi carry no spurs. The head is often crested and in most species the sexes are different.

Old World quail (14–20 cm). This group includes 10 species usually placed in 3 genera; they are very small and rounded, and appear tailless with weak bill and legs. The sexes are dissimilar in most species, the males heavily, and in some cases, colourfully marked with blue, brown, black and white.

Partridges (16–72 cm). The partridges (84 species in about 17 genera) are a large and diverse group of Old World birds with larger bills, stronger legs and longer tails than the preceding groups. The group includes bush quail, francolins, spurfowl, snowcocks and pheasant-grouse as well as grey-, red-legged-, sand-, snow-, stone-, tree-, wood-, and bamboo-partridges. In most species the sexes are similar and cryptically patterned. In a few forest species, notably the Roulroul *Rollulus roulroul*, the male is brightly coloured and crested. They vary in size from the quail-sized bush quail *Perdicula* to the Himalayan Snowcock *Tetraogallus himalayensis* which may weigh up to 3 kg.

Pheasants (40–235 cm). The pheasants proper comprise 48 species in 16 genera, of large but generally more slender birds, often with long, pointed tails and giving lateral displays. In all but one genus, the eared pheasants *Crossoptilon*, the sexes are different, the males being boldly and sometimes iridescently patterned with blues, reds, greens, and whites, and often adorned with elaborate structures used in display. The group includes Junglefowl *Gallus*, Peafowl *Pavo*, and several species well known from captivity such as Golden Pheasants and Silver Pheasants *Lophura nycthemera*, as well as the 'true' or 'game' pheasants *Phasianus*.

Distribution and habitat. The family in general is distributed throughout the world with the exception of a number of oceanic islands and the polar regions. Most members are natives of the Old World, and apart from artificial introductions, the family is represented in the New World only by the American quails. These are found in the temperate and warm parts of North, Central and South America, from the northern United States (one reaches southern Ontario in Canada) to Peru, Bolivia, Paraguay, and southern Brazil. They are particularly numerous and diverse in the southern United States, Mexico, and Central America. Some live in forests, others on woody or bushy plains and deserts, and a number are found on cultivated land, for example the Bobwhite *Colinus virginianus*. Some are adapted to life at a high altitude, although they never transcend the limit of the trees.

The Old World quail are widely distributed in all the continents of the Old World from Australia to Europe and Africa. There are separate species on Madagascar and New Guinea, but the New Zealand species is now extinct. Quail are typically birds of open country, preferring grassy plains but adapting to cultivated land as well. At least some species roost in tight circles, heads pointing outwards.

Partridges are found from Europe to Indonesia, their distribution centred on southern Asia with many species in India, Burma, and Malaysia. Francolins are found mostly in Africa, with only one other (monospecific) genus, the Stone Partridge *Ptilopachus* present south of the Sahara. Although most partridges live in grassland, scrub and farmland, they inhabit a wide variety of habitats from desert and alpine meadows to dense tropical rainforest.

Pheasants are almost entirely confined to Asia. The startling exception to this is the Congo Peacock *Afropavo congensis* which is restricted to the rainforests of central Africa, where it was only discovered in 1936. Several species have been successfully introduced in other parts of the world, notably *Phasianus colchicus* which is now established in Europe, North America and New Zealand. Most pheasants inhabit forests, either in the mountains of central Asia and China, or in the tropical rain forests of south-east Asia. A few species are adapted to forest edge (e.g. *Gallus*), open woodland (e.g. *Syrmaticus* spp., *Pavo*), or scrub (e.g. *Chrysolophus*, *Crossoptilon*). *Ithaginis*, *Lophophorus* and *Catreus* inhabit scrub, woodland and open grassland on steep, rocky hillsides, and *Phasianus* prefers patches of dense cover such as tamarisk, scrub or reedbeds, near cultivation, in steppe or in desert.

Populations. Pheasants, partridges and quail are of great importance to man as game-birds, providing sport and food. Wild populations are hunted and in Europe and America are sometimes protected and managed. Pheasants (*Phasianus*) and sometimes partridges (*Alectoris* and *Perdix*) are raised in captivity and released to supplement wild populations in some areas.

Most species are fairly numerous, but hunting pressure and habitat destruction have already exterminated 2 species (*Ophrysia* the Indian Mountain Quail, and *Coturnix novaezealandiae* the New Zealand Quail) and have seriously threatened the survival of at least 16 other species. Most of these are pheasants from tropical and montane forests. However, a number of the endangered species can be bred in captivity and in certain cases (for example the Cheer *Catreus wallichii*) captive-bred stock has been reintroduced to the wild. There are rumours, too, of rediscovery of the Indian Mountain Quail.

Movements. Most pheasants are sedentary in habits and often show strong local attachments. Some mountain species migrate up and down hill at different seasons, and Bulwer's Wattled Pheasant *Lophura bulweri* is said to be nomadic in search of fruiting trees, but only a few quails of the genus *Coturnix* are truly migratory. *C. coturnix* migrates from Europe and central Asia to Africa and India, an astonishing feat for such heavy, round-winged little birds, and Harlequin Quail *C. delegorguei* of Africa periodically invade suitable areas in large numbers, deserting them again after breeding.

Food. The family is mainly vegetarian, but the amount of animal protein taken varies from none to a large proportion of the diet. Pheasants are catholic feeders and rarely specialize on one type or species of food. Important foods include seeds, shoots, berries, roots, bulbs, and insects. Those living in grassland or scrub eat mainly seeds and shoots, while in woodland berries may be more important. In tropical forests, fallen fruit and invertebrates such as grubs and termites are the main items of diet, while at high altitudes in particular, some species (notably eared *Crossoptilon*, Cheer *Catreus*, and monal *Lophophorus* pheasants) are adapted to unearthing bulbs, roots and worms with their feet or bill (*Lophophorus* uses only its bill and is capable of excavating holes up to 30 cm in depth in search of bulbs). Peafowl are known to eat lizards and snakes. Desert-dwelling partridges may depend on grasshoppers and locusts, but most partridges and quail are vegetarian as adults. However, the chicks of almost all species in the family are raised on insects and other invertebrates (an exception being snowcock young, which feed on legumes). The current decline of Grey Partridges *Perdix perdix* in Britain is attributed largely to the increased use of pesticides which kill chick food.

Behaviour. A variety of patterns of social organization is found in the family, depending largely on habitat. Most of the American quail and the partridges, living in scrub and open country, are highly gregarious, found for much of the year in 'coveys' comprising one or more family parties. Typically these number between 4 and 10 but in some species living in very bare habitats, such as *Callipepela*, *Colinus*, *Ammoperdix*, *Tetraogallus*, *Lerwa*, and *Francolinus* spp., such groups may amalgamate to form flocks of 20–40 birds. Most partridges and American quail are monogamous, pairs being formed and maintained all year round; in spring these pairs leave the coveys and remain dispersed during breeding, but they do not defend territories. Some partridges do not gather in coveys, but remain in pairs all year, the broods fragmenting on reaching maturity. These are generally birds such as *Rollulus* and *Melanoperdix* that live in dense tropical forests.

Except on migration most Old World quail are solitary. Some, however, live, like partridges, in coveys. On the breeding grounds, the males occupy territories which they defend against other males, and in which they sing to attract females who then nest within the territory; they are sometimes polygynous. On migration, they may travel in coveys or larger temporary flocks.

Among the pheasants, social patterns are varied and often poorly understood. Those that live in open scrub or open woodland are found in coveys like those of partridges, and are monogamous. Eared (*Crossoptilon*) and blood pheasants (*Ithaginis*) often gather in larger flocks of up to at least 20. Coveys break up into pairs in the breeding season. Species living in dense scrub or around the edges of forest are often found in single sex groups or are organized into harems with one male defending each group of females, and surplus males remaining in bachelor groups (for example junglefowl). Alternatively, the males may defend territories in which live one or more females (for example true pheasants *Phasianus* and long-tailed pheasants *Syrmaticus*). Peacocks *Pavo* defend small aggregated territories resembling leks. Most species are polygynous, and the males take no part in rearing the young. Species that live in dense forest tend to be more solitary and secretive. Some live in pairs (for example tragopans and the Congo Peacock *Afropavo*) but others are solitary, and the sexes meet only briefly during the mating season, when males attract females to special display grounds or seek them out (for example argus and peacock pheasants *Polyplectron*). In some gallopheasants *Lophura*, the sexes live separately for most of the year, each bird in its own home range, but may gather in flocks at other times.

Display and voice. In the quail and partridges, displays are relatively simple affairs; courting males strut around the females with body feathers erected, wings lowered, and tail spread. Patches of colour on the face or flank may be exaggerated by the adoption of special postures or the crest may be raised and spread. Such display precedes pairing and is not generally repeated before copulation. American quail are on the whole noisy birds; those that live in open country have harsh, repetitive, staccato voices used in alarm calls, choruses at dawn and dusk, or for advertisement by unmated males. Forest species give whistles or hoots, the most elaborate forms being the loud, hooting choruses of the tree quails *Dendrortyx* and the piping, nocturnal song of the singing quails *Dactylortyx*. Old World quail are more silent except in the breeding season when males give their distinctive song to advertise their territories and attract females (the song is a series of high-pitched whistles, *quit quit quit* repeated many times). Partridges are talkative birds with loud alarm calls, and they are fond of choruses at dawn and dusk. They make a variety of sounds: low, grating creaks (*Perdix*, *Ammoperdix*); harsh, staccato sounds, as suggested by the name 'chukar' (*Alectoris*); cackles (*Galloperdix*); sharp, high-pitched creaks and twitters (*Francolinus*, *Perdicula*, *Bambusicola*), and low, melodious whistles (*Tetraogallus*). Forest partridges give shrill, piping whistles, and some species are fond of duetting, for example *Rhizothera longirostris* the Long-billed Partridge, and *Caloperdix oculea* the Ferruginous Wood Partridge.

In pheasants, displays are elaborate, colourful and varied. The males of most species display laterally, that is by presenting one flank of their body to the female, with the body feathers and wing lowered on that side, raised on the other, and the tail spread vertically either, in species with flat tails such as tragopans, Koklass *Pucrasia* and true pheasants, by opening the tail and tilting it on one side, or, in species with compressed arched tails such as gallopheasants, by opening the tail vertically. Such displays exaggerate the size of the performer and reach their most extreme form in the Crested Argus in which the enormous tail feathers (the largest feathers in the world, 15 cm wide and reaching over 1.5 m in length) are spread, like a sail, in front of the female. Lateral displays are also used in, for example, *Phasianus* to intimidate other males. Some species do not display laterally or have in addition, different methods. Eared pheasants have simple partridge-like displays, and in long-tailed pheasants *Syrmaticus* the males strut in front of the females with the feathers of the neck and head erected to give a swollen appearance. Peacock pheasants have both lateral and frontal displays. Monals *Lophophorus* also display in flight. But the most spectacular displays of all are the great frontal shows of some of the larger, flat-tailed species. In these the tail is erected over the back and spread like a fan, while the wings are lowered or spread and the head is retracted between the shoulders. The effect is to show off the colours of the back (e.g. *Lophophorus*), wings, tail or tail coverts: in peacocks the latter are enormous and beautifully patterned with metallic ocellae. In the Great Argus *Argusianus argus*, the secondary feathers are very long and broad and in display they are spread over the back, with the head hidden behind them, so that the bird looks like a huge painted fan.

As well as lateral and frontal displays, many pheasants use so-called 'tid-bitting' ceremonies to call their mates to proffered items of food, over which they then display. Displays are often enhanced by the use of special structures, notably bare patches of skin on the face which can be enlarged or flushed at moments of sexual or aggressive excitement. These are normally red, sometimes, in forest species, blue. The commonest forms are the red wattles or facial 'roses' of the true, eared and gallopheasants. In junglefowl, a 'comb' is also present on the crown of the head, and in Bulwer's Wattled Pheasant, the blue facial wattles can be extended beyond the head in front and behind, which, together with the enormous white tail gives this species a bizarre and spectacular display. Tragopans have erectile, bare horns on the head and lappet below the face which can be greatly expanded in display to form a large, blue or yellow bib, patterned with orange, which resembles a brightly coloured piece of silk. Other species possess crests or ruffs used in display. The long, double crest of the Koklass *Pucrasia macrolopha* can be raised vertically and out from the head, as can the short 'ears' of true pheasants, while in *Chrysolophus* (Golden and Lady Amherst's Pheasants) the lateral display is enhanced by a beautiful yellow or white ruff, boldly marked with black, which can be spread from the nape to the bill, completely hiding one side of the face.

Some pheasants, particularly gallopheasants *Lophura*, long-tailed pheasants and tragopans, whirr their wings in advertisement displays to announce territory ownership or attract females. Others have loud advertisement calls which may be harsh and grating (*Chrysolophus*), raucous and deep (*Phasianus* and *Pucrasia*), high-pitched and whistling (*Ithaginis*, *Lophophorus*, *Lophura*, *Polyplectron*), or a plaintive, musical wail (*Tragopan*, *Pavo*, *Argus*, *Rheinartia*). The crowing call of the junglefowl is the well known sound of the domestic cockerel. Apart from crowing calls, some pheasants are talkative and noisy, particularly those that are gregarious like *Ithaginis*, *Catreus*, *Gallus* and *Crossoptilon*, and make continual clucking or crooning sounds. Others are very silent or like *Syrmaticus* have weak, quiet voices. Male true pheasants have a raucous, repetitive alarm call, the well known *cock cock cock* . . . .

Breeding. The nest is very simple, usually placed on the ground, perhaps protected by a rock or bush, or situated at the foot of a tree; it may be lined with grass or leaves but not with feathers. In the Crimson-headed Wood Partridge *Haematortyx sanguiniceps* the nest may be raised on a tussock to avoid flooding, and wood quail *Odontophorus* of South America are reported to build domed nests; tragopans are unique in building bulky nests in trees. The eggs are plain (white, buff, olive green) or spotted. Clutch size is highly variable: argus and peacock pheasants lay only 2 eggs and most tropical species of all groups lay 3–5 eggs in a clutch. But open country birds lay larger clutches, typically about 8–12; some species lay even more and the Grey Partridge lays probably the largest clutch of all birds, at least 20 eggs in many cases. Clutch size is complicated in *Phasianus* by egg-dumping habits (several birds may lay in one nest) and in *Alectoris* by 'double-clutching' where the male sometimes incubates a second clutch. There is normally only one clutch in a season, but nest predation is often heavy and birds may re-lay several times. In most cases the males take no part in incubation, although in monogamous species they may help to rear the young. In at least 2 species, the Golden Pheasant and the Great Argus, the female incubates continuously without ever leaving the nest, even to feed or drink, and without moving for much of the time. The chicks of all species are born fully covered with down and they leave the nest soon after hatching; some have well-developed wing feathers and are soon able to fly and to roost up at night with the mother. Most species mature in their first year, but in a few large pheasants maturation of males in particular is deferred for one or more years and in certain cases (peacocks and argus pheasants) full adult male plumage is not attained for 3–5 years. Such species are often long lived, and one Great Argus survived for more than 30 years in captivity.

See photo AGGRESSION. J.T.D. and M.W.R.

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PHEASANT, CROW-: see CROW-PHEASANT; and for family see CUCKOO.

PHENETIC: term applied in taxonomy to a grouping or arrangement based on observable resemblances that may or may not also be evidence of phyletic relationship.

PHENOLOGY: literally the study of visible appearances, and thus used in respect of seasonally recurring events in animate nature, such as—in the ornithological field—first arrival of a migratory species, first laying of a species, last singing of a species, and the relation of these with meteorological data.

PHENOTYPE: the group in which an individual falls by reason of its appearance, which is the result of interaction between external factors and the GENOTYPE; see also GENETICS.

PHILEPITTIDAE: see under PASSERIFORMES, suborder Deutero-Oscines; ASITY.

PHILOPATRY: fidelity to home area—a term introduced as the English equivalent of ORTSTREUE (see DISPERSAL).

PHILYDORINAE: see OVENBIRD (1).

PHOEBE: substantive name of *Sayornis* spp. (see FLYCATCHER (2)).

PHOENICOPTERIDAE: see under PHOENICOPTERIFORMES; FLAMINGO.

PHOENICOPTERIFORMES: an order, comprising the sole Recent family Phoenicopteridae (see FLAMINGO). In Wetmore's system treated as a suborder Phoenicopteri of the order Ciconiiformes, but other authors consider them more closely related to the Anseriformes, and, more recently, to the Charadriiformes, suborder Charadrii, next to the Recurvirostridae.

PHOENICULIDAE: family of CORACIIFORMES; WOOD-HOOPOE.

PHOENIX: see FABULOUS BIRDS.

PHORESY: transport of one species of organism by another that is not parasitic upon it; the term is applied particularly to insects, e.g. Mallophaga carried by louse-flies on a bird (see ECTOPARASITE).

PHORORHACI: see under FOSSIL BIRDS.

PHOTOGRAPHY: as applied to birds—a comparatively young aspect of ornithology. Although its pioneers were active in the 1890s, it was in fact only during the first decade of the present century, and especially after the First World War, that its impact became important and its practice widespread, until today the camera may be regarded, in varying degrees and with different purposes, as a tool of ornithologists. At one extreme, its object may be purely scientific; at the other, merely recreational—a field sport as it were, with the bird taking second place to the artistic effectiveness of the result.

Whilst it is for its scientific value as an aid to ornithology that the camera appeals to the serious student, it is of wide importance in more general directions. Fundamentally, the ornithologist is a collector, as are all naturalists. The museums and private collections are the foundation stone of the science. But as these grew more and more complete, interest turned to the living bird, and with the advent of conservation, as we know it today, aimless collecting fell into disrepute. Here it was that the camera came into its timely own, for with it the instincts of the collector could be satisfied without the need to take life.

Again, if today the public is much more 'bird-minded' than even 20 years ago, photography, more than scientific awareness, is one of the main causes. Ornithology, once the hobby of the few, was the interest of those to whom leisure and opportunity gave access. Today it is shared, with vastly differing degrees of seriousness, by all the many who subscribe to societies and clubs that serve birds and their observers (see BIRD-WATCHING).

Illustration. In this minor revolution of our age the bird photographer has played a decisive part. Without illustration it was of little avail to write about, or appeal for, an unknown bird with some strange name. The photograph has added reality and substance to the written word; and the ease with which it can be reproduced has made it available to the public press. Its rise has been at the expense of, or at least has coincided with the decline of, the coloured Plate, and none would for a moment fail to regret that fact. The age, however, of the stately coloured Plate was the age of patronage, and with its passing the photograph filled a vital gap. Moreover, the skill of the painter was confined to the gifted few; the ability to take a photograph, albeit with different degrees of perfection, was open to all capable of mastering its fundamental technique. Thus those who visit distant places are able, either by illustrated books or lectures, to convey visually to the layman their experiences, the countryside, and its birds. This has been the case especially with the moving film, and the influence of bird photography on the public has reached a new peak with its adoption by television. In short, photography in all its guises—monochrome, colour, and cinematography—has gained for birds a very wide audience, not necessarily knowledgeable, but sympathetic and interested; and it is largely from this pool that has sprung modern 'ornithomania' and the general acceptance of the concept of conservation.

Scientific applications. In the scientific field, the camera stands supreme in recording bird behaviour, e.g. displays and the like. However vivid the written word, it can never compete with the visual record, with the possibility of frame-by-frame analysis. Electronic flash has enabled the student of avian aerodynamics to see in detail wing positions too fast for the human eye to register. Its ability to stop all movement has assisted in the exact identification of insect food brought by birds to their young.

Photography can also give valuable aid in the enumeration of birds, e.g. sea birds breeding densely on a cliff-face, or flocks of birds such as Anatidae in the open photographed from the air (see CENSUS). Mention may also be made of the photography of radar screens showing birds flying overhead (see RADAR). In systematic work, monochrome or colour photographs of a series of skins are often useful to illustrate an author's point.

Trends. Heralded at its advent with acclaim, bird photography has with its increasing popularity come under the fire of criticism. Today pictures of outstanding merit and technical excellence have become the rule, so that the serious ornithologist tends to be scornful of the man who uses a camera but, too often, in his eyes, fails to make any biological contribution along with the photograph. Moreover, photography at the nest, which has for long been the chief focusing point, does entail disturbance. The fact that correct technique and due care of approach can minimize this danger was satisfactory so long as bird photographers were few in number and therefore of little importance. But today many have adopted the pursuit as a field sport, and with numbers the element of possible disturbance becomes of more significance, particularly in the case of rare birds which by their very rarity present a challenge to the photographer. To counter this danger recent legislation has made it an offence deliberately to disturb birds at the nest, and permission for any such photography in Britain has now to be obtained from the Nature Conservancy Council. Consequently there has been a marked reaction from bird-at-the-nest portraits to bird-in-habitat—waders on the tide-line, carrion-eaters at bait, birds in flight—in short to illustrate activities rather than to make portraits.

Equipment. Until the 1960s most serious bird photography was undertaken with large camera, large lens, and large film or plate and with its going went the infinite beauty of the delicate tones in monochrome and the superb detail of plumage. Such equipment was not easy to use, was cumbersome and heavy and limited in its use. But with the advent of the 35 mm camera bird photography was revolutionized. Small and lightweight bodies, high definition lenses with a great variety of focal lengths ideal for either nest or wait-and-see photography; electronic flash now coupled with the metering system on the camera giving accurate exposures whether used as the main lighting source or as a fill-in to soften harsh shadows; high resolution films in colour and in black and white, with faster speeds making it possible to take photographs that would have been impossible before. Who knows what the future holds in store with the continued rapid advance in photographic technology? One thing is certain: that the computer and video-tape will replace many of the methods used today and these developments will give bird photography new life, new purpose and new areas to conquer. G.K.Y. and E.J.H.

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PHOTOPERIODISM: the use of the daily light/dark cycle as a source of predictive information, chiefly in the regulation of seasonal changes in physiological conditions and behaviour. At a given latitude, predictable changes in daylength allow its use by birds and other animals as a proximate factor controlling annual cycles of, for example, breeding, moult and migration in many non-equatorial species. Some species respond directly to increases in photoperiod, beginning the development of, for example, reproductive condition when daylength reaches a threshold value, so that it may be completed in time for the production of young at an opportune season (see BREEDING SEASON). In other species, the seasonal changes in photoperiod may serve also, or only, as a synchronizer for circannual rhythms (see RHYTHMS AND TIME MEASUREMENT). (See also ENERGETICS; MIGRATION; MOULT). Most photoperiodic species become insensitive at a certain time of year to photoperiods which normally would stimulate reproductive development. This phenomenon is described as photorefractoriness and its adaptive value is to prevent breeding at seasons when it is disadvantageous. The complex endocrine events associated with photostimulation are reviewed in Murton and Westwood (1977).

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PHYLETIC: used in the same sense as 'phylogenetic' (see PHYLOGENY).

PHYLOGENETIC TAXONOMY: see TAXONOMY.

PHYLOGENY: sometimes written 'phylogenesis', the evolutionary history of a taxon—contrasted with 'ontogeny', the development of an individual within its own life-span; both 'phylogenetic' and 'phyletic' are used as adjectives. (See TAXONOMY).

PHYLUM: a taxonomic category higher than class (see ANIMAL KINGDOM).

PHYSIOLOGY: the science of bodily function. The use of chemical and physical methods for this study involves the disciplines of biochemistry and biophysics; or the subject may be divided, according to the particular function studied, into such specialities as neurology and endocrinology. The physiology of birds is dealt with in this work under the names of the various systems of the body, and under other special heads, e.g. HEAT REGULATION; METABOLISM; NUTRITION.

PHYTOTOMIDAE: see under PASSERIFORMES, infraorder Tyranni; PLANTCUTTER.

PIAPIAC: *Ptilostomus afer* (see CROW (1)).

PICAE: the second order of Linnaeus.

PICARIAE: formerly used as the name of an order, placed next to the Passeres, which included a motley assemblage of groups now placed in the Piciformes, Apodiformes, Caprimulgiformes, Coraciiformes, and Cuculiformes (and by Stresemann in a still greater number of orders), and originally also the birds now placed in the Psittaciformes.

PICATHARTINI: see BABBLER.

PICI; PICIDAE: see below.

PICIFORMES: an order, alternatively 'Pici', comprising 2 suborders, Galbulae, Pici; 6 families: Galbulidae (JACAMAR), Bucconidae (PUFFBIRD), Capitonidae (BARBET), Indicatoridae (HONEYGUIDE), Ramphastidae (TOUCAN), Picidae (WOODPECKER). The Galbulae are here divided into 2 superfamilies comprising 5 families; but some authors prefer to place all but the first 2 families in the suborder Pici. The Picidae are divisible into 3 subfamilies—Picinae (typical woodpeckers), Picumninae (piculets), and Jynginae (wrynecks). The relationship of the families is indicated by certain anatomical characters common to all. These include a zygodactyl foot, with a distinctive arrangement of the flexor tendons; also, except in the Galbulidae, absence of down plumage at any age in most species. A specialized form of bill is characteristic of each family. Other characters shared by all of them include those of the bony palate, the rather weak structure of the plate of the breast bone and the general appearance of arboreal birds, reminiscent of early arboreal Passerines, to which they may be actually related. Their wide ecological radiation suggests long periods of development and hence the antiquity of all the families in this order.

PICULET: substantive name of Picumninae spp. (see WOODPECKER).

PICUMNINAE: see WOODPECKER.

PIE: see MAGPIE; TREE-PIE (for family see CROW(1)).

PIEDTAIL: substantive name of *Phlogophilus* spp. (for family see HUMMINGBIRD).

PIGEON: substantive name, with 'dove' as a frequent alternative, of the species of Columbidae (Columbiformes): in the plural general term for the family. In popular speech in England 'dove' is used for the smaller and 'pigeon' for the larger forms, but this usage has not been followed by ornithologists; thus, the Stock Dove *Columba oenas* is a typical pigeon in every way.

Characteristics and distribution. Pigeons vary in size from the Diamond Dove *Geopelia cuneata* no bigger than a Skylark *Alauda arvensis* to the crowned pigeons *Goura* spp., which are nearly as large as hen Turkeys *Meleagris gallopavo* (*c.* 17–90 cm). They have soft, dense plumage with feathers that detach easily, and plump, compact bodies with rather small heads. The wings are usually medium sized but may be rather short and rounded or rather long. The tail may be square ended, rounded or pointed and of variable length. The bill is usually rather small, hard at the tip but soft at the base and with a naked cere over the nostrils. The legs are usually short but are longer in some of the terrestrial species. In most species the female is slightly duller than the male; in some the sexes are alike, but in others the male differs strikingly in colour from the female.

The family has been divided into numerous genera, 43 are recognized here; 12 of these are monotypic. The subfamily Columbinae includes not only all the more typical pigeons and doves but also the various superficially partridge-like forms such as the quail doves *Geotrygon* spp. of Central and South America, the Pheasant Pigeon *Otidiphaps nobilis* of New Guinea, the many rather small South American doves, and the Australian bronzewings (see later). Most members of this subfamily are primarily seed-eaters; they differ much in colour, but are mostly clad in soft shades of brown, grey or vinous in various combinations. Often they have iridescent, white, or black areas on the neck, wings, or tail that are exhibited in display or when the bird takes wing.

The subfamily Treroninae consists of a probably bi-phyletic and possible polyphyletic assemblage of arboreal fruit-eating species. Among them are the green pigeons *Treron* spp. of the Afrotropical and Oriental regions. These are primarily soft green in colour, often with beautiful yellow, orange or mauve markings and brilliantly coloured eyes and ceres. Unlike other fruit pigeons they have hard, muscular gizzards, and digest the seed of the wild figs on which they largely feed. The often brilliantly coloured fruit doves of the genus *Ptilinopus* and the larger imperial pigeons *Ducula* spp. differ from each other in size and in the more diverse colours found in the smaller species; they are widespread in the Indo-Malayan and Pacific areas, a few species reaching India proper and Australia. The New Zealand Pigeon *Hemiphaga novaeseelandiae* and the very distinct Top-knot Pigeon *Lopholaimus antarcticus* of eastern Australia are probably related to them, as the blue fruit pigeons *Alectroenas* spp. of the islands of the Indian Ocean almost certainly are. All these forms have a broad gut and void intact the (often large) seeds of the fruits which they swallow whole.

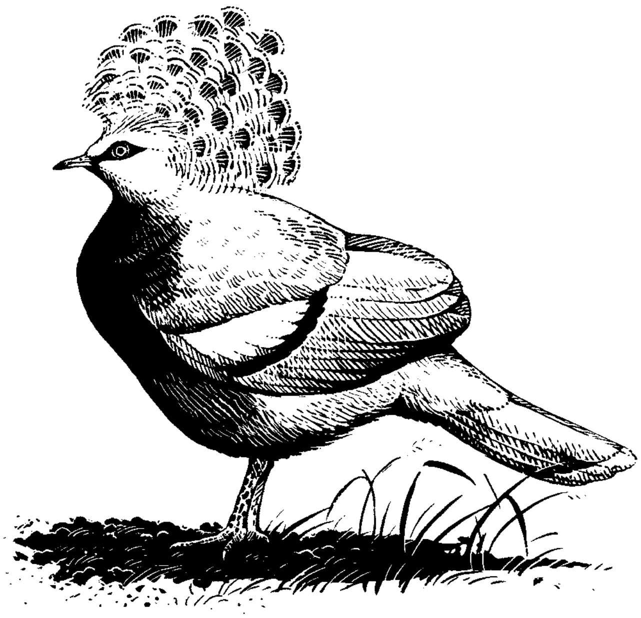
The subfamily Gourinae consists of 3 closely related crowned pigeons *Goura* spp. of New Guinea. They have large, laterally flattened crests of lacy-looking disconnected or spatulate-tipped feathers.

The subfamily Didunculinae comprises only one species, the Tooth-billed Pigeon *Didunculus strigirostris* of Samoa.

Only a few of the more noteworthy of the 255 species of pigeons can be mentioned individually here. The Rock Pigeon or Rock Dove *Columba livia*, a native of Europe, western Asia, India and north Africa, is the ancestor of the many breeds of domestic pigeons and of their feral descendants now common in towns (and often also in the country) throughout most of the world (see DOMESTICATION; HOMING PIGEON). The wild form is bluish grey with two black wing bars and an iridescent neck. It roosts and breeds in caves and on sheltered cliff ledges and feeds on the ground, usually in open areas.

The long-tailed Passenger Pigeon *Ectopistes migratorius* of eastern North America was remarkable for its extreme gregariousness, nesting and migrating in enormous flocks. Unfortunately this made it very vulnerable to human predation and it was exterminated in the wild by 1894 after a long period of relentless exploitation by man (see EXTINCT BIRDS). A closely related but smaller and less brightly coloured species, the Mourning Dove *Zenaida macroura*, is still common, ranging from Alaska to Panama.

The African Collared Dove *Streptopelia roseogrisea* is the ancestor of the domesticated Barbary Dove or Blonde Ringdove and its white variety the so-called 'Java Dove'. A related Asian species, the Collared Dove *Streptopelia decaocto*, has recently spread across Europe in a remarkable manner; the first one to be seen in Britain was in 1952; now it is a common and characteristic bird of lowland villages, suburbs, farmsteads and some towns, throughout Britain.



Victoria Crowned Pigeon *Goura victoria*. (*D.A.T.*).

The little Masked or Namaqua Dove *Oena capensis* of Africa and Madagascar frequents open country and is of nomadic habits. It has a very long, graduated tail and shows marked sexual dichromatism, the male having a black face and breast bordered with pale grey, while these areas are light drab in the female. Another strongly dichromatic species, with a most unusual type of sexual difference, the Flame Dove or Orange Dove *Ptilinopus victor* of Fiji is unique in colour: the male is vivid orange with an olive-yellow head, and the female dark green but with her head the same colour as her mate's.

The Australian bronzewing pigeons of the genera *Phaps*, *Geophaps*, *Ocyphaps* and *Petrophassa* are good examples of adaptive radiation. Although they have diverged greatly in the course of their speciation and adaptation to different biotopes, their colour patterns and behaviour still show their close phylogenetic affinities. They include the only 2 genera, *Ocyphaps* and *Geophaps* (subgenus *Lophophaps*), which have long, pointed crests.

Habitat. Pigeons, of different species, inhabit many types of country, from rocky uplands and scrub-grown semi-desert to tropical forest. Most species are at least partly arboreal but a few are terrestrial or cliff-dwelling. The family is almost cosmopolitan, being absent only from the Arctic, sub-Arctic, Antarctic and sub-Antarctic areas and some oceanic islands. Feral populations of *Columba livia* now exist in some places where no wild species lives or is thought formerly to have done so.

Food. Seeds, fruits, berries, flowers and young leaves are the main foods of pigeons but many species also take small snails and/or other invertebrate animals. Some, perhaps most or all, also take such mineral substances as salt-impregnated earth and crushed shell. Most pigeons have strong, muscular gizzards and long, narrow intestines, but in some of the fruit-eating species, the stomach is designed for rubbing off the pulp or pericarp of fruits rather than grinding seeds and the gut is short and wide. These latter birds digest only the pulp of the fruits they eat, voiding the stones intact. Pigeons drink by immersing the bill and sucking, a habit shared with some estrildid finches but one which many species that do not habitually practise it, can and do use when necessary.

Behaviour. Most pigeons are strong flyers and some are migratory or nomadic. Some species, however, spend much of their time on the ground and make use of their wings only in an emergency or to fly up to perch on a branch or rock. Most of the species whose behaviour is known are to some extent gregarious when not breeding, some gathering into large flocks. Some species often or usually breed colonially; and in others large numbers of individuals may congregate at good feeding places even in the breeding season.

An old writer on domestic pigeons noted that 'These birds have many pretty and whimsical gestures when that they are salacious'. It would be difficult to make a more succinct and yet appreciative statement. Suffice to say that courtship displays are often similar to, though seldom identical with, those used in threat and that, as in other birds, they exhibit bright or striking parts of the plumage or soft parts to best advantage. Pigeons pair at least for the duration of a nesting cycle, in most known cases for an entire breeding season and sometimes for life. In many species the male drives his mate away from potential sexual rivals during the period that she is sexually receptive. The copulation ceremonial may be comparatively short and simple as in the doves of the genus *Streptopelia* or surprisingly involved and 'complicated' as in some of the Australian forms such as the Diamond Dove *Geopelia cuneata*.

Voice. Typically pigeons utter cooing, crooning or booming calls and inflate their necks when so-doing. Some utter whistling, screaming, harsh or cackling cries in lieu of or additionally to cooing. Some usually or often punctuate their display flights with loud wing-clapping. Rather similar, but less deliberate-seeming, more rattling or clattering wing claps may be made (by some species, including the Rock Pigeon and its feral descendants) when the bird suddenly takes wing in alarm or when it intends to fly fast for some distance, for example to a feeding site some miles away.

Breeding. All species whose behaviour is known build a shallow, usually slight but often strongly interwoven nest of twigs, wiry stems, thin roots or similar materials; species that nest on the ground, on ledges or in holes may sometimes dispense with nesting material although more usually they build some sort of nest. One or (in a majority of species) 2 white or (less often) buffish, unmarked eggs are laid. From these hatch helpless nestlings clad sparsely in coarse down which is usually yellow or buff in colour. The young insert their soft bills into their parents' mouths and are fed by regurgitation. They grow rapidly as a rule; some of the smaller species can fly before they are 2 weeks old. Some of the larger species, such as the New Zealand Pigeon, take longer than most and the Nicobar Pigeon *Caloenas nicobarica* is said to grow astonishingly slowly, not fledging until 3 months old (Nicolai 1969). The female usually does most or all of the building, the male bringing her materials. Both sexes share in incubation (from 14–18 days) and care of the young. Both produce 'pigeon's milk', a nutritious curd-like substance formed by the proliferation and sloughing off of the cells of the lining epithelium of the crop (see CROP MILK); for the first few days this constitutes the sole food of the young. The fledged young are fed by both parents, or by their father only, until at least some days after they are strong on the wing. D.G.

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PIGEON, CAPE: sailors' name for the Pintado Petrel *Daption capense* (see PETREL).

PIGEON, HOMING: see HOMING PIGEON.

PIGEON MILK: see CROP MILK.

PIGMENT: see COLOUR; EGG; PLUMAGE.

PIGMENTS, VISUAL: see VISION.

PIHA: substantive name of *Lipaugus* spp. (for family see COTINGA).

PILEATED: crested or capped, referring to the shape of the crown-feathers.

PILOT-BIRD: *Pycnoptilus floccosus* (for family see WREN (2)).

PINEAL BODY: see NERVOUS SYSTEM (Fore-brain).

PINFEATHER: a growing feather still in its sheath.

PINION: poetical word for a wing; sometimes applied to the part of the wing comprising the primary feathers, or even to a single one of these.

PINIONING: rendering a captive bird permanently incapable of flight by cutting one wing at the carpal joint and so removing the basis from which the primary feathers grow (compare CLIPPING). This procedure makes it possible to keep waterfowl and reasonably large ground-birds in the open; it is the lopsidedness, more than the reduction in wing area, that is effective.

PINKFOOT: colloquial short name (plural 'pinkfeet') for the Pink-footed Goose *Anser fabalis brachyrhynchus* (see under DUCK).

PINTAIL: substantive name of certain *Anas* spp.; used without qualification for *A. acuta* (see DUCK).

PIOPIO: native name for *Turnagra capensis*, also known as the New Zealand Thrush, a bird of uncertain affinities but usually placed in the Turnagridae (see THRUSH, NEW ZEALAND).

PIPIT: substantive name of species of *Anthus* and related genera (see under WAGTAIL).

PIPPED: see HATCHING.

PIPRIDAE: see under PASSERIFORMES, suborder Deutero-Oscines; MANAKIN.

PIQUERO: alternative name for *Sula nebouxii* (see GANNET).

PIRACY: term describing a range of inter- and intraspecific food-stealing activities (also called clepto- or kleptoparasitism). Food items procured by one individual (the 'host') are forcibly stolen by another (the 'pirate' or kleptoparasite). What distinguishes piracy from the many other types of feeding interaction is the fact that the host is usually harassed, often violently and for long periods, into giving up items of food. The pirate may snatch food from the host's grasp or the host may drop an item on being chased. Frequently, however, the host is harried into regurgitating food which has already been swallowed. Several pirates may harass one host individual at a time and may steal food from each other once it has been secured. 'Piracy' of nest material also occurs, but this article is only concerned with food-stealing.

The distribution of piracy among birds. Piracy occurs in many animal groups but it is particularly widespread among birds. Its distribution across the various orders, however, is far from random. Only one duck, the American Wigeon *Anas americana*, is a regular pirate although ducks are frequently found in mixed species flocks and are themselves hosts for a number of pirate species. Piracy has never been recorded among the seed and fruit-eating Galliformes, Columbiformes and Psittaciformes and is sporadic among passerines even though these constitute the vast majority of bird species. On the other hand piracy is extensive among the Accipitriformes, Falconiformes and Charadriiformes (particularly the families Stercorariidae and Laridae). These 3 orders together contain 60% of recorded pirate species but only 7% of the known bird species of the world. The frequency of piracy within an order is therefore not simply a reflection of the number of species it contains but appears instead to depend on particular ecological conditions which make piracy profitable. Species of some orders encounter these conditions more often than those of others and the pirate individuals are favoured by natural selection.

Conditions favouring piracy. Regular association of one type or another is an obvious prerequisite for the development of piracy. When raptors pursue prey the latter may drop or regurgitate food to avoid capture. Raptor species may then begin to harass rather than capture 'prey' to obtain already immobilized food. Turkey Vultures *Cathartes aura*, for example, which commonly prey on young Great Blue Heron *Ardea herodias* chicks, sometimes attack older nestlings. As part of their (successful) defence mechanism, older chicks regurgitate food which the vultures then feed to their own offspring. Various raptor species have also been recorded snatching food from one another including one observation of a triple piracy where a Sparrowhawk *Accipiter nisus* was robbed by a Merlin *Falco columbarius*, the Merlin by a Honey Buzzard *Pernis apivorus* and the Honey Buzzard by a Peregrine Falcon *Falco peregrinus*. Piracy is commonest in mixed species colonies of seabirds. In tern colonies, adults steal both from each other and from feeding chicks, and gulls nesting in the colony steal from the terns and from conspecifics. In colonies of Puffins *Fratercula arctica* and Black Guillemots *Cepphus grylle*,

Arctic Skua *Stercorarius parasiticus* parasitizing Lesser Black-backed Gull *Larus fuscus*. (*Photo: P. Munsterman*).

Jackdaws *Corvus monedula*, gulls and even terns operate as ground-based pirates while skuas (*Stercorarius* spp.) and some gulls attack the auks as they return with food to their burrows. Other associations in which piracy is common are single and mixed species feeding flocks (e.g. Black-headed Gulls *Larus ridibundus* robbing Lapwings *Vanellus vanellus* of earthworms), and associations based on scavenging and predator mobbing responses. The mobbing response appears to be the origin of Magpies *Pica pica* stealing from Golden Eagles *Aquila chrysaetos* and of crows stealing from harriers, falcons and kites. Pirates are most likely to attack when food carried by the host is large, visible, of high quality or is scarce and when the host is unlikely to escape.

Many species which show piracy are dietary opportunists. In these cases piracy is one of many feeding strategies which may be employed at different times. For example the omnivorous House Sparrow *Passer domesticus* has been recorded stealing immobilized katydids (Orthoptera) from female digger wasps (*Sphex* spp.). Several gull and egret species are similarly opportunistic pirates. Some species, however, obtain a large proportion of their food through piracy. The frigatebirds (*Fregata* spp.), skuas and jaegers (*Stercorarius* spp.) are probably the best known 'professional' pirates. Specializations for piracy in frigatebirds include a vestigial uropygial gland which greatly reduces the amount of oil in the feathers and the largest wingspan: body-weight ratio of any bird species. These features enhance aerobatic flight but they also mean the birds can no longer enter the water from which most of their food originates.

(R.M.) C.J.B. (1)

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PISCIVOROUS: fish eating.

PISHING: squeaking (see HUMAN IMITATION OF BIRD SOUNDS).

PITOHUI: substantive name of the 7 species of Australasian pachycephaline flycatchers of the genus *Pitohui* (see THICKHEAD).

PITTA: substantive name of the species of Pittidae (Passeriformes, suborder Deutero-Oscines, infraorder Pittae); in the plural, general term for the family. The pittas comprise a rather uniform family of 29 species, usually placed in the single genus *Pitta*. They are mostly confined to the Old World tropics, with their centre of diversity in South-east Asia where 22 species are found.

In 1876 the pittas were placed with the New World Deutero-Oscines on the basis of syringeal morphology, but it is a simple type of syrinx and now considered to be unreliable as an indicator of relationships. However, the result of recent anatomical and biochemical studies is that the pittas occupy an isolated and highly enigmatic position nearest to the New World Deutero-Oscines. Further to this, the latest volume of Peters' 'Check-list of birds of the world' (1979) chose to include the Pittidae in the suborder *Incertae Sedis*. The wing has 10 primaries, the outermost long, and 12 rectrices. The tarsus has a long anterior and a posterior plate.

Characteristics. Pittas' size range is 15–28 cm; weights vary between 42 and 218 g. Fifteen male Fairy Pittas *Pitta nympha* collected on Taiwan in May had a range of 67.5–155 g and a mean of 109 g. They are stocky, long-legged, short-tailed birds and in the field some species might be confused with ground thrushes, the group with which they were originally placed. They have also been called 'ant-thrushes' or 'jewel-thrushes'. The plumage of many pittas is highly colourful. Much of the bright coloration, however, is on the underparts, while the more protectively patterned upperparts effectively conceal them in the dim light of the tropical forest floor. Nine species are sexually dimorphic, 4 with brightly coloured males and drab females. Juvenile birds are more brownish and mottled or spotted.

Habitat. Moist evergreen or deciduous forests, bamboo groves, mangroves, dense secondary scrub and wooded ravines in more open areas; up to 2,500 m.

Distribution. Widespread in the Oriental Region as residents and/or migrants, extending north to Japan (one species), east to Australia (3) and the Solomon Islands (one) and also tropical Africa (one).

Populations. Many forms are considered rare, but this is partly due to their retiring habits; pittas may be locally common.

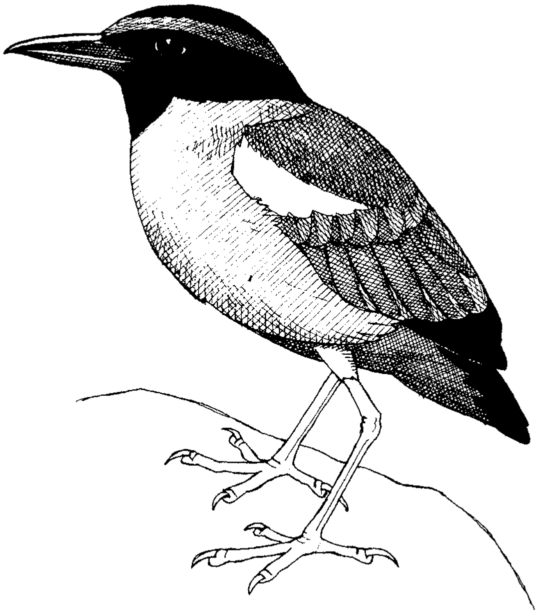
Movements. Generally sedentary, with local or seasonal dispersal, also altitudinal. Eight forms are migratory, including the Indian Pitta *P. brachyura* from the Himalayan region to southern India and Sri Lanka, the Fairy Pitta from Japan to Borneo and the African Pitta *P. angolensis* in east and central Africa. Some long distance vagrancy has been recorded, e.g. the Blue-winged Pitta *P. moluccensis* has reached NW Australia. Pittas are nocturnal migrants and their attraction to lights has provided many records. A study of migrating birds at Fraser's Hill, West Malaysia, revealed the following periods for the 2 regular migrants, the Blue-winged Pitta and the Hooded Pitta *P. sordida*: 25 September–22 December and 7 April–9 May.

Food. Insects, spiders, worms and particularly snails; small shrimps, crabs, lizards or snakes may also be taken. Other food has seldom been recorded, e.g. the Garnet Pitta *P. granatina* on Borneo taking large seeds and Schneider's Pitta *P. schneideri* of Sumatra taking vegetable matter. A captive Hooded Pitta studied for one month ate approximately its own weight in food each day.

Behaviour. Normally all pittas live singly or in pairs, but larger groups may occur during migration. Pittas spend most of their time foraging on the ground where they hop about, often flicking and bobbing their tails. If disturbed, they will hop away or fly a short distance, keeping near the ground; in some commoner species this reveals a conspicuous white wing patch. When foraging, pittas flick the leaves and other vegetation over with their strong bills and may sometimes use slight wing flicking movements to flush small prey ahead of them. A stone or log is used as an anvil to break snail shells. An ability attributed to pittas of locating prey by smell is supported by a study of their olfactory system, with the largest olfactory ratio among the Passeriformes. This is exemplified by the captive Hooded Pitta mentioned above that actively sought worms by digging the entire bill into the soft earth provided. Pittas are shy and retiring birds and often only located by calls, an imitation of which will usually bring them into view; outside of the breeding period they may be more silent. When calling, pittas have been observed up to 10 m above the ground and short looping flights may be performed from a perch. At night pittas usually roost in trees. An aggressive display observed in a few species involves crouching with fluffed out feathers, wings spread and bill pointed upwards. The distinctive Eared Pitta *P. phayrei* has long plumes at the side of the nape that may have a special function, as all species have erectile crown feathers, elevated when excited.

Voice. A short series of variably pitched whistles, often dissyllabic, is characteristic; also trilling, rolling sounds. Calls may be heard during the day from some species but most often at dawn and dusk, before rainstorms, and on moonlit nights, when some neighbouring birds may call against each other or in chorus.

Breeding. The breeding season is variable. In distinctly seasonal areas, pittas are summer breeders, especially the migratory species. Otherwise, as in South-east Asia, they breed in all but the wettest months. The nest may be found up to 8 m above the ground, but usually under 3 m or even on the ground. Sites include stumps, amongst root buttresses of large trees, against banks or fallen trees, in tangled clumps of vegetation or rock clefts. The nest is an untidy globular or elliptical structure of twigs and rootlets often decorated with moss, lined with finer materials and with a low side-entrance. A doormat of animal dung outside the nest is made by the Australian Noisy Pitta *P. versicolor*. Average dimensions for some nests of the Blue-winged Pitta were: external diameter 20 cm, internal 16 cm, depth 7.5 cm, and entrance 10 cm wide. When disturbed, the bird may cover the entrance with a small, leafy twig. So far as is known, both sexes share in nest building, incubation and the care and feeding of the young. The clutch size is 2–7 eggs, but usually 3–5; they vary from a broad blunt oval to a spheroidal shape, some with a large amount of gloss, and are white or buffish with reddish or purplish spots or speckles and fine grey or lilac undermarkings. Fifty eggs of the Indian Pitta measured 23.3–28.2 × 20.0–22.4 mm, with a mean of 24.7 × 21.2 mm; average egg weight from a clutch of the Blue-winged Pitta was 5.2 g. The incubation period for a captive Hooded Pitta was 17 days. This was for the first breeding in captivity by J. Delacour (1934). Pittas are difficult to keep and have seldom been bred, partly due to their pugnacious nature. The young hatchlings are fleshy or purplish coloured, sometimes with tufts of natal down on the upperparts. M.D.B.



Noisy Pitta *Pitta versicolor*. (*N.W.C.*).

Benson, C.W. & Stuart Irwin, M.P. 1964. The migrations of the pitta of eastern Africa (*Pitta angolensis longipennis* Reichenow). N. Rhodesian Journ. 5: 465–475.

Delacour, J. 1934. Breeding the Hooded Pitta (*Pitta cucullata*). Avic. Mag. (4) 12: 222–226.

Garrod, A.H. 1876. On some anatomical characters which bear upon the major divisions of the Passerine birds. Part I. Proc. Zool. Soc. Lond. 1876: 506–519.

Harrisson, T. 1964. Food capacity of a Green-breasted Pitta *P. sordida*. Sarawak Mus. Journ. 11: 611–615.

King, B.F., Woodcock, M.W. & Dickinson, E.C. 1975. A Field Guide to the Birds of South-east Asia. London.

McClure, H.E. 1974. Migration and survival of the birds of Asia. Bangkok: ASRCT.

Peters, J.L. 1979. Check-list of Birds of the World, vol. 8 (Traylor, M.A. Jr, ed.). Cambridge, Mass.

PITTA, ANT-: see ANTPITTA; ANTBIRD.

PITTIDAE: family of PASSERIFORMES; suborder Deutero-Oscines; PITTA.

PITUITARY GLAND: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; NERVOUS SYSTEM.

PITYRIASIDIDAE: a family of PASSERIFORMES, suborder Oscines; BRISTLEHEAD.

PLAINRUNNER: substantive name of *Coryphistera alaudina* and *Clibanornis dendrocolaptoides* (see OVENBIRD (1)).

PLAINS-WANDERER: alternatively 'Collared Hemipode', *Pedionomus torquatus*, sole member of the Pedionomidae (Gruiformes, suborder Turnices). *Pedionomus* is placed apart from the buttonquails (Turnicidae) on account of the persistent hind toe, the pyriform instead of oval eggs, and the persistence of paired carotid arteries: but many consider separation as a subfamily (Pedionominae) sufficient.

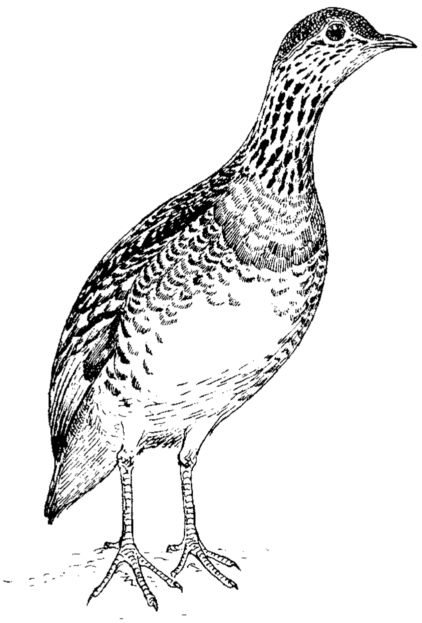
Characteristics. The Plains-wanderer is a small bird (male *c.* 10 cm, female *c.* 12 cm). Although superficially like a buttonquail *Turnix* sp., the Plains-wanderer typically does not exhibit the crouching posture but stands erect like a bustard (Otididae); an interesting photograph published by Purnell (1915) shows clearly the bird's habit of standing 'elevated on its toes' so as to achieve a wide view of the surroundings.

The bill is slender and of medium length. The wings are short and rounded, the tail is very short, and the whole body is compact. The plumage shows a cryptic pattern of reddish-brown, buff, and black, paler below; there is a 'collar' of black spots on a white ground. Sexual dimorphism is marked, the female having a chestnut-coloured breast. They are usually loth to fly, preferring to run or 'freeze', and have on occasions been caught by hand. They have a whirring flight like that of a buttonquail.

Habitat. Plains-wanderers inhabit open grasslands and plains of south-eastern Australia, where they keep to open areas and avoid the scrubby sections and stubble that are favoured by most buttonquail species.

Distribution. The breeding range is from Duaringa, Queensland, in the north, to western New South Wales, Lake Frome (one or two records) and south-eastern South Australia. Most recent records are from Victoria. D'Ombrain (1926) has reviewed certain aspects of the scanty knowledge of the habits of the species, speculating about the reason for its rarity in modern times. Recent records in South Australia, Victoria and New South Wales are widely dispersed but uncommon. Alteration of habitat due to sheep, rabbits, and fires, and the introduction of the fox and feral cat, have undoubtedly contributed to the numerical reduction of the species.

Food. Such stomach analyses as have been carried out disclose the presence of insects, seeds, vegetable matter, and sand.



Plains-wanderer *Pedionomus torquatus*. (*C.J.F.C.*).

Breeding. The breeding season is described as being from September to January. The nest is a slight depression in the ground, and 4 eggs make up the clutch; they are pale yellowish or greenish, spotted with grey and olive. The male incubates the eggs and raises the young. (A.K.) H.J.F.

Crome, F.H.J. & Rushton, D.K. 1975. Development of plumage in the plains-wanderer. Emu 75: 181–184.

D'Ombrain, E.A. 1926. The vanishing Plains-wanderer *Pedionomus torquatus*. Emu 26: 59–63 (map).

Purnell, H.A. 1915. The Plains-wanderer in captivity. Emu 15: 141–143 (photograph).

PLAINTAIN-EATER: substantive name (unfortunately misleading) of some species of Musophagidae (see TURACO).

PLANTAR: pertaining to the posterior surface of the tarsus (equivalent to the sole).

PLANTCUTTER: substantive name for 3 species of Phytotomidae (Passeriformes, infraorder Tyranni); in the plural, general term for the family. *Phytotoma* is a single, polytypic and purely neotropical genus, its 3 species being very alike.

Characteristics. Plantcutters are heavily built finch-like birds about the size of an European Hawfinch *Coccothraustes coccothraustes* (18–19.5 cm), having short wings, rather long tails and with crown feathers pileated to form a slight crest. The plumage on the upper parts is plumbeous and/or brown, in the male streaked more heavily with black. The throat, breast and underparts of the female are light buff and dull ochre with dark streaks; these colours being replaced in the male by bright rufous and chestnut. The males of all species present a conspicuous white wing-bar. Tails in *Phytotoma rutila* and *P. raimondi* are blackish with white tips; in the case of *P. rara* they are black-tipped with chestnut coloured inner webs. Immatures tend to look like females. Legs are short and feet large in comparison; the bill is stout, short, conical and finely serrated in both mandibles. Eyes are bright amber or yellow in both sexes.

Habitat and distribution. Plantcutters are typical of bushy and low woodland, preferring rather open country; also well adapted to cultivated fields and orchards where they may cause damage. They are found from about 3,000 m in Andean valleys down to the coast. They have enlarged their range and, locally, their numbers due to increasing cultivation. But intensive pesticide spraying on parts of this artificial habitat may eradicate a whole population.

The genus is mainly distributed in western and southern South America. The smallest species, *Phytotoma raimondi*, the Peruvian Plantcutter (total length *c.* 18 cm) is confined to the coastal fringe of northern Peru between Tumbes and Lima. The Chilean Plantcutter *Phytotoma rara*, the largest representative (19.5 cm), has been observed in Chile from Atacama to Magallanes and along the Andean foothills of Argentina from Neuquén to northern Chubut. The Red-breasted Plantcutter *Phytotoma rutila* (19 cm) is distributed in SE Bolivia, Paraguay, Uruguay and Argentina south to Río Negro.

Movements. Plantcutters are generally sedentary in lowlands, but high-level and southern populations migrate respectively down and/or north during autumn and winter seasons.

Food. The genus is entirely vegetarian. The bill is admirably adapted for plucking buds, shoots, tender leaves and different fruits. The birds, being provided with such an instrument of destruction, are considered one of the worst enemies to fruit and horticultural plantations.

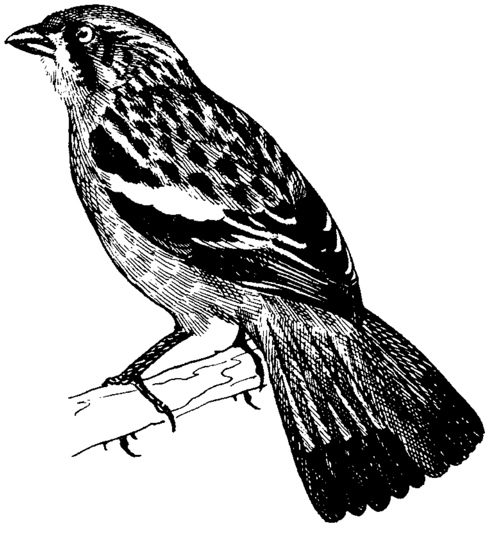
Behaviour and voice. Plantcutters are commonly observed in pairs and, at the end of the breeding season, family groups are typical. Small flocks of 6 to 12 individuals may be observed flying or foraging together in loose association. They tend to be territorial during the breeding season, males making their presence known by an oft-repeated rasping metallic wheeze. When approached they fly off with an undulating rather sluggish flight to perch on top of another nearby shrub and utter again their unmusical rattle.

Breeding. Nesting starts in October and continues into January for Andean populations. The nest is loosely made, flat, untidy and built almost entirely with root fibres. It measures about 10–12 cm in diameter and is usually placed in the fork of horizontal branches near the top of low trees or shrubs. Clutch-size 2–4 eggs; these are greenish-blue, sparsely dotted with dark markings which have a tendency to zone at the broad end. (J.D.G.) R.P.S.

PLASMA: see BLOOD.

PLATALEINAE: see SPOONBILL.

PLAY: an activity performed by a wide variety of bird species; although probably less common in birds than in mammals (Kilham 1974; Ficken 1977). Playful behaviour in young animals may be important in the development of social behaviour and social relationships and may also be useful in the development and/or 'polishing' (or practising and learning) of specific motor skills (but see BEHAVIOUR, DEVELOPMENT OF.) Also, play may result in increased flexibility of behaviour (Ficken 1977). Some birds, as do many mammals (Bekoff and Byers 1981), even use play invitation signals to solicit play from other individuals. Play behaviour in birds may take on a number of different forms including mock-fighting, sexual behaviour and courtship, reciprocal chasing and fleeing, and the performance of rapid motor sequences such as 'nose-diving' at other birds or performing somersaults in water, and may involve playing with food objects or even making snowballs (Kilham 1974; Keller 1975; Ficken 1977). Social play is probably less common than object play.



Chilean Plantcutter *Phytotoma rara*. (*C.E.T.K.*).

Young raptors have been observed to make hunting movements towards inedible objects and Red-bellied Woodpeckers *Centurus carolinus* will try to put miscellaneous objects such as bent nails in crevices otherwise used to store food (Kilham 1974). Young Christmas Island Frigatebirds *Fregata minor minor* will swoop at, pick up, and then drop, leaves and other objects floating on the surface of the sea. Vocal play also may occur. Subsong shows some close similarities with characteristics of nonvocal mammalian play (Ficken 1977).

Play by adults is more difficult to understand than is play by young (as is the case in many mammals). Rooks *Corvus frugilegus* will commonly indulge in tumbling acrobatics; Ravens *C. corax* have been described as carrying up twigs or pieces of heather, which they drop and then catch again in the air. Various aquatic birds, e.g. Eider *Somateria mollissima* and Black Guillemot *Cepphus grylle*, have been seen to disport themselves in swift currents in a way that suggests that the birds are 'having fun'. Similarly, Adélie Penguins *Pygoscelis adeliae* have been described as riding in vociferous parties on small iceflows in a tide race, only to swim back to the starting point and begin once again. That play may indeed be enjoyable has been suggested for mammals as well (Bekoff 1976). Adults (and probably young) seem to play most when they are undisturbed and when other more pressing needs (such as food, shelter, warmth) have been satisfied. As in mammals, play rarely occurs when individuals are disturbed or stressed.

In many cases it is very difficult to separate playful from non-playful activities, regardless of how amusing the behaviours appear to the human eye. More quantitative data are needed regarding avian play and it would be useful if a list of play criteria could be developed. One should not expect *a priori* that avian play will necessarily be very similar to mammalian play. Avian play should be studied as an entity in itself before detailed comparisons are made with mammalian play, especially concerning its structure (what animals do when they play), function(s), adaptive significance, development, and evolution. M.B.

Bekoff, M. 1976. Animal play: problems and perspectives. Perspectives in Ethology 2: 165–168.

Bekoff, M. & Byers, J.A. 1981. A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: an ethological hornet's nest. *In* Immelmann, K., Barlow, G., Main, M. & Petrinovich, L. (eds.). Issues in Behavioural Development: the Bielefeld Conference. Cambridge.

Ficken, M.S. 1977. Avian play. Auk 94: 573–582.

Keller, R. 1975. Das Spielverhalten der Keas (*Nestor notabilis* Gould) des Zürcher Zoos. Zeitschrift für Tierpsychologie 38: 393–408.

Kilham, L. 1974. Play in hairy, downy, and other woodpeckers. Wilson Bull. 86: 35–42.

PLAYBACK: refers to the broadcasting of recorded songs or calls, usually in the field. Since portable recording equipment became available in the 1950s, this technique has been employed increasingly for research on bird sounds, for censusing, viewing, photographing and capturing birds, and as a control method where birds are regarded as pests. It is suitable for use with any kind of bird which uses any sort of sound for communication. Although birds often respond to poor recordings, playback of good quality and adequate volume is important for most applications. Portable equipment is usually sufficient. Although there is little evidence that playback is harmful, it should be used with restraint. Birds are protected by their tendency to lose interest in repeated sound signals.

Alone or with visual models, playback enables researchers to use experimental methods to investigate the meaning of sound signals by observing responses of listeners. The investigator can vary the location, time of day, stage of the breeding cycle, type of listener to be studied and the individual whose signal is to be broadcast. Various studies have shown that birds can distinguish between sounds of their own and other species and may recognize sounds of mates, parents, offspring and individual territorial neighbours. In certain cases responses between species have been demonstrated. By playing altered or artificial sounds, it is possible to determine which features are sufficient to elicit a particular response. Thus, the acoustic basis of species and individual recognition has been investigated. For most purposes, brief playback experiments are more meaningful than prolonged exposure of birds to an unresponsive sound source.

Playback is especially valuable in the study of territorial behaviour. For example, territory-holders have been removed and recordings played in their territories to investigate the role of song as a 'keep out' signal. Birds that advertise by song usually respond aggressively if recorded songs are played within their territories. By moving the loudspeaker, their defended boundaries can be mapped. Where territories are contiguous, mapping by playback provides an accurate census of the breeding population. However, if members of a species are few and far between, a bird may follow a loudspeaker far beyond the area it normally occupies. Playback is useful for locating rare, inaccessible or nocturnal species. Song or distress calls can be played near traps or mist nets to capture particular individuals. This is useful in studies of breeding birds.

Since playback may attract birds which are otherwise difficult to approach, it facilitates close observation, sound recording and photography. It is most effective early in the breeding season (often prior to mating) and when the recording is of the bird's own voice or that of an unfamiliar member of the same population. If the response wanes it may be restored temporarily by changing songs or locations.

As a control method, alarm or distress calls have been broadcast to disperse undesirable roosts, reduce bird hazards at airports, and to protect crops. The effectiveness of such measures may diminish with prolonged use. J.B.F.

Blackburn, F. 1974. The uses of play-back tape. *In* Turner Ettlinger, D.M. (ed.). Natural History Photography. New York.

Falls, J.B. 1978. Bird song and territorial behaviour. *In* Krames, L., Pliner, P. & Alloway, T. (eds.). Aggression, Dominance and Individual Spacing. New York.

Falls, J.B. 1981. Mapping territories with playback: an accurate census method for songbirds. *In* Ralph, C.J. & Scott, J.M. (eds.). Estimating the numbers of terrestrial birds. Studies in Avian Biology, 6.

Falls, J.B. 1982. Individual recognition by sounds in birds. *In* Kroodsman, D.E. & Miller, E.H. (eds.). Acoustic Communication in Birds, vol. 2. New York.

Murton, R.K. 1971. Man and Birds. London.

PLENARY POWERS: of the International Commission, see NOMENCLATURE.

PLOCEIDAE: a family of the PASSERIFORMES, suborder Oscines; WEAVER; also SPARROW (1)).

PLOCEPASSERINAE: see SPARROW-WEAVER AND SCALY-WEAVER.

PLOVER (1): substantive name of the majority of species of the Charadriidae (Charadriiformes, suborder Charadrii); in the plural, general term for the family. The other substantive name widely used in the group is 'lapwing', but not all the species that are generically lapwings are in practice so called. A few members of the family have particular names, and one of these, 'dotterel', is sometimes used also as a substantive name of other species of Charadriidae, especially in Australia and New Zealand.

Characteristics. Plovers are birds of from small to medium size (15–40 cm long), compactly built and thick-necked, with large eyes. They run swiftly and fly strongly. The bill is usually straight, fairly stout, and of only moderate length compared to the size of the head—not showing numerous specialized forms such as are found in the Scolopacidae (see SANDPIPER). The wings are long, the tail is short to medium, the legs are of various lengths, and with or without a vestigial hallux. The plumage differs from that commonly found in the Scolopacidae in that it shows bold colour patterns (in brown, olive, grey, black, and white), but it is nevertheless cryptic owing to the disruptive effect. Common features are a white band on or behind the nape, a dark thoracic band or area, and a dark terminal or subterminal band on the tail. The downy chicks of most species have the white band on the nape, and also a dark cap. A few species show pronounced seasonal change; the sexes are alike or nearly so, and the juvenile plumage is also not strikingly different.

Bock (1958) recognized about 50 species of plovers, with a few others doubtfully belonging to the group. They can be broadly divided into the lapwings, recognized by Bock as a single genus *Vanellus* comprising 24 species; and the true plovers, 5 genera comprising 26 species. This classification amalgamated many genera recognized hitherto, the majority of them monotypic. The earlier classification had been based on characters of doubtful validity—notably the shape of the skull, which is in fact particularly affected by the size of the nasal glands, this in turn depending on adaptation to a fresh-water or saline environment. The classification adopted here recognizes some subdivision of the lapwings at a generic level.

Of additional forms sometimes included in the Charadriidae, *Phegornis* is retained here on the basis of relationship with the dotterels *Eudromias* spp. (see Storer in Burton 1974); and the Australian Dotterel *Peltohyas* *australis*, sometimes included with the coursers, is treated as a plover on the basis of the review by Maclean (1976); but the turnstones (Arenariinae) are firmly placed in the Scolopacidae (see SANDPIPER) (Jehl 1968, Burton 1974); and the MAGELLANIC PLOVER *Pluvianellus socialis* has been removed from the Charadriidae and placed in a monotypic family Pluvianellidae by J.R. Jehl.

The plover family is cosmopolitan in its distribution, but whereas the Scolopacidae are predominantly native to the Northern Hemisphere, the Charadriidae are to a large extent tropical.

Lapwings. Although the general appearance of the several species of *Vanellus* is diverse, the tail is always white basally and usually has a broad black band distally, while the wing always has black primaries and usually a broad white stripe. Characters frequent among the lapwings, but not found in other plovers, are a crest, facial wattles, and wing-spurs; the last correlate with the aggressive nature of the birds, and in species which have no actual spur on the carpal joint a bony knob is present beneath the skin. Africa has the largest number of species. North America has no lapwings, apart from the occasional occurrence of vagrant individuals or flocks of the European *Vanellus vanellus*; South America has 3 species, probably descended from birds crossing directly from Africa. New Zealand had none, even as regular visitors, until its successful invasion by an Australian form (*V. miles novaehollandiae*).

The English name was originally given to the Lapwing *Vanellus vanellus* and refers to the rather slow wing-beat. It is a crested species native to middle Palearctic latitudes. The Sociable Plover *Chettusia* ('*Vanellus*') *gregarius* has a circumscribed inland breeding range on both sides of the Ural mountains. The handsome Spur-winged Plover *Hoplopterus* ('*Vanellus*') *spinosus* is found in south-eastern Europe, the Middle East, Egypt and tropical Africa (mostly north of the Equator); in eastern Africa its range is largely allopatric with that of the Blacksmith Plover *V. armatus*, which replaces it to the south, though the 2 species are patchily sympatric in Kenya where they have both been recorded nesting around the same water hole. Africa seems to have been the centre from which the lapwings have radiated, as judged by present-day distributions and specializations. Separation in eastern Africa by altitude is found between *V. lugubris* and *V. melanopterus* and by habitat between *V. tectus* (in arid thorn scrub) and *V. coronatus* (on grassland). The former is also a more northerly species, but the ranges are sympatric in Kenya, though with a fair degree of ecological separation. Amongst further habitat specializations may be cited the jacana-like habits of *V. crassirostris*, which makes a floating nest, and the exploitation of rivers with extensive sandbanks by *V. albiceps* and other plovers during the dry season.

Of the smaller number of species in the Oriental Region, the Red-wattled Lapwing *V. indicus* and the Yellow-wattled Lapwing *V. malabaricus* are well-known birds in India, where the latter often nests on flat roofed houses. The River Lapwing *V. duvaucelii*, ranging from India to S. China, is often considered conspecific with the Spur-winged Plover *Hoplopterus* ('*V.*') *spinosus*. Australia holds the Banded Plover *V.* ('*Zonifer*') *tricolor* and 2 subspecies of the Masked Plover *V. miles*.

Golden Plovers. The 4 species of *Pluvialis* are exceptional in their plumage pattern; the white band on the nape is not present even in the downy chick, and the colour of the back is 'spangled' instead of uniform. These 'spangles', pale feather edgings, often wear off during the winter months. The under parts are largely black in the breeding season in the 3 northern species. They are relatively larger birds than the sand plovers (see below).

The Golden Plover *P. apricaria* (northern and southern races) breeds in northern Europe and the extreme north-west of Asia, reaching the Mediterranean countries and northern India on migration; the southern race is present throughout the year in Britain. The closely related Lesser or American Golden Plover *P. dominica* (Atlantic and Pacific races) is native to high latitudes in North America and Siberia east of R. Yenesei. Its migrations extend as far as Australia, Argentina and East Africa (e.g. Ethiopia and Somalia). The Grey Plover *Pluvialis* ('*Squatarola*') *squatarola*—called Black-bellied Plover in America—has a Holarctic breeding distribution at very high latitudes; and migrations extending as far as Chile, Cape Province, and Australia. The so-called New Zealand Dotterel *P. obscurus* has reddish-brown underparts in the breeding season; it is restricted to New Zealand, and one may suppose it to be descended from migrant ancestors of the northern species remaining in the south to breed.

Sand plovers. This is sometimes used as a convenient general term for the species here regarded as constituting the genus *Charadrius*, often termed 'dotterels' in Australia. They are mostly rather small plovers, but some are of medium size. In general the plumage is brown or grey above and white below except for some expression of a pattern of darker markings that is characteristic of the genus—a dark band across the breast, a black forehead, and a black line from bill to eye.

Bock recognized 24 species and divided them into (a) a typical group; (b) sand plovers in the narrow sense; (c) mountain or plains plovers; (d) a number of aberrant forms. The genus is cosmopolitan in its distribution. Of group (a), the familiar Ringed Plover *Charadrius hiaticula* of Europe also breeds in Greenland and arctic Canada, where it has been known to interbreed with the Semipalmated Plover *C. semipalmatus* of North America; they are often considered to be conspecific. The Kentish Plover *C. alexandrinus* of Europe (Snowy Plover of North America) is a small and pale species with only an interrupted breast-band. It is practically cosmopolitan, in different subspecific forms, the most colourful being the Red-capped Dotterel of Australia. The Killdeer *C. vociferus*, which is larger than those just mentioned, has two breast-bands; it is a bird of inland pastures and breeds from Canada to Peru. Another species with 2 black bands (leaving 3 white areas) is the Three-banded Plover *C. tricollaris* of Africa South of the Sahara, including Madagascar. The Double-banded Dotterels *C. bicinctus*, which breed in New Zealand, and some of which then visit Australia, have an upper black band and a lower chestnut one.

Typical of group (b) is the Great Sand-plover (or Large Sand Dotterel) *C. leschenaultii* which has no black on the chest, but a broad band of rufous in the male only; it is a notable migrant, breeding in Central Asia and reaching South Africa and Australia. Amongst group (c), the Mountain Plover *C.* ('*Eupodia*') *montanus* inhabits semi-arid plains in the southern area of the Rocky Mountains, and is notable for its flexible mating system (see later), a supposed adaptation to unpredictable food supplies which vary in quantity from year to year. The Caspian Plover *C. asiaticus*, which may be conspecific with the larger Oriental Plover *C. veredus*, breeds in the eastern Palearctic and reaches South Africa and Australia on migration. It seems closely related to the Winter Plover *C. modestus* of South America.

Other genera. In similar habitats to the montane plovers are found the Dotterel *Eudromias morinellus*, a native chiefly of northern Europe and western Siberia, migrating to the Mediterranean and south-western Asia, and the congeneric *E. ruficollis* of South America. Also found in South America is Mitchell's Plover *Phegornis mitchellii*, a bird of the edges of mountain torrents, where it feeds on animal prey picked from aquatic plants. The Wrybill Plover *Anarhynchus frontalis* of New Zealand, breeding in the South Island and migrating to the North Island, is unique among birds in having a laterally deflected bill, the distal quarter being turned to the right; with this it probes for insects under stones on beaches.

Habitat. Lapwings are found in a wide variety of habitats during the breeding season, from areas of human habitation (*V. malabaricus* in India, *V. miles novaehollandiae* in Australia), through farmland, both arable and grazed pasture (*V. vanellus* in Europe), sparsely vegetated ground (*V. tricolor* in Australia), thorn scrub (*V. tectus* in E. Africa) to sandbanks in major African rivers during the dry season. The 3 species of golden plovers that breed in the northern hemisphere do so in sparsely vegetated mountainous areas or on the arctic tundra. Of the sand plovers, some breed on sandy or pebbly seashores, often nesting only a short distance above the tide-line (*C. hiaticula* in Europe, *C. alexandrinus*), whereas others of the same species may nest inland on shingle beds in rivers or beside lakes, as well as on stony tundra (*C. hiaticula* in Greenland). *C. pallidus* breeds around soda-lakes in East and SW Africa. Other species frequent open ground, often far from water, whilst breeding: either lowland fields (*C. vociferus*) or dry prairies at higher altitudes (*C. montanus*).

Movements. Those species breeding at high latitudes are migratory, some of them performing journeys of up to 10,000 km. Immature birds of the larger species may stay south of the arctic breeding grounds for 1 or 2 years. The migrations of the golden plovers, particularly *P. dominica*, involve long sea-crossings e.g. from Alaska to Hawaii, and consequently require the storage of large quantities of fat before departure and an accurate navigation system which can be used over the open ocean. In temperate latitudes, many species migrate towards the Equator in autumn but few cross it. Some populations of some species are partial migrants, e.g. the British population of *C. hiaticula*, and the New Zealand *C. bicinctus*. In tropical regions, most species move only short distances, though this may involve a change of habitat e.g. from riverine sandbanks to nearby ricefields in Nigeria when the large rivers come into flood. European species that feed inland on damp pastures or ploughed land in the non-breeding season, e.g. *V. vanellus*, move west or south during severe weather in winter or during very dry summer weather, when their foods become unavailable.

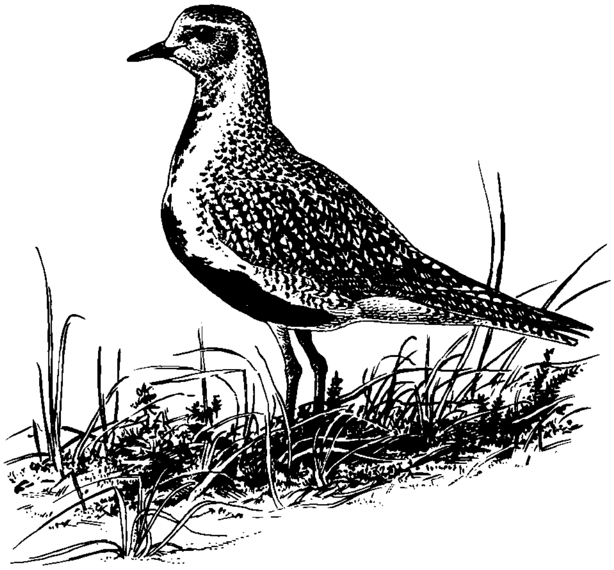
Food. Plovers forage in a characteristic way, by repeated runs of a few metres at a time, interrupted by pauses spent in an upright or 'head-lowered' attitude. A peck at the ground often follows a pause, with a change from the upright to the 'head-lowered' attitude sometimes intervening. Successive runs may involve changes in direction of more than 90°, presumably because birds have detected prey to the side of, or behind, them. Although it has been claimed that plovers hunt by auditory cues (and have been shown to be able to do so in the laboratory), it is unlikely that these are of major importance in field conditions, where sight is used almost exclusively (Pienkowski 1983). Plovers can detect prey when these are active on the surface of the substratum, and they may use foot-trembling to make prey move. They do not search by probing, as do many sandpipers. Their food is mainly animal. On coasts and estuaries, it comprises the larger intertidal polychaetes, small crustacea and small bivalves and gastropods, swallowed whole. Terrestrial plovers take many annelids, dipteran larvae and carabid beetles. Many species feed at night, some probably obtaining a greater proportion of their daily food intake then than by day, as a result of the greater variety and size of invertebrates that become active at the surface of the substratum by night.

When feeding, plovers space out much more than sandpipers, and often feed away from the water's edge, even in intertidal areas. In this way, they are able to reduce physical disturbance to the substratum, which might otherwise make prey unavailable. (When disturbed, many prey either become immobile or move to depths beyond the range of a plover's bill.) Some individuals of some species, e.g. *P. squatarola*, defend feeding territories during the non-breeding season, partly to reduce disturbance to prey, partly to conserve food resources and sometimes to ensure sheltered sites in which to feed during gales (Townshend *et al* 1984).

Behaviour. Many plovers are also territorial during the breeding season, though some species, e.g. *V. vanellus* in Europe and *V. tricolor* in Australia, form what have been termed 'loose colonies', in which nests are well spaced, but some co-operation occurs between adjacent pairs in mobbing potential predators. (These loose colonies appear to be determined only in part by suitability of habitat.) Outside the breeding season, plovers tend to be gregarious inland in Europe (e.g. flocks of thousands of *P. apricaria* and *V. vanellus*) though never in such large numbers on coastal sites, nor inland in Africa. On the coast, birds that have been feeding while well-dispersed over many sq km of mudflats usually come together to roost, often with sandpipers.

Display and voice. Territorial plovers display on the ground at the boundaries of their territories and in the air above them, particularly at the beginning of the breeding season. When in flight, with slow butterfly-like wing-beats, they often 'sing' with melodious long trills. Call-notes, which are usually short whistles or shrill cries, are often reserved for flights to and from roost and feeding areas, and are not always given when birds are disturbed. Other displays connected with nesting include injury-feigning to distract predators from the vicinity of nests (e.g. by shore-nesting plovers such as *C. hiaticula*), and attacks, by jumping with spread wings, in the faces of large herbivores approaching nesting areas, as shown by African vanellids. *V. vanellus* in Europe will mob and dive-bomb corvids alighting near their nests.

Breeding. Plovers employ a variety of mating systems—monogamy (as in *C. hiaticula*, although the mate may be changed from one year to the next); polyandry, associated with sex reversal in dotterels, in which the female is brightly coloured and the male incubates; polygyny; and polygamy involving mate-changing by both sexes, as found in *C. montanus*. Many monogamous species attempt to raise only one brood per year, but this may involve many layings, since predation of the ground nests is heavy. Most breeding habitats are open, either bare or thinly vegetated, and the nests are mere scrapes with little or no lining. Several *Charadrius* spp. partly cover their eggs with sand when leaving them, a habit most fully developed in the African *C. pecuarius* which, in a few seconds, completely covers its eggs by stereotyped kicking movements. Tropical plovers may also damp the eggs and substrate with water brought in their belly feathers (see BELLY-SOAKING). Two to 5 eggs are laid; in many temperate species very consistently 4, in African *Charadrius* spp. equally consistently 2. They are buff, brown or grey, heavily marked with black, and well camouflaged. In monogamous species, both parents usually incubate and share care of the brood after hatching. First breeding may occur at one-year-old in smaller species, but often not until 2 or 3 in larger species. The chicks are downy and nidifugous, and losses to predators occur chiefly during the first 10 days after hatching, which takes place after 3–4 weeks incubation. Fledging takes from 3 weeks in the smaller to 5 or 6 weeks in the larger species. Annual survival of adults in high, especially of larger species e.g. 80–90% for *P. squatarola*.



Golden Plover *Pluvialis apricaria*. (*A.H.*).

See photos BELLY-SOAKING; COLORATION, ADAPTIVE; ENERGETICS.

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PLOVER (2): used as substantive name of certain species not included in the Charadriidae—Egyptian Plover *Pluvianus aegyptius* (see COURSER); Norfolk Plover (or Stone-curlew) *Burhinus oedicnemus* and Stone Plover *Esacus magnirostris* (see THICKKNEE); Upland Plover (or Bartram's Sandpiper) *Bartramia longicauda* (see SANDPIPER); Crab-plover *Dromas ardeola* (see CRAB-PLOVER); and, not even in the Charadriiformes, Quail-plover *Ortyxelos meiffrenii* (see BUTTONQUAIL).

PLOVERCREST: *Stephanoxis lalandi* (for family see HUMMINGBIRD).

PLOVER, MAGELLANIC: see MAGELLANIC PLOVER.

PLOVER, QUAIL-: see BUTTONQUAIL.

PLOVER, SAND: see SAND-PLOVER; for family see PLOVER (1).

PLUMA: alternatively 'plumage feather', one in which the barbs are free instead of forming a coherent vane (see FEATHER; PLUMAGE; and compare PENNA).

PLUMAGE: also called 'ptilosis', the aggregate of which the feather is the unit, and the outstanding character distinguishing the Class Aves from all others (see FEATHER). While the general nature of plumage is constant for all birds, differences in its characteristics are found between one species and another, and to a minor extent between populations of a species (whether sharply separable into races or not); and certain broad differences are common to particular taxonomic groups of species. Further, there are differences related to age, sex and season. There is also individual variation, strongly marked in some species; and occasional abnormalities occur (see PLUMAGE, ABNORMAL). The plumage of the individual bird is periodically renewed (see MOULT).

Functions. The plumage constitutes a mechanical and thermal protective covering for the body. Parts of it are essential components of the organs of flight—the wings, and to a lesser extent the tail (see FLIGHT). In addition, the plumage helps to streamline the body, reducing friction during movement on the ground, in the air, and—in the aquatic environment of many species—on or below the surface of the water. For all these it combines high efficiency with minimal weight. It exerts its influence on the energy economy of the body (see HEAT REGULATION) partly through the insulation provided by the air trapped among the feathers and partly by its coloration. During incubation the plumage has a special role in that the feathers and associated brood patches of bare skin are important in maintaining the eggs at optimum temperature (see INCUBATION).

Other functions of the plumage are: to make aquatic birds waterproof (but the feathers of cormorants (Phalacrocoracidae) soak water, which has the function of reducing buoyancy), to carry water (see BELLY-SOAKING; SANDGROUSE), to facilitate the catching of insects in flight and as tactile organs (bristles), to collect acoustic energy and direct it into the ear (the ear coverts of owls (Strigiformes)) and to facilitate the escape from a predator by the sudden shedding of part of it, in analogy with a lizard shedding part of its tail ('fright moult').

The plumage is also the most important element in the external appearance of the bird. As such, the differences which it shows play a great part in determining recognition of other members of the same species. In some, also, the plumage is mainly responsible for a cryptic, mimetic, or aggressive appearance of the bird (see COLORATION, ADAPTIVE). In very many it includes the principal manifestations of the secondary sexual characters and parts of the plumage are often specially adapted for use in DISPLAY. Apart from providing visual stimuli, feathers—sometimes specially modified—play a part in the production of auditory signals (see MECHANICAL SOUNDS). In all these relations to behaviour the plumage is important for the perpetuation of the species.

Terminology. A bird which attains maturity has, in succession, a number of plumages. The plumages of a temperate zone bird, which has a breeding plumage differing from that outside the breeding season, the latter being identical at 1½ years old with that at 2½ years old, can be named in one of the following two ways:

(Dwight 1900)	(Humphrey and Parkes 1959)
Natal	Natal
Juvenile	Juvenal
1st non-nuptial	1st basic
1st nuptial	1st alternate
Adult non-nuptial	Definitive basic
Adult nuptial	Definitive alternate

If the plumage is the same during and outside the breeding season it is termed annual or basic. If there are three plumages per cycle the third may be termed supplemental.

Plumages may also be defined with respect to the age of the bird, the season of the year or the brightness of the feathers. In most cases, especially in technical studies of plumage succession and moult, the terminology of Humphrey and Parkes probably is to be preferred (see MOULT for further explanation), but it was criticized by E. Stresemann. Humphrey and Parkes also defined the plumage in a new way, namely as a single generation of feathers that is brought about by a moult. The aggregate of feathers of a bird at a given time is then termed the feather coat, which may consist of one or several 'plumages' (= feather generations); e.g. a 4 month old domestic hen has three 'plumages'. There is, however, a very long tradition for using plumage either in a general way to describe the feather coat or the appearance of a given bird at a given time, and this is adhered to here.

Natal plumage. The plumage of the chick on hatching is downy. But in many species, e.g. pigeons (Columbiformes), parrots (Psittaciformes) and passerines, this is sparse, providing virtually no covering, and in some, e.g. kingfishers (Alcedinidae) and woodpeckers (Picidae), it is entirely absent; in others e.g. ducks (Anatidae) and waders (Charadriiformes), it is thick, soft and beautiful—and in these instances often of cryptic coloration. In some species, e.g. cormorants, the nestling is naked at hatching, but later develops down. A few groups of birds, e.g. penguins (Spheniscidae) and owls, produce a second set of down or semiplumes. The two successive sets may be termed protoptile and mesoptile, respectively. In the megapodes (Megapodiidae) the natal plumage consists of contour-like feathers, not down (Becker), and the young are able to fly almost at once.

Juvenile plumage. This is the first plumage in which contour feathers are present. Usually the growing juvenile feather bears the preceding natal down on its tip, but soon the down falls off. It was formerly held that the natal down and the juvenile feather comprised only one feather generation, the natal down being merely the downy tip of the juvenile feather. This view has been abandoned.

Juvenile feathers are simpler in structure than corresponding adult ones (fewer barbs per unit length, fewer barbules with hooklets, etc. (Göhringer 1951)).

Where sexual dimorphism occurs, the juvenile plumage of both sexes usually resembles quite closely the plumage of the adult female. There are exceptions to this rule, for in the Koel *Eudynamus scolopacea* and the Somali Chestnut-wing Starling *Onycognathus blythii* the juvenile birds of both sexes resemble the male.

In some species, e.g. the Gannet *Sula bassana*, where the adults show no broad differences between the sexes, the juvenile plumage differs totally from that of the adult. In others, the juvenile plumage resembles that of the adults, but is nevertheless distinguishable, e.g. in the Kingfisher *Alcedo atthis*, where the young have similar colouring but lack the brilliance of the adults.

Yet another pattern, in which the young have a distinctive dress, is exemplified by the Great Spotted Woodpecker *Dendrocopos major*; juvenile birds of both sexes have the top of the head red but, after moulting from the juvenile plumage, they acquire the distinctive sexual dimorphism of the parents, i.e. the black crown in both and the red nuchal band that distinguishes the male. This may be an instance of ontogeny repeating phylogeny, indicating that an ancestral form had at one time the red crown both in adults and in the young, and that the present sexual dimorphism represents a later specialization.

Spotting and longitudinal striation is often more marked and cryptic in juvenile than in adult (definitive) plumages. The cryptic effect can be related to the juveniles' lack of environmental experience and consequently greater vulnerability to predators. In a few species, e.g. the Red-backed Shrike *Lanius collurio*, two similarly coloured juvenile plumages follow each other.

Plumage change with age. In many species (passerines in particular) the plumage that follows the juvenile plumage is so similar to that of the adult bird in the same season, that close inspection is necessary to disclose a difference (e.g. in European Robin *Erithacus rubecula* some rectrices tend to be more pointed and some wing-coverts tend to have larger bright spots in first year birds). In a few instances, e.g. the Shore (or Horned) Lark *Eremophila alpestris*, there may be no observable distinction at all, so that the definitive basic plumage is assumed direct from the juvenile plumage. In other species, e.g. the male European Blackbird *Turdus merula*, this second plumage is clearly intermediate between those of the juvenile and adult birds. Often flight and tail feathers belonging to the juvenile feather generation are retained for the succeeding plumage.

In small birds, in general, the plumage does not change appreciably with age after the bird is about 1½ years old. In male Pied Flycatcher *Ficedula hypoleuca*, however, the brown or black plumage colour continues to intensify up to an age of perhaps 5 years (Winkel *et al* 1970). Also many larger species e.g. geese *Anser*, show only minor plumage changes after their first year to year and a half.

In some species the plumage succession may extend over a span of years. Examples are provided by albatrosses (Diomedeidae), gannets, large birds of prey and the larger gull *Larus* species, but also by some passerine birds, such as the males of some species of birds-of-paradise (Paradisaeidae) with their elaborate display plumages. In the Twelve-wired Bird-of-Paradise *Seleucidis melanoleuca* the period may be as long as 7 years (at least in captivity).

The attainment of the final plumage roughly coincides with the age at which breeding starts, but the correlation is not always close. In the European Sea Eagle *Haliaeetus albicilla* breeding starts when the birds are about 4 years old, by which age the dark brown juvenile plumage has changed through gradually lighter plumages into the light grey-brown plumage of the adult; the tail also has changed from brown to predominantly white, but it may be several more years before it becomes pure white. In captivity the Bald Eagle *Haliaeetus leucocephalus* may take 10 years to reach the definitive plumage.

The plumages intervening between the juvenile plumage and the adult or definitive plumage are most precisely termed first, second (etc.) basic/non-nuptial and alternate/nuptial. Collectively the less accurate term 'immature plumage' may be used; for the later stages also 'sub-adult plumage'.

Seasonal plumage changes. In species with a seasonal change of plumage, the plumage worn outside the breeding season is the non-nuptial or basic, while the plumage worn during the breeding season is the nuptial or alternate.

The non-nuptial or basic plumage is usually duller than the nuptial or alternate plumage, and the term 'basic' stems from considering the dullness primitive (Humphrey and Parkes). To give an example, the basic plumage in many waders is characterized by white under parts as opposed to black or red in the alternate plumage.

Striking nuptial plumages and accessories are assumed by both sexes in the grebes (Podicipedidae), the divers (Gaviidae) and the herons (Ardeidae)—the plumes of the head, mantle and other regions of the last-named forming most impressive additions to the breeding dress. SEXUAL DIMORPHISM is very common and usually more marked in the alternate i.e. breeding plumage, than in the basic plumage. Where a dull basic/non-nuptial plumage is worn for only a short period, as in ducks and some sunbirds (Nectariniidae), it is sometimes referred to as eclipse plumage (see MOULT); but it is not certain that this plumage corresponds to the basic/non-nuptial plumage of other birds. Some sunbirds have a bright plumage the whole year. If this corresponds to the annual/basic plumage of other birds, the eclipse plumage of some sunbirds must be regarded as a specialized interpolated plumage serving a protective function (E. Stresemann).

In some species, e.g. the Sharp-tailed Sparrow *Ammospiza caudacuta*, there are two nearly identical plumages per year. This may be related to abrasion caused by the species' habit of foraging in wet vegetation.

The length of the period during which each plumage is worn varies with the species; in the Dunlin *Calidris alpina* the basic plumage is present for 7–8 months (September–April) while in the Mallard *Anas platyrhynchos* it is worn for only 2–3 months.

Other terms for the basic/non-nuptial/eclipse plumage are off-season, non-breeding and winter plumage, though in northern temperate dabbling ducks the 'winter' plumage is actually worn during the later summer months. The alternate or nuptial plumage is also termed breeding, nesting or summer plumage.

Some species have more than two plumages annually. In the adult male Long-tailed Duck *Clangula hyemalis* four plumages are recognized: transitional autumn, winter, transitional summer and full non-breeding. It is assumed that the first two correspond to the nuptial plumage of other ducks, the latter two to the non-nuptial plumage, but some tracts bear three feather generations in a year. The major moults are not continuous, but interrupted or halted for several weeks, so that annual plumages are produced.

In ptarmigans *Lagopus* as well as in the male Ruff *Philomachus pugnax* three annual plumages are present. In the Ruff the third plumage is related to display, while in the Long-tailed Duck and ptarmigans the plumage succession probably favours camouflage in changing habitats.

Component units. Outwardly, most birds appear to be uniformly covered with contour feathers. In most species, however, the feathers, other than down, grow only from definite tracts (pterylae) of skin (see PTERYLOSIS).

The total number of feathers usually runs into thousands (see FEATHERS, NUMBER OF), but the plumage weight usually equals only 5–7% of the body weight. More than 95% of the plumage volume consists of air.

The plumage comprises feathers of several different types (for details of development and structure see FEATHER):

1. *Contour feathers.* Except for the natal plumage, these constitute the most important element of the ordinarily visible plumage. They include the primary and secondary remiges of the wings and the rectrices of the tail, the coverts that—above and below—cover the bases of the remiges and rectrices and also cover the ear orifices, and feathers on other parts of the body (see TAIL; TOPOGRAPHY; WING).

2. *Down.* Except in the natal plumage, down rarely contributes to the appearance of the plumage, being hidden from view as a separate layer beneath the contour feathers, where it forms an undercoat in many species. Sometimes down is partly visible, as at the neck in vultures, where the contour feathers have become suppressed as an adaptation to the method of feeding. Some groups of birds entirely lack down in the adult plumage, e.g. ratites, pigeons, and coraciiform birds except kingfishers. In such cases the downy portion of the contour feathers fulfils the corresponding function; but contour feathers with downy portions are present as well as down in many species.

3. *Semiplumes.* These, like adult down, are hidden from view by the contour feathers. They are often abundant in the abdominal region.

4. *Filoplumes.* Although these are normally associated with and concealed by the contour feathers they may be visible in some species, e.g. Chaffinch *Fringilla coelebs*, at the nape. They are seen very strikingly on the nape and back of the Hairy-backed Bulbul *Hypsipetes criniger*. The white feathers found on the heads, necks and thigh patches of some cormorants are presumably also filoplumes.

5. *Bristles.* In a few species bristles are found on the toes, but otherwise bristles are confined to the neck and to the head, most frequently at the base of the bill (rictal bristles), the lores, the eye, the malar and the gular regions. Those above the base of the bill and on the lores are sometimes known as 'vibrissae'. Bristles specialized as eyelashes and other bristles in the eye region may serve to keep foreign particles out of the eye.

Most groups of birds possess bristles, but some groups, e.g. tubenoses (Procellariiformes) and flamingos (Phoenicopteridae), seem to lack them (Stettenheim 1974).

6. *Powder feathers.* Where these are densely packed in patches, they may be recognized outwardly in the plumage, e.g. on the Kagu *Rhynochetos jubatus* and herons (Ardeidae). In other species, e.g. some pigeons and parrots, they are dispersed among the contour feathers and so hidden from view. Powder feathers are widespread among birds, but many groups lack them, including nearly all passerine families. Their function is not well understood; the powder may contribute to making the plumage waterproof or to changing the plumage's colour, so that it becomes more bluish grey.

Adaptive differences. Some degree of specialized adaptation can be recognized in practically all the feathering of a bird. Most important of all is the modification of wing feathers to serve the vital function of flight, to which they are most perfectly suited. Minor examples are the beautifully graded and shaped feathers of the facial disc and 'ears' of many owls and the curious rosette of feathers surrounding the uropygial gland (see OIL GLAND).

During the course of evolution, notable differences of plumage quality have become established between different taxonomic groups. Contrast, for example, the scale-like feathers of penguins—a character already discernible in embryonic life—and the soft, abundant feathering of owls, in which flight as near silent as possible is essential to the birds' mode of predation. Take again the water-resistant property of the feathering of the Anatidae and other aquatic birds, which is primarily a structural adaptation: the barbules bear many relatively long outgrowths (E. Rutschke), which, together with the barbules themselves, break up the interface between the surrounding water and the air in the plumage into numerous minute areas. Due to its surface tension, the water is not able to displace the air present in these minute areas and a stable water–air interface is produced. Probably the main function of uropygial gland secretion as a water-repellent is to impregnate the feather substance of the barbules and their outgrowths so that they retain their flexibility and do not break or become disordered.

Plumage variation. Individual birds of a given population normally differ from each other slightly with respect to plumage characteristics. Corresponding feathers may vary between individuals in length, shape, pattern of pigmentation and colour, and in at least two *Accipiter* hawks there is evidence that these features are constant over the years, so that they can be used for the recognition of individual birds (Opdam and Müskens 1976).

In addition to this normal, continuous variation there are more striking types of variation. A given plumage of a species may show several colour phases (see POLYMORPHISM) or individuals may show abnormalities (see PLUMAGE, ABNORMAL).

A further type of variation appears to have phylogenetic significance as an atavistic manifestation. The study of the subject received a great stimulus from the classical experiments of Darwin in back-breeding fancy varieties of domestic pigeon to the similitude of the original stock, the Rock Dove *Columba livia*. Another example is provided by the occurrence, in the Britsh race of the Robin *Erithacus rubecula melophilus*, of a variant in which the breast pattern approximates closely to that found in the Japanese Robin *Luscinia akahige*.

A recurring character in the gulls of the genus *Larus*, namely an oblong white patch in the region of the carpal joint, has been noted in individuals of Heermann's Gull *L. heermanni*, the Herring Gull *L. argentatus* and the British race of the Lesser Black-backed Gull *L. fuscus graellsii*, indicating the extremely close affinity of these three forms.

A white neck ring, which is a constant character in the drake Mallard, and which can occur also in the duck of that species, occurs on occasions in the Gadwall *A. strepera* both in immature and adult drakes, in the Shoveler *A. clypeata*, in the Wigeon *A. penelope*, in the Yellow-billed Teal *A. flavirostris* and in the European race of the Teal *A. crecca crecca*, although in the last two it is at best vestigial and incomplete; it also occurs in some Pintail *A. acuta* drakes in eclipse plumage.

In all the above examples interspecific hybridization is not involved. Where this has been the case, more striking instances have occurred (see also HYBRID). An example is provided by the progeny of a drake European Teal and a duck Shoveler *A. clypeata* in which appeared the striking facial bridling that is the most characteristic feature of the drake Baikal Teal *A. formosa* when in adult nuptial plumage.

A summary of plumage variants in the Anatidae is given by Harrison and Harrison (1963).

Associated behaviour. Some species make use of their own or other down and feathers as nesting material. The habit of plucking their own breast down to use as a nest lining is well developed among ducks. In the bowerbirds (Ptilonorhynchidae) any available bright feathers are among the objects used for decorative purposes in the surroundings of the bower (see BOWERBIRD).

There is also the physiological value of ingested feathers. Among birds of prey feathers are taken in the course of ingesting avian prey and facilitate pellet formation (see PELLET). In grebes the feathers are apparently plucked from the bird's own body surface, but subserve the same purpose.

Preening, ANTING, DUSTING, SUNNING and flirting with smoke and fire form part of the behaviour of a bird towards its own plumage (see COMFORT BEHAVIOUR). ALLOPREENING is a social response in some species, while mutual preening by a pair occurs in the normal relations between the sexes. An apparent perversion is the feather picking indulged in by domestic fowls and by game-birds (Galliformes) in captivity. (J.M.H.) J.D.

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PLUMAGE, ABNORMAL: plumage abnormalities may be due to changes in the amount and distribution of the pigments normally present, chemical changes in the pigments producing abnormal colours, changes in feather patterning, or changes in the structure of feathers. Such abnormalities are in many cases extremes of tendencies apparent in the individual variation of a species. They are, of course, to be distinguished from normal differences in colour and pattern resulting from geographical variation or POLYMORPHISM.

Abnormal pigmentation. This is the most frequently occurring type of plumage abnormality, at times affecting most of the commoner pigments, the melanins—black or grey Eumelanin, brown or buff Phaeomelanin and chestnut-red Erythromelanin—and the red and yellow lipochrome pigments.

Atypical pigmentation. The more extreme variations of this type are sometimes grouped under the term 'heterochroism'. Occasional individuals of a wide range of species, from penguins to passerines, show a marked reduction or loss, or a considerable increase, in the pigments normally present. Although often referred to as chance mutations, in the form in which they occur they are remarkably consistent, genetically controlled and usually recessive, and can predictably be produced by subsequent controlled breeding.

Under natural conditions individuals showing such variations are usually at a disadvantage and short-lived, mainly because their greater conspicuousness makes them more liable to predation. In addition, reduced pigmentation weakens the feather structure, causing accelerated abrasion and wear, particularly of flight feathers, and this may affect mobility. Loss of pigmentation also affects the retina of the eye and can lead to impaired sight in bright light. There is evidence in some species of a failure to recognize abnormally-coloured individuals as potential partners in pair-formation. In captive Greenfinches *Carduelis chloris*, nestlings with variant plumage are at a disadvantage compared with normal youngsters in the same brood and often fail to survive until fledging.

Of variations resulting from an increase in the pigment present, the best-known is probably 'melanism' in which the amount of black and/or brown melanin present increases, and may spread to parts of the plumage which normally lack melanin, masking other colours where these are present. The bird usually appears entirely black or dark brown or a mixture of both. Apparent melanism is sometimes due to a staining of feathers by industrial wastes, soot or oil. The term 'erythrism' is sometimes used for cases in which chestnut-red replaces other melanins. 'Flavism', an excess of yellow pigment spreading into parts of the plumage where it does not normally occur, is rare in the wild, but is apparent in some domesticated strains of the Canary *Serinus canaria* and Budgerigar *Melopsittacus undulatus*.

Partial loss of pigment, affecting all the colours present and reducing them in intensity, is rare. It is called 'dilution' by bird breeders and 'leucism' in scientific writings, although the latter term is also used at times for various forms of schizochroic loss (see below) of single pigments which make the plumage appear paler. The complete loss of feather pigment is more common. This may occur as true 'albinism' in which pigment is absent throughout the body, a condition resulting in red eyes and pale pink legs and bill. In other cases, genetically different from true albinism, pigment is absent from the plumage but the normal body colours are retained. In species in which some or all of the plumage is normally white, the normal condition can often be distinguished from these white variants by the presence of small amounts of greyish pigmentation in the downy bases of the white feathers.

Partial whiteness, usually in the form of one or more asymmetrical patches of plumage, is more frequent than total whiteness. It is controlled by recessive genes which appear to carry the capacity for partial loss of plumage pigmentation, but not to control its location on the body, resulting in individual differences also apparent if the variation is passed on to offspring. However, within any group of related species, partial whiteness is likely to occur more consistently on some areas of plumage than on others. The amount of white may increase in area on an individual with successive moults, but it appears not to have been established whether this is an aspect of ageing due to a hereditary factor or the result of some increasing physiological disorder.

Schizochroism. The other major source of colour abnormality is a phenomenon sometimes called 'schizochroism'. In this a pigment normally present in the plumage is absent, or several pigments may be missing. This changes coloration or affects patterns by leaving white areas on feathers where the missing pigments would normally be present, unless another pigment also occurs on this part of the feather and now appears alone.

The predominant colour of many bird plumages is a dull brown formed by a mixture of both brown and black melanin. In the non-eumelanic form of schizochroic plumage abnormality only the black colour is lacking, and the bird appears a pale buffish-brown, with white markings where black alone was present. If other pigments are normally present they will be unaffected. In captive birds this condition is usually described as 'buff', 'fawn' or 'cinnamon'. It is controlled by a sex-linked gene and is usually found only in females in the wild.

The non-phaeomelanic variation is less frequently seen. It usually appears mainly ash-grey, and is sometimes referred to as a 'silver' variety. It is under different genetic control from the last, being apparently autosomal, and birds showing it are as likely to be male as female. In both types of loss the feathers, with reduced quantities of melanin, are subject to more rapid abrasion than are normal feathers, and also bleach rapidly. By the time that they are due to be moulted, the normally-exposed portions of feathers may have lost their melanin, and the bird may appear white unless closely examined.

The chestnut-red melanin, when present, seems little affected in such variant plumages. The loss of both black and brown with retention of chestnut-red is known in the Zebra Finch *Poephila guttata*, and has been recorded once in the Waxwing *Bombycilla garrulus*. Loss of chestnut-red with retention of other melanins seems unknown in wild birds but occurs in the 'penguin' strain of the domesticated Zebra Finch.

Schizochroic variants in which all melanins are lacking from the plumage appear albino or white-feathered except where red and yellow pigments are also present, the latter persisting as coloured areas on otherwise white plumage. Such variations are known in the finches (Fringillidae), waxbills (Estrildidae), and weavers (Ploceidae); while loss of black in normally green parrots such as the Budgerigar and the Ring-necked Parakeet *Psittacula krameri* produces yellow individuals in which normally dark markings are white. In some cases loss of melanin reveals a more extensive distribution of red or yellow, which is normally masked by other pigments.

The converse of the last variation produces individuals having the normal melanin pigments, with white areas where red or yellow would occur, and modification of areas of mixed pigmentation. In parrots this produces blue forms, lacking the yellow pigment which would make them appear green, and with the black melanin modified to blue by Tyndall scattering (see COLOUR). Other examples lacking red and yellow pigments are known in the finches and in the Yellow Wagtail *Motacilla flava*.

Once the general pigment distribution in the plumage of any species is known, it is usually possible to predict what potential plumage abnormalities there might be, and their likely appearance; but unexpected abnormalities sometimes occur. The distinctive patterns which are characteristic of the display plumages of males of many species appear to be to some extent under independent genetic control and not necessarily responsive to changes in the pigmentation of the remainder of the plumage. This is particularly true of the patterns on head and breast; thus in what would otherwise be recognized as non-eumelanic variants of the House Sparrow *Passer domesticus* and Painted Quail *Coturnix chinensis*, these parts of the plumage retain much of the black patterning.

Pigment replacement. Rarely, one colour is replaced by another. An abnormal change to chestnut-red melanin occurs in individuals of some wader species (Charadriiformes), particularly in the Woodcock *Scolopax rusticola* and Common Snipe *Gallinago gallinago*. It is also found in gamebirds (Phasianidae), as in the rufous or 'montana' variant of the Grey Partridge *Perdix perdix*. The abnormal replacement of red by orange has occurred in individuals of the Red-eared Waxbill *Estrilda troglodytes* and Senegal Firefinch *Lagonosticta senegala*, in the latter proving to be a recessive inherited character.

Gynandromorphs. A striking abnormal variation in pigment distribution results from a possible chromosomal accident which produces an individual that is visually half-male and half-female, possessing both an ovary and testis. In sexually dimorphic species the two sides show the different plumage colours and patterns of the two sexes (and differences in other characters such as wattles, if present), joining abruptly along the mid-line. This phenomenon has been recorded in a number of passerine species, and in the Pheasant *Phasianus colchicus*, Flicker *Colaptes auratus* and Budgerigar. In species with marked sexual size dimorphism, this abnormality may produce an individual with dissimilar legs and wings and with distortion of the bill and other medial features.

Pigment deficiency. Plumage abnormalities sometimes very similar to those of genetic origin, already mentioned, may be the results of deficiencies or excesses in diet. They occasionally occur in wild birds but are more often seen in captive individuals. Some may be distinguished from genetic variants in that they are temporary and may be partially or wholly corrected in later life. Others are permanent and may be the outward evidence of pathological disorders. The former are sometimes evident in hand-reared birds which show a lack or excess of normal pigment in the plumage, corrected when the individual has greater opportunity to select its own food and moults into adult plumage.

Inadequacy of diet is likely to be cumulative in its effects, and during feather growth is sometimes apparent as a gradual reduction in pigmentation, producing feathers that are increasingly whitish towards the bases. The white bases to remiges occurring on some individual wild Carrion Crows *Corvus corone* and Rooks *C. frugilegus* have been ascribed to diet deficiencies but may be of genetic origin. An initially deficient but gradually rectified diet may produce pale-tipped feathers. Brief or intermittent periods of starvation may produce one or more narrow transverse bands across feathers, indicating the extent of growth during the period of deficiency. Such inadequacies of diet will not affect feathers once they are fully grown. On a nestling where all feathers are growing simultaneously, pale transverse bands may occur in similar positions on most feathers, creating a plumage pattern similar to some of genetic origin. Such barred patterns have been described for young crows *Corvus* spp. White transverse bands of this type have been experimentally induced by hormone injections during moult.

Abnormal white feathers may appear when injury to individual feather follicles or to areas of skin results in follicles continuing to produce feathers but unable to produce melanin. An abnormality of unknown origin in the African Grey Parrot *Psittacus erithacus* results in the replacement of normal grey body feathers by red ones lacking melanin and similar to those normally present in the tail.

Unsatisfactory diet in captive birds may produce melanism which is in some instances irreversible. In captive finches this has been attributed to an excess of oily seeds, particularly hemp seed. It may result in wholly black plumage but in the early stages the melanin is sometimes irregularly distributed, affecting only some feathers and producing an asymmetrical spotted appearance.

Excess of red-pigmented material in the diet may affect the appearance of the plumage. Prior to the production of Red Factor canaries in which red and orange colour is genetic in origin, powdered red peppers were fed to give an orange tint to yellow canaries. Orange-tinted plumage in wild birds has been recorded for a Yellow Wagtail feeding around a red palm-oil effluent, and in Greenfinches feeding on yew berries.

Diet deficiency, particularly a lack of carotene, may result in a reversible reduction or loss of red and yellow pigments in feathers. Birds showing a complete loss of these colours may resemble some schizochroic variant forms. This most frequently occurs as an abnormality of captive birds. Blue-grey and white plumage may replace green and yellow, and a bronzy tint occur instead of red. The red colour of captive flamingos (Phoenicopteridae) is largely lost if the diet lacks a substitute for the crustaceans from which this is normally derived.

A similar effect may occur in some species due to loss of fugitive pigment from plumage after a period of exposure to light, without any deficiency of diet. A pink tint on freshly-moulted white plumage of some gulls (Laridae) and ducks (Anatidae) is soon lost; and in some tropical bee-eaters (Meropidae) and kingfishers (Alcedinidae) the green feathers of the plumage fade to a light blue through loss of yellow pigment by the time that they are moulted. In the Hunting Cissa *Cissa chinensis* the normally bright green plumage rapidly becomes light blue in captive birds and also in stored museum skins.

Pattern variations. The patterns created by variations in melanin distribution on feathers are a distinctive plumage character of many species, and within populations marked variation in visible pattern is unusual. From a study of the pigment patterns on feathers it seems probable that the patterns apparent on the plumages of many species have undergone a series of progressive changes in the past to evolve that which is now present, and that a uniform colouring may mask earlier patterns. The occurrence on feathers of markings differing from simple transverse bars, such as those induced by experimental hormone injection in some game birds and domestic fowl, may therefore be due to the revelation, when complete pigmentation is inhibited, of earlier evolved patterns.

Similarly, earlier patterns on areas of plumage may have been lost, but the genetic potential for their production may remain. This would appear to be the underlying cause for the appearance on some hybrid birds of patterns not apparent in either parent but present on closely-related species. The bimaculate face patterns of some *Anas* duck hybrids may be an example of this. Variant individuals showing elements of pattern or colour characteristic of other subspecies or related species occur sporadically in a wide range of taxa, and these variations may be of similar origin. In some instances a recurrent variation is not a character of any extant species, as in the case of the white carpal patch which has been noted on individuals of several different species of gulls.

In normal plumage the appearance is controlled not only by direct genetic factors but also by the relative levels of hormones which determine the occurrence of sexually dimorphic plumages and the seasonal breeding and non-breeding plumages. Any imbalance of the endocrine system is likely to have a noticeable effect on plumage, and in some instances this has been studied in experimentally created conditions, as well as in individuals showing changes which are of pathological origin.

In some gamebirds such as the Pheasant and the domestic fowl a reduction in the level of the female hormone may result in females assuming male plumage. This may also occur through the atrophy of ovaries from age or disease. It may not necessarily imply a loss of all female functions since exceptionally individuals have laid eggs when in male plumage. This can occur in other species and there is a record of a male-plumaged Common Redstart *Phoenicurus phoenicurus* laying eggs in the wild. Female birds have only a single ovary on the left side of the abdominal cavity and if this is removed a mixed gland (ovotestis) develops in a similar site on the right hand side. In game birds the plumage assumed by the castrated female is of a male type and becomes increasingly male with successive moults. Conversely, in castrated Pheasants the male assumes a plumage resembling that of the female. In some breeds of domestic fowl most of the males are hen-feathered. Paradoxically, if such birds are castrated, a more typical male plumage is produced. The hen-feathered condition is controlled by the testes but appears to be hypersensitive to such female hormones as are normally present in the sexually active male.

In the House Sparrow, the male of which retains the sexually dimorphic plumage throughout the year although it is partially concealed by dull feather edges in winter, the sexual plumage is under genetic control, but a character affected by hormone levels and lost through castration is the black bill colour of the male breeding dress.

Feather structure abnormalities. Abnormalities of feather structure occur infrequently and in wild birds are usually lethal. Like pigment abnormalities, they may be the result of disease or temporary food deficiencies, or may be genetically determined and can be maintained by controlled breeding in captive birds.

The more rapid abrasion and loss of portions of plumage deficient in melanin has been mentioned above. Structural abnormalities may have a similar effect. An abnormal weakness of structure resulting in rapid wear of the distal part of the feather vane with retention of a tapering rachial zone, to give a 'needle-tailed' effect to the rectrices, has occurred on both rectrices and remiges of individuals of the Guillemot *Uria aalge* and Black Guillemot *Cepphus grylle*. A complete breakdown of the structure of these feathers, resulting in flightlessness, has been recorded for the Eurasian Jay *Garrulus glandarius* and Shelduck *Tadorna tadorna*.

Abnormally loose and fluffy plumage may be produced by failure of the interlocking barbule structure, or absence of the necessary barbicels. If the abnormality affects the remiges and rectrices, such a variation is usually lethal in the wild. In captivity hereditary strains of a similar type have been selected to produce the 'silky' form of the domestic fowl, domestic pigeon *Columba livia* and Barbary Dove *Streptopelia roseogrisea*. A similar breakdown of feather structure associated with reduced pigmentation, possibly resulting from disease and producing plumage with a 'hairy' appearance, has been noted in the Eurasian Jay and the Moorhen *Gallinula chloropus*.

A structural defect resulting in a twisting of the rachis of contour feathers to produce a frizzled effect occurs at times in captive finches, and hereditary strains have been established. Hereditary strains with a complete absence of all feathers have been produced in the domestic fowl and domestic pigeon but have failed to survive for long.

Although most of these structural abnormalities are rare, one type of defect is of more frequent occurrence. If a bird undergoes one or more days of inadequate diet when feathers are growing, the deficiency may result in a narrow transverse zone or line of weakness across the vane of the feather. (As already mentioned, pigmentation may also be affected.) This transverse line of defective structure is usually referred to as a 'hunger trace' or 'hunger fault'. Feathers with such faults are liable to break off after a time along the line of weakness, and if this occurs on a number of flight feathers it may make flight difficult or impossible. It was particularly a matter of concern to man in the early practice of falconry.

C.J.O.H.

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PLUMAGE MIMICRY: see MIMICRY.

PLUMAGE VARIATION: see PLUMAGE.

PLUMBEOUS: lead coloured.

PLUME: a feather, usually long and showy, developed for the purposes of display.

PLUMELETEER: substantive name of *Chalybura* spp. (for family see HUMMINGBIRD).

PLUMULA: a down feather (see PLUMAGE). Natal or nestling down plumage, when present, is called 'neossoptile'.

PLUNGING: see SWIMMING AND DIVING.

PLUSHCROWN: substantive name of *Metopothrix aurantiacus*, a South American furnariid (for family see OVENBIRD (1)).

PLUVIANELLIDAE: see under CHARADRIIFORMES; PLOVER, MAGELLANIC.

PNEUMATIZATION OF BONE: a term denoting the air-holding properties of the skeleton or parts of the skeleton. Aerated bones are characteristic of the class Aves, but also occur in the skull of crocodiles and, according to Bellairs and Jenkin (1960), were very probably features of the fossil pterodactyls. Since very light and hollow bones are also found in dinosaurs, it is not inconceivable that the origin of pneumatization is to be sought in the early archosaurs, from which all these groups stem (see EARLY EVOLUTION OF BIRDS). Pneumatized bones are hollow, the hollow parts communicating with the air-sac system. Air is supplied to the cranial bones via the air-sacs of the nasal and tympanic cavities, and to the postcranial skeleton via the air-sacs of the respiratory apparatus proper (see RESPIRATORY SYSTEM).

Skull pneumatization. The extent of pneumatization can easily be examined in the skull-roof. Unpneumatized parts (so-called windows) appear featureless and more or less translucent. They consist of a single layer of bone. Pneumatized parts of the skull-roof appear speckled in passerines and have a labyrinthine conformation in non-passerines. They consist of bilaminate bone, the two layers sandwiching the spongiosa, bony tissue rendered cancellous by action of bone-excavating cells. The extent of pneumatization can vary markedly both between and within different orders, families and species. No universally applicable rule can be formulated about this. Skulls which are for the most part weakly or not at all pneumatized are seen in e.g. kiwis (Apterygiformes), divers (Gaviiformes), herons (Ardeidae) and auks (Alcidae). Quite varied development of pneumatization occurs e.g. among wildfowl (Anseriformes), raptors (Accipitriformes, Falconiformes), gulls (Laridae) and woodpeckers (Picidae). Predominantly strongly or even fully pneumatized skulls are possessed by e.g. ostriches, rheas and cassowaries (Struthioniformes), pigeons and doves (Columbiformes), parrots (Psittaciformes) and nightjars (Caprimulgidae). The only two orders in which all members pneumatize completely are the owls (Strigiformes) and—apart from a very few exceptions—the passerines (Passeriformes). Numerous examples of the amount of pneumatization of the skull-roof in various groups of birds are given in papers by Harrison (1957), Verheyen (1953) and Winkler (1979).

In young birds the available studies show a different process of development of pneumatization in non-passerines and passerines. This phenomenon is closely correlated with differences in brain-development: in non-passerines the brain grows evenly to its adult volume and in most species the pneumatization-process terminates with attainment of the ultimate body-size. In the few non-passerines in which pneumatization continues beyond this point, additional bone is laid down on the outer surface of the skull, as Stork (1972) has established for pigeons. Pneumatization on the inner surface would cause pressure on the brain. But in young passerines the brain goes through an overweight phase, after which it shrinks to the adult volume. For this reason the skull in this group remains unpneumatized until maximum brain-volume is attained. The pneumatization process only sets in when the brain begins to contract to its adult volume. This point approximately coincides with the fledging of the passerine nestling. In contrast to non-passerines, pneumatization takes place against the internal skull-surface. Its function here is to fill out the gap between the unpneumatized skull-roof and upper brain-surface left by the shrinkage-process of the brain.

Pneumatization of skull-roof and ageing. In passerines the state of pneumatization of the skull-roof has long been used in establishing age. Since Baird (1963) first demonstrated how the state of pneumatization can be examined through the skin even in live birds, this method of ageing has become important in bird ringing. As nearly all passerines are fully pneumatized when adult (exceptions are noted in Winkler), all incompletely pneumatized birds can be recorded as immatures. However fully pneumatized individuals may only be definitely termed adult during the part of the year in which no juveniles with completed pneumatization can be expected. The dates from which fully pneumatized juveniles can occur have been given by Wood (1969) for certain North American passerines and by Winkler for European species. Depending on species the pneumatization process takes 2 to 8 months, beginning in the occipital region and finishing over the forehead. Among European species pneumatization takes least time in the Willow Warbler *Phylloscopus trochilus* (2 months) and longest in the Yellowhammer *Emberiza citrinella* (over 8 months). Occasionally the latter fails to achieve complete pneumatization.

In general the stage of pneumatization in non-passerines cannot be employed as an ageing criterion.

Pneumatization of postcranial skeleton. This has been far less well studied than that of the skull-roof and again is far more extensively developed in some species than in others. Diving birds like penguins (Spheniscidae), divers *Gavia* spp. and cormorants *Phalacrocorax* spp. are more poorly pneumatized than large flying birds like albatrosses (Diomedeidae) and eagles *Aquila* spp. A number of examples are contained in Bellairs and Jenkin and in Stresemann (1934). Generally the skeleton of large species in a related group appears to be more highly pneumatized than that of smaller species. As demonstrated both by Bellairs and Jenkin, and Stresemann, pneumatization of the postcranial skeleton begins with the penetration of developing bone by fine air-sac diverticula. The air-sac diverticula follow the resorption of the bone marrow and expand through the interior of the bone until they occupy its entire cavity.

Function of pneumatization. It is obvious that pneumatization primarily serves to save weight and so enhance flying ability. In addition, a pneumatized bone proves to be structurally more stress-resistant than an unpneumatized one. However, the great differences in extent of pneumatization between different orders of birds remain unexplained. Adaptations to specialized modes of life certainly play an important role here. Thus Harrison comments on the fact that almost all deep-diving birds are but very poorly pneumatized. They thereby minimize the natural tendency to buoyancy during diving. Stork ascribes a function of brain-insulation to the pneumatization of the skull. Winkler considers the significance of skull-pneumatization to lie in, among other things, its balancing out the two functions of the skull-roof, namely on the one hand to enclose securely the brain and on the other to provide insertions for musculature and sockets for the large eyes. Since pneumatization has above all a functional character, its extent cannot be employed as a taxonomic criterion. R.W.

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POCHARD: substantive name of some *Aythya* spp. and of *Netta* spp.; used without qualification in Britain for *A. ferina*; in the plural, general term for the tribe Aythyini (see DUCK).

PODARGIDAE: see under CAPRIMULGIFORMES; FROGMOUTH.

PODICIPEDIFORMES: an order, comprising only the cosmopolitan family Podicipedidae (see GREBE). The ordinal name, which on the basis of a different view of the etymology of the type genus *Podiceps* was for a short time called Podicipitiformes, is derived from the family name Podicipedidae, which in its turn was validated in Opinion 981 of the Bulletin of the International Commission on Zoological Nomenclature 29 (1) 1972: 152. Before 1956 the name of the order used by the American Ornithologists' Union was Colymbiformes, for which see COLYMBIDAE.

PODICIPITIFORMES: obsolete term, see PODICIPEDIFORMES.

PODOTHECA: the horny covering of the unfeathered parts of the legs and feet (see LEG).

POETRY, BIRDS IN: for birds, as for man, the dominant senses are those of sight and hearing; the world of their experience seems, therefore, more comprehensible than one perceived mainly through scent or touch. Their form is often elegant and their colours attractive; the songs of some have long pleased man; their power of flight is enviable. Some build their nests not only in gardens and orchards but even in man's farm buildings and houses, so that these are familiar to man as no other wild animals are. Their domestic behaviour—the nests they build, the care they give to their young—are, again, not remote from human experience. And yet they are rendered mysterious and a cause of curiosity by their migrations. All in all, birds are a natural source of myth and of poetry; but the amount of actual observation of their lives which is available to a poet is necessarily limited.

Perhaps the earliest folk-song of Europe to survive was that sung by Rhodian boys to welcome the Swallow, but 7 or 8 centuries earlier a Minoan artist on Santorini had painted a Spring fresco of Swallows, with a pair rising beak to beak against a background of rocks and lilies. Hesiod, Simonides, Aristophanes and other Greek poets associated the return of the Swallow with spring, for even three and a half millennia ago it nested about man's buildings and so made itself more noticeable than other summer migrants. ('Swallow' for the poets often included the House Martin and the Red-rumped Swallow, both of which nest on buildings. The poets are always 'lumpers' not 'splitters'.) But the Swallow's twitter, which has pleased many an English poet—Sir John Davies even preferred it to the Nightingale—seemed to the Greeks no more than a barbarous gabble.

The Cuckoo's call—for Shakespeare, with his love of puns, a 'word of fear unpleasing to a married ear'—was a sign of spring to Hesiod, and Aristophanes recognized in it a warning to be off to work in the fields. The spring arrival of these birds was noted, but they were not, like storks and cranes, observable while on migration. Homer compared the clamour of the Trojan host to the noise of migrating cranes, and Hesiod and Aristophanes took the sound in autumn to be a sign that it was time to plough and to sow; Euripides seems to have been more impressed by the spectacle of the long-necked birds in flight 'passing beneath the Pleiads and Orion in the night', probably the first mention of moon-watching. And the winter quarters of cranes were not, like those of Swallows, beyond the limits of the known world.

The song of the Nightingale has evoked the charmed response of poets from Homer to our own time, and from Persia to Britain. Some of them—Aristophanes, Nashe, Lyly, Barnfield—have even attempted to transcribe its song into human syllables. Dafydd ap Gwilym addressed a poem to the Nightingale in the Birch Grove (was this in Wales?) and Milton saluted the bird

> 'that on yon bloomy spray
> Warblest at eve when all the woods are still',

in the earliest of his sonnets, and often referred to it elsewhere. His friend Marvell, whose poetry gives precise descriptions of birds, observed that

> 'Low Shrubs she sits in, and adorns
> With Musick high the squatted Thorns.'

And Izaak Walton, their elder contemporary, shows that he had chosen to listen to the song: 'He that at midnight, when the very labourer sleeps securely, should hear, as I have very often, the clear airs, the sweet descants, the natural rising and falling, the doubling and redoubling of her voice, might well be lifted above earth, and say, "Lord, what music hast thou provided for the Saints in Heaven, when thou affordest bad men such music on Earth!"' Collins noted Sophocles's 'peculiar fondness for the song' which he heard at Colonus, and Peacock also referred to this. Keats, hearing the song at Hampstead, was prompted to write perhaps the best known of all poems in its praise, and Robert Bridges wrote a sensitive lyric on the song. Throughout the bird's range the poets have celebrated its song: in English and Welsh, in German and Italian, in Greek and Persian; no other bird has been so universally admired.

Much of the poetry about the Nightingale derives from the primitive and savage myth of Tereus, Procne and Philomela (the Hoopoe, Nightingale and Swallow), on which Sophocles wrote a tragedy, of which only a fragment remains. Ovid retells the myth in *Metamorphoses* VI (the source of later versions) but with Philomela now the Nightingale not, as in Greek sources, the Swallow. For the poets the Nightingale was feminine, and she sang her sad song 'leaning her breast against a thorn.' But these things are the effects of myth, not of observation. Another myth, of Aedon who murdered her child Itylus in error and prayed to be changed into a Nightingale, was known to Homer: in the *Odyssey* Philomel

> 'in bow'ry shades unseen
> To vernal airs attunes her varied strains,
> And Itylus sounds warbling o'er the plains.'

Swinburne's poem is the best known version of this story in English. Probably more English poets knew the myths than had ever listened to the song, and one cannot help questioning whether the bird whose song Cowper heard on New Year's Day, 1792, was, as he supposed, a Nightingale.

No other song-bird has attracted so much myth as the Nightingale, and poetry about Song Thrush, Blackbird and Skylark owes rather more to personal observation. Robert Browning, in *Home Thoughts from Abroad*, recalled the song of the Chaffinch and of

> 'the wise thrush; he sings each song twice over
> Lest you should think he never could recapture
> The first fine careless rapture.'

The same characteristic repetition was noted by Tennyson and, 250 years earlier, by William Browne of Tavistock. John Clare, a most observant countryman who mentions many birds, heard

> 'a merry thrush
> Sing songs of rapture,'

and he watched her skilful modelling of her nest, where Marvell noted with pleasure how he might

> 'through the Hazles thick espy
> The hatching *Throstles* shining Eye.'

Spenser, in *The Faerie Queene*, singles out the refreshing quality of the song when Calepine, released from captivity, and now regaining strength,

> 'Upon a day he cast abrode to wend,
> To take the ayre, and heare the thrushes song.'

And the song made a similar appeal to Hardy, when 'every spirit upon earth seemed fervourless as I',

> 'At once a voice arose among
> The bleak twigs overhead
> In a full-hearted evensong
> Of joy illimited;
> An agéd thrush, frail, gaunt, and small,
> In blast-beruffled plume,
> Had chosen thus to fling his soul
> Upon the growing gloom.'

Michael Drayton, who has some claim to be the best ornithologist among English poets, said 'Of all birds, only the blackbird whistleth', and with 'the blackbird whistles from the thorny brake' Thomson recognized the same quality. Theocritus, 2,000 years before, had remarked the clarity of its notes, and poets in the Greek Anthology leave no doubt of their preference for its song to that of the thrush—in Greece, no doubt, the Mistle Thrush.

The 'early, cheerful, mounting lark' both by its conspicuous song-flight and by the quality of its song makes a strong contrast with the Nightingale singing its plaintive song at night in 'verdurous glooms and winding mossy ways', and it has delighted many English poets. Wordsworth drew the contrast in a poem addressed To a Skylark:

> 'Leave to the nightingale her shady wood;
> A privacy of glorious light is thine;
> Whence thou dost pour upon the world a flood
> Of harmony, with instinct more divine;
> Type of the wise who soar, but never roam;
> True to the kindred points of Heaven and Home!'

When Romeo must leave Juliet she says:

> 'It was the nightingale, and not the lark,
> That pierced the fearful hollow of thine ear;
> Nightly she sings on yond pomegranate-tree:
> Believe me, love, it was the nightingale.'

But Romeo is not convinced:

> 'It was the lark, the herald of the morn,
> No nightingale: look, love, what envious streaks
> Do lace the severing clouds in yonder east:
> Night's candles are burnt out, and jocund day
> Stands tiptoe on the misty mountain tops.'

Gray, like Wordsworth, notes song-flight and song:

> 'the skylark warbles high
> His trembling thrilling ecstasy;
> And, lessening from the dazzled sight,
> Melts into air and liquid light.'

Meredith attempted to describe the song:

> 'He drops the silver chain of sound,
> Of many links without a break,
> In chirrup, whistle, slur and shake ...
> A press of hurried notes that run
> So fleet they scarce are more than one.'

In the finest of all the poems inspired by the Skylark, which Shelley heard 'while wandering among the lanes' near Leghorn, he devised a stanza to represent its continuous, trilling melody:

> 'Sound of vernal showers
> On the twinkling grass,
> Rain-awakened flowers,
> All that ever was
> Joyous, and clear, and fresh, thy music doth surpass.'

Shelley heard his Skylark 'on a beautiful summer evening', but most of the poets associate the song with break of day. This is especially the time for song, before the busy human world has filled the air with discordant sounds, and the dawn chorus must have delighted many when getting up with the lark was the normal custom. The best description of this is Michael Drayton's in *Poly-Olbion*, where he writes of the birds of his native Warwickshire greeting the dawn in the Forest of Arden—where else, indeed, should a friend and neighbour of Shakespeare choose?—and he names many birds which

> 'with their cleere open throats
> Unto the joyfull Morne so straine their warbling notes
> That Hills and Valleys ring, and even the ecchoing Ayre
> Seemes all compos'd of sounds.'

Among these he names the Woodlark, which Gerard Manley Hopkins made the subject of an unfinished poem, where he transcribes the song:

> '*Teevo cheevo cheevio chee*:
> O where, what can that be?
> *Weedio-weedio*: there again!
> So tiny a trickle of song-strain.'

William Browne has a description of 'a musical concert of birds' no doubt in his native Devon:

> 'The lofty treble sung the little wren;
> Robin the mean, that best of all loves men;
> The nightingale the tenor, and the thrush
> The counter-tenor sweetly in a bush ...
> The crow was willing they should be beholding
> For his deep voice, but being hoarse with scolding,
> He thus lends aid; upon an oak doth climb
> And nodding with his head, so keepeth time.'

Poets of the greatest age of English music, in the 16th and 17th centuries, were especially responsive to the song of birds. Henry Vaughan, different from other poets as always, thought of a bird waking from sleep:

'Hither thou com'st: the busie wind all night
Blew through thy lodging, where thy own warm wing
Thy pillow was. Many a sullen storm
(For which course man seems much the fitter born,)
Rain'd on thy bed
And harmless head.
And now as fresh and chearful as the light
Thy little heart in early hymns doth sing.'

John Clare may rival Skelton and Drayton for the number of birds whom he mentions, among them some which seldom enter poetry, such as the Snipe, Yellowhammer, Blue Tit, Sand Martin, Corncrake and Firetail (Redstart) which, apprehensive when a hedger stops a gap near her nest in a hollow tree,

'Of everything that stirs she dreameth wrong
And pipes her "tweet tut" fears the whole day long.'

And, when his mind had broken, he could still delight in the birds he knew:

'Little trotty wagtail he went in the rain,
And twittering, tottering sideways he ne'er got straight again.
He stooped to get a worm, and looked up to get a fly,
And then he flew away ere his feathers they were dry.'

But it is not the province of the poet to contribute detailed knowledge of the lives and habits of individual species and it is often pointless to try to make precise identifications.

One of the strangest legends about the song of birds is of the swan-song—the song which the swan was said to sing only as a prelude to its own death. Certainly the Greeks, among whom the legend arose, would not have differentiated between Mute and Whooper Swans, both of which occur in the north, but it is tempting to suppose that the species which gave rise to the legend was the Whooper. Alcaeus said that swans transported Apollo to the land of the Hyperboreans, to the uttermost north, and Aristophanes said that the birds 'clattered their wings together in praise of Apollo, and through an aery cloud came their cry.' Perhaps someone noticed the musical cry of Whoopers before they left in the spring and, not seeing them again, devised the legend of the swan-song. The unrelated myth of Zeus taking the shape of a swan to woo Leda, who laid the egg (or two eggs) from which hatched Helen of Troy and the Heavenly Twins, was first told by Euripides and has attracted many painters and poets since his time, including W.B. Yeats who wrote a fine sonnet—his only sonnet—on the theme. But that story cannot reward ornithological research. *The Wild Swans at Coole* shows Yeats watching unmythical birds at a favourite place of his, and yet imagining them to have that timelessness which Keats imagined for his Nightingale. Birds' lack of individual characteristics seems to deprive them of those personal qualities whose passing is the source of so much human grief.

Swans are large and conspicuous not small and retiring like so many song-birds, but these man has long kept in cages and aviaries, where the poets have praised or lamented them. Catullus' address to and elegy on Lesbia's sparrow are probably the most famous of these, but by no means the earliest. The Greek Anthology includes a number of epitaphs on tame partridges—Alcibiades kept a pet Quail—or on song-birds, some of which had been killed by cats, and Catullus knew Simias' epitaph on a partridge. Some have doubted whether Lesbia's pet was a humble sparrow, but it chirruped (*pipiabat*) and sparrows are still kept as pets in Italy, as in England in the 16th century. Skelton wrote a long poem, and his best, when Jane Scrope's pet sparrow was killed by the nunnery cat, and though he was more interested in Jane than in her pet there is no reason to doubt that it was a sparrow: indeed the lecherous disposition of sparrows was something that Skelton could exploit. Sidney pretended to be jealous of Stella's pet sparrow which, like Jane Scrope's and George Gascoigne's and like himself, was called Philip. Skelton, who names 75 birds in his poem—far more than Shakespeare in all his works—followed the medieval tradition of birds attending a requiem mass, as does Shakespeare in *The Phoenix and Turtle*; but this tradition derived ultimately from Ovid who, in his elegy on a parrot (*Amores* II.6) summoned the birds to its funeral.

'Psittacus, Eois imitatrix ales ab Indis,
occidit: exsequias ite frequenter, aves;
ite, piae volucres, et plangite pectora pinnis
et rigido teneras ungue notate genas.'

Later Statius also wrote a lament for a dead parrot. They were fashionable pets in Imperial Rome.

If the poets' sympathies are usually with the owners of the pet birds there are, nevertheless, some whose imagination is touched by the bird's imprisonment in a cage. Everyone knows Blake's

'A robin redbreast in a cage
Puts all Heaven in a rage,'

but the exaggerated violence of expression is far less acceptable than Chaucer's gentle understanding:

'Tak any brid, and put it in a cage,
And do al thyn entente and thy corage
To fostre it tendrely with mete and drinke,
Of alle deyntees that thou canst bithinke,
And keep it al-so clenly as thou may;
Al-though his cage of gold be never so gay,
Yet hath this brid, by twenty thousand fold,
Lever in a forest, that is rude and cold,
Gon ete wormes and swich wrecchednesse.
For ever this brid wol doon his bisinesse
To escape out of his cage, if he may;
His libertee this brid desireth ay.'

Thomas Hardy, seeing a caged bird whose eyes had been put out, and hearing it singing, made a subtle contrast with man by adapting St Paul's words on charity:

'Who hath charity? This bird.
Who suffereth long and is kind,
Is not provoked, though blind
And alive ensepulchred?
Who hopeth, endureth all things?
Who thinketh no evil, but sings?
Who is divine? This bird.'

Cowper, who wrote an elegy *On the Death of Mrs Throckmorton's Bulfinch* (which was killed by a rat) wrote a better poem *On a Goldfinch starved to death in his cage*:

'Time was when I was free as air,
The thistle's downy seed my fare,
My drink the morning dew;
I perch'd at will on ev'ry spray,
My form genteel, my plumage gay,
My strains for ever new.'

But man's cruelty and neglect brought this happy liberty to an end. A more unusual epitaph, for this is on a wild bird, is Samuel Rogers' On a Robin-Redbreast, which was 'inscribed on an urn in the flower-garden at Hafod.'

'Tread lightly here, for here, 'tis said,
When piping winds are hushed around,
A small note wakes from underground,
Where now his tiny bones are laid.
No more in lone and leafless groves,
With ruffled wing and faded breast,
His friendless, homeless spirit roves;
—Gone to the world where birds are blest!
Where never cat glides o'er the green,
Or school-boy's giant form is seen;
But Love, and Joy, and smiling Spring
Inspire their little souls to sing!'

Poems about Robins are innumerable, for it is familiar in most English gardens where its confiding nature and attractive song, which is repeated in autumn when most other birds are silent, endears it to man. The nursery rhyme, *Who killed cock robin?* has been known to generations of children, probably from the 15th century on; and the strange legend that the robin 'fynding the dead body of a Man or Woman, wyll cover the face of the same with Mosse', was attached to the story of the Babes in the Wood, and so again made known in the nursery. Both the ballad and the legend date from the late 16th century, if not earlier. Only a bird as well known to man as the Redbreast could have acquired a nickname, which indeed has now become its usual name, just as 'Jackdaw' has supplanted the older 'daw'. The rascally repute of this bird has also been established by the Ingoldsby Legend of *The Jackdaw of Rheims*, one of the most amusing poems about a bird. By contrast with such anthropomorphic accounts of birds Marvell has a vivid description of the Hewel (Green Woodpecker) who

'walks still upright from the Root,
Meas'ring the Timber with his Foot;
And all the way, to keep it clean,
Doth from the Bark the Wood-moths glean.'

Clearly he had enjoyed watching a wild woodpecker about its daily life.

Emigrants from Britain to the New World were seldom poets, but Alexander Wilson, the Scottish pedlar poet author of the *American Ornithology* (1808–14), wrote of American birds which had not previously been celebrated in verse: the Ruby-throated Hummingbird which

'Sips with inserted tube the honeyed blooms,
And chirps his gratitude as round he roams.'

And he notes the iridescence of the plumage, where

'Each rapid movement gives a different dye.'

He has poems descriptive of other American birds, among them the Blue Jay and the tyrant flycatcher or Kingbird. This then was persecuted and Wilson sought to dispel prejudice by presenting the reader with a short poetical description of its life-history. Edna Millay's *Bobolink* is more about herself than the bird, and Robert Frost's charming poem *On a Bird Singing in its Sleep* does not identify the species. Poe's *Raven* has the traditional, sinister qualities but is as mythical as Coleridge's albatross.

Men have kept birds not only as pets, for the beauty of their plumage and the charm of their song, and for food, but also for sport, especially the noble sport of FALCONRY which provided imagery for medieval poets and for Shakespeare. In *2 Henry VI* there is reference to flying at the brook, and Michael Drayton, again, provides the best poetic account of this sport in the Norfolk section of *Poly-Olbion*, where the quarry is wildfowl. Drayton clearly had first-hand knowledge of the sport through Sir Thomas Monson and Sir Henry Goodere, both of whom he knew well, and both of whom were noted falconers. The later and less aristocratic sport of shooting has also been noted by the poets, perhaps best of all by Pope in *Windsor-Forest*, though the prey here would not all be at risk from modern sportsmen:

'With slaught'ring Guns th' unweary'd Fowler roves,
When Frosts have whiten'd all the naked Groves;
Where Doves in Flocks the leafless Trees o'ershade,
And lonely Woodcocks haunt the watry Glade.
He lifts the Tube, and levels with his Eye;
Strait a short Thunder breaks the frozen Sky.
Oft, as in Airy Rings they skim the Heath,
The clam'rous Lapwings feel the Leaden Death:
Oft as the mounting Larks their Notes prepare,
They fall, and leave their little Lives in Air.'

Thomson's humanitarian sentiment deflected him from describing the sport:

'These are not subjects for the peaceful muse,
Nor will she stain with such her spotless song—
Then most delighted when she social sees
The whole mix'd animal creation round
Alive and happy.'

The ancient Japanese custom of fishing with trained cormorants has been celebrated in tankas and it may be that the training of cormorants demands similar patience and skill to the training of falcons.

Hopkins' poem *The Windhover* is a masterpiece on a falcon (Kestrel) but has no reference to the sport; there are few poems about birds of prey outside the context of falconry, though Alexander Wilson has one on the Osprey. Even eagles have not found much favour with the poets, apart from their legendary ability to gaze at the sun and their identification in Greek myth with Zeus as was fitting for the 'feathered king'. Tennyson's six lines, which recall the legend, surpass all others:

'He clasps the crag with crookèd hands;
Close to the sun in lonely lands,
Ringed with the azure world, he stands.

The wrinkled sea beneath him crawls;
He watches from his mountain walls,
And like a thunderbolt he falls.'

Seabirds are as remote from man as eagles, and the most famous of them in poetry, the Ancient Mariner's albatross, is a symbol rather than a bird—a bird which Coleridge had never seen. As we might expect, it is poets from the highland zone of Britain who have written of seabirds: Dafydd ap Gwilym has an elegant cywydd to a snow-white gull on the margin of the sea, and in the Anglo-Saxon *Seafarer* there is mention of the clamour of Gannets and the crying of 'sea-mews'. But the finest description is James Thomson's in *Autumn*:

  Or, where the Northern Ocean in vast whirls
Boils round the naked melancholy isles
Of farthest Thule, and th' Atlantic surge
Pours in among the stormy Hebrides,
Who can recount what transmigrations there
Are annual made? what nations come and go?
And how the living clouds on clouds arise,
Infinite wings! till all the plume-dark air
And rude resounding shore are one wild cry?

Thomson's birds are immersed in activities which have nothing to do with man. In Norway, too, Ibsen has some well-observed poems about seabirds. With these one might place Shakespeare's well-known lines about a Dabchick, which he had clearly observed, though, as usual, he requires it only for a simile for human behaviour:

'Like a dive-dapper peering through a wave,
Who, being looked on, ducks as quickly in.'

The nocturnal owls, remote from man in another way, have, by their stealthy flight and eerie cries, always seemed sinister, and this has perhaps been enhanced by their facial discs and frontal gaze, 'the staring owl' of Shakespeare, which has some human suggestion. The 13th century poem of *The Owl and the Nightingale*, in which the two birds debate the matter of what benefits they confer on man nevertheless has some natural charm of observation though the two birds are very anthropomorphic.

Aristophanes' comedy *The Birds*, first produced at Athens in 414 BC, remains the most comprehensive and in many ways most remarkable of all European tributes to birds. It exhibits man's world seen through the eyes of birds, and, inevitably, seen as comic, an ornithomorphic view of man, so to say. It includes 'scraps of birdlore culled from every quarter—from history, poetry, legend, fable, proverb, and personal observation,' from all the varied responses of man to the fascination of birds. It could only have been written by a man who enjoyed looking at and listening to birds, and perhaps better than any other piece sums up what European poets for nearly 3,000 years have been writing about birds. E.J.M.B.

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POIKILOTHERMAL: 'cold-blooded', opposite of HOMOIOTHERMAL (see HEAT REGULATION).

POINTED-TAIL: substantive name of *Berlepschia rikeri* (see OVENBIRD (1)).

POISONING: see TOXIC CHEMICALS.

POISONING, LEAD: see DISEASE; and under GRIT.

POLIOPTILINAE: see GNATCATCHER.

POLLINATORS: agents—avian in this context—in the pollination of plants. Birds may be predators on plants or they may be used by plants as agents of pollen flow or SEED DISPERSAL. In the latter cases, the plants have adaptations for attracting birds and often for restricting less efficient visitors. There has evidently been a long history of co-evolution between birds and plants, in the course of which mutual adaptations have been acquired.

In typical bird-pollinated flowers the corolla tube is long and generally narrow, the ovary is inferior, and the nectar, which is produced mostly during the day when the flower is open, is stored at the base of the corolla. The colour is very often (but by no means always) red. Bird-flowers usually do not produce a scent or have nectar guides that might facilitate insect visits. Within bird-flowers there are even more refined specializations that limit the range of bird species that can visit each flower efficiently.

Birds of a wide variety of families (hummingbirds, honeyeaters, sunbirds, orioles (Icteridae), tanagers, finches, estrildid finches, flowerpeckers etc.) visit flowers and, at least sometimes, remove nectar. Not all of these visitors effect successful pollination. Some birds (e.g. estrildids and finches) remove and mandibulate the flower to force nectar out; others, such as some honeycreepers (Thraupidae), may probe into the nectar chamber through the corolla wall, contacting neither the stigma nor stamens. These nectar thieves have probably been important selective agents for the evolution of thick corollas and inferior ovaries.

Birds adapted for feeding on flower nectar often have relatively long bills, and extensible tongues with fringed bifurcated tips. The tongue of sunbirds and hummingbirds has a longitudinal trough in which nectar moves by capillary action. In neither group is the trough sufficiently enclosed to permit a 'soda straw' sucking action. Other, less specialized nectar feeders among birds have fringe-tipped tongues (e.g. the 'brush-tongued' parrots), but generally lack the bifurcated tip. Legitimate visitors to flowers probe through the distal corolla opening to reach the nectar chamber at the base of the corolla, at the same time either depositing or removing pollen. The position of stamens and stigma differs in different bird-flowers, and this may help to ensure that the pollen removed by a bird is transferred to another flower of the same species. The pollen of bird-flowers is generally sticky and may coat the bird's surfaces.

There is very little evidence that birds regularly eat pollen (though this may be an important source of amino acids for some insects and bats) or are searching for insects in the flowers that they probe (despite categorical statements in the earlier literature). They visit the flowers only for the nectar, which in the case of specialized nectarivores provides their main energy source.

The composition of floral nectar includes (in addition to water) sugars, usually composed primarily of sucrose, glucose and fructose; small amounts of polysaccharides; and small quantities of other substances (see below). Nectar in bird-pollinated flowers varies at least from 10% to about 50% sugar concentration by weight, the majority being in the range 15–25%. Insect-pollinated flowers tend to have somewhat higher concentrations of sugar, and also nectar that varies widely in concentration through time as a result of evaporation from the more open flowers.

The other substances contained in nectar include amino acids, proteins and lipids. While some of these are of some nutritional potential for birds the concentrations tend to be lower in bird-pollinated than insect-pollinated flowers. The few hummingbirds that have been tested in the laboratory either reject or show no preference for sugar solutions containing amino acids at approximately natural concentrations. It seems to be the general rule that nectarivorous birds derive most non-energetic nutrients from insects captured away from the flowers.

Most hummingbird-pollinated plants do not have perches that provide direct access to the flowers. Hummingbirds must usually hover while feeding, although where possible they will use an available perch, such as an adjacent leaf. Most other nectar specialists visit plants with convenient perches. Large nectar feeders such as orioles and parrots are facultative visitors although some tropical trees may use orioles as their principal pollinators.

Nectarivorous birds may increase the benefit from foraging by preferentially visiting flowers that have accumulated the largest amounts of nectar. Sunbirds, Hawaiian honeycreepers (Drepanididae) and hummingbirds have been shown to organize their visits so as to make the nectar reward per flower more than could be expected from random foraging. This probably involves some memory of locations in a foraging area. Long-term memory has been recorded in hummingbirds that, for example, return to the location of a feeder after a migratory absence.

Foraging patterns by nectarivores influence gene flow among the plants at which they feed. Non-random foraging (see above) will tend to equalize the visitation rate to each potential pollen donor and recipient. Behavioural interactions among the pollinators will also influence gene-flow between plants. Thus a territorial bird, defending a concentrated group of flowers, will generally carry pollen only over short distances, while a bird that feeds on flowers that are too sparse to be suitable to defend as a feeding territory will carry pollen over longer distances. The effect on the plants will depend on the degree of local adaptation. For at least one insect-pollinated plant, *Delphinium nelsoni*, there is evidence that pollen flow over relatively short distances increases individual reproduction. Shorter or longer distances of pollen movement may disrupt local adaptations and lower reproductive success through reduced seed set or reduced viability of offspring.

Colour, especially red, is often assumed to play an important role in attracting bird visitors to flowers. However, hummingbirds will visit flowers (and feeders) displaying colours from near ultraviolet to red, provided that they obtain nectar rewards. The importance of red may lie in the contrast with green foliage as well as in the ability of birds to discriminate red wave lengths. Some insects, at least, are less capable or incapable of red discrimination, so that colour may function to restrict insect visitors to hummingbird-flowers.

See photo FEEDING HABITS. L.L.W.

POLYANDRY: general term for mating systems in which individual females regularly mate with two or more males in the course of a breeding season. Polyandrous mating systems are confined to a few groups of non-passerine nidifugous birds, in nearly all of which each nest is tended by a single parent—in most cases the male only, in a few cases by the male and female at separate nests. It is often combined with a reversal of the usual sex roles in courtship, the female being larger and more brightly coloured than the male and playing the dominant role. In contrast to POLYGYNY, which is characteristic of seed-, fruit- and nectar-eating birds, polyandrous species mostly eat animal food.

The main feature of typical polyandrous breeding systems is that the male takes charge of the eggs laid by his mate, thus freeing her to lay another clutch for another male. Hence polyandry is normally successive (or serial). Simultaneous polyandry is known in two species of hawks, one species of jacana, the Tasmanian Waterhen *Tribonyx mortierii*, and the Noisy Miner *Manorina melanocephala*, a honeyeater with a highly developed group breeding system.

The reasons for the original reversal of the sex roles in families in which polyandry is the rule are not known. When the contributions of the two sexes to the care of the nest and young are unequal, the female will normally be expected to take the greater part, as her investment in the reproductive effort is the greater (see MATING SYSTEM). Whatever the original causal factors in the various groups in which it occurs, polyandry is clearly adaptive in making possible an increase in the reproductive output, especially when conditions suitable for breeding are short-lived. In principle it can easily be derived from a monogamous breeding system in which the female lays 2 clutches of eggs, the first of which her mate incubates while she takes charge of the second.

The following treatment is systematic, and includes all groups of birds in which polyandry has been reliably reported.

Ratites. The Australian Cassowary *Casuarius casuarius* practises successive polyandry. Pairs are formed, but after laying the female leaves the clutch to the male and may mate with one or more further males. (The nesting behaviour of the Emu *Dromaius novaehollandiae* is similar, but females apparently do not normally pair with a second male.) In the Greater Rhea *Rhea americana* successive polyandry is combined with harem polygyny. The male collects a harem of females, all of whom lay in his nest. He then takes sole charge of the nest and eggs and the females move on and mate with another male. Mating systems vary geographically in the Ostrich *Struthio camelus*; in the East African race at least (*S. c. massaicus*), females mate promiscuously with several males.

Tinamous. The breeding systems are varied in this family, but in all species that have been studied in detail the male takes charge of the nest and its contents. Some species are monogamous; in others there is successive polyandry, and in at least 3 species successive polyandry is combined with harem polygyny (see POLYGYNY).

Hawks. The Galapagos Hawk *Buteo galapagoensis* practises what has been called 'co-operative polyandry' (Faaborg *et al* 1980). One to 4 males mate with a single female, and all males help in the care of the eggs and young. Polyandrous groups apparently breed more successfully than monogamous pairs. Less complete evidence indicates that the breeding system of Harris's Hawk *Parabuteo unicinctus* of desert areas of North America is similar. In these cases polyandry seems to be an adaptive response to breeding in habitats where food resources are poor or unpredictable.

Partridges. In the Red-legged Partridge *Alectoris rufa* in captivity, after pair formation the female lays a clutch of eggs which her mate incubates and then a second clutch which she herself incubates. In the wild, however, there is evidence that females may lay clutches for successive males.

Buttonquail. Successive polyandry appears to be the rule. There is some evidence for it also in the related Plains-wanderer *Pedionomus torquatus* (sole member of the Pedionomidae), and in one of the 3 species of mesites (Mesitornithidae), another related family. Possibly therefore the system evolved early in the evolutionary history of this section of the Gruiformes.

Rails. The Tasmanian Waterhen lives in groups, each female associating with one to 3 males. All of them mate with her and help to raise her young.

Jacanas. Successive polyandry is the rule in the Indian species *Hydrophasianus chirurgus*, and probably in *Metopidius indicus*. The Neotropical species *Jacana spinosa* has a system of simultaneous polyandry. Each female has from one to 4 males which hold sub-territories within her own territory. Females are generally larger than males in all species; in *Jacana spinosa* the difference is extreme, females weighing 75% more than males.

Painted snipe. Successive polyandry is the rule, at least in the Old World species *Rostratula benghalensis*. The female is larger and more brightly coloured than the male.

Sandpipers, plovers and phalaropes. Most sandpipers and plovers seem to be normally monogamous, but successive polyandry occurs in a number of northern and montane species. The initial stage in the evolution of polyandry in this group is probably shown by Temminck's Stint *Calidris temminckii*, a species which seems normally to be monogamous: the female lays 2 successive clutches, the first of which is incubated by the male and the second by the female. A similar system probably occurs in the Little Stint *C. minuta*, Sanderling *C. alba*, and Mountain Plover *Charadrius montanus*. In the Spotted Sandpiper *Actitis macularia* polyandry is more advanced, females laying a succession of up to 4 clutches for different males, the last of which they help in incubating. In the Dotterel *Eudromias morinellus* the system seems to be essentially the same, but females are not recorded as laying more than 2 successive clutches. In the phalaropes the mating system has long been controversial. Polyandry (successive) was assumed, and recent research has confirmed it for the Red-necked Phalarope *Phalaropus lobatus* and Grey Phalarope *P. fulicarius* (see PHALAROPE).

Honeyeaters. The Noisy Miner of eastern Australia has a highly developed communal breeding system (Dow 1978). Females may mate with several males of the group to which they belong, and as many as 14 different males have been seen feeding the young in one nest. Though the system qualifies as polyandrous, it is rather one of promiscuity modified by the dominance relations obtaining among the males, the dominant male of a group achieving most of the copulations. D.W.S. (1)

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(See also references under MATING SYSTEM.)

POLYBOROIDINAE: see HAWK.

POLYGAMY: see MATING SYSTEM.

POLYGYNY: general term for mating systems in which individual males regularly mate with two or more females in the course of a breeding season; thus excluding the cases of occasional bigamy recorded in many normally monogamous species. For general considerations of the part played by the two sexes in the care of eggs and young, see under MATING SYSTEM.

A clear-cut classification of the many forms of polygyny is hardly possible, partly because of their variety and variability and partly because of inadequate knowledge of the biology of many of the species concerned. A distinction is usually made between (1) harem polygyny, in which a male maintains simultaneous pair-bonds with two or more females, (2) successive (or serial) polygyny, in which a male pairs with two or more females in succession, and (3) promiscuity (often associated with LEK displays), in which the male mates with as many females as offer themselves to him, and no pair-bonds are maintained. 'Promiscuity' is, however, not a very suitable term, as females of such species are by no means promiscuous but highly selective in their choice of mates, though males may be relatively undiscriminating. The term 'polybrachygamy' (many brief matings) has been proposed by Selander (1972). In some ratites and tinamous harem polygyny is combined with POLYANDRY. A distinction may also be made between 'resource-based' polygyny, in which the male makes some resource, over which he has control, available to the females with which he mates, and polygyny that is not based on any resource, in which the male contributes nothing but his genetic material to the reproductive effort of the females with which he mates. This distinction is biologically important, but in particular cases it is not always possible to decide, on the evidence available, whether a system is resource-based or not. A further difficulty arises, in some cases, in attempting to distinguish polygyny from promiscuity in species which have not received detailed study with marked individuals.

One of the main preconditions for the evolution of polygyny is that the female should be able to tend the eggs and young single-handed, or with only a small amount of assistance from her mate. This condition is met in several of the groups of birds in which polygyny occurs (e.g. game-birds, waders, hummingbirds), but it applies less obviously to polygynous species in passerine families in which monogamy is the rule. In these cases it seems that polygyny results from certain features of the habitat and associated food resources. It is found especially in species that exploit highly productive but structurally simple habitats, in which food is concentrated in a narrow spatial range (e.g. some marsh birds), or habitats that offer widespread feeding areas but restricted nest-sites (e.g. some colonial tree-nesters). In such conditions some males may be able to control territories in which two or more females may be able to breed successfully, while less successful males may obtain suboptimal or unsuitable territories, or none at all. A further factor favouring polygyny may be a domed or hole nest, which reduces the energetic costs of incubation and feeding the young and so may make it easier for the female alone to tend the nest (e.g. wrens, dippers).

Since the functional classification is difficult, for the reasons given above, the following treatment is systematic, and includes all groups of birds in which polygyny has been reliably reported. Lek species are mentioned but not dealt with in detail; for a fuller treatment see under LEK.

Ratites. In the Greater Rhea *Rhea americana* the male collects a harem of up to 15 females, all of whom lay in his nest. He then takes sole charge of the eggs and young while the females move on and lay for another male (harem polygyny combined with successive polyandry). In the Ostrich *Struthio camelus* mating systems differ in different populations. Males of the southern race (*S. c. australis*) collect a harem of females who all lay in one nest, but the dominant female helps the male in incubation and all the females help in care of the young. In the E. African race (*S. c. massaicus*) several females lay in one nest but a harem is not formed; only one female, the 'major' female, remains associated with the male and his nest. (In the Emu *Dromaius novaehollandiae* monogamy seems to be the rule.)

Tinamous. In at least 3 species (*Nothocercus bonapartei, Nothoprocta cinerascens* and *Crypturellus boucardi*) the breeding system is essentially the same as in the Greater Rhea: the male collects a harem of several females, which lay in his nest and then move on to another male. Other tinamous are monogamous or serially polyandrous; in all of them the male takes charge of the nest and its contents.

Bittern. Males of the Bittern *Botaurus stellaris* (and possibly other *Botaurus* spp.) may have several females nesting within their territories. Presumably this is a case of harem polygyny, but it needs further study. Nothing comparable has been recorded in other members of the Ardeidae.

Ducks. In contrast to the great majority of the species, the tropical ducks of the closely related genera *Cairina* and *Sarkidiornis* (Muscovy and Comb Ducks) are reported to be promiscuous, each drake copulating with several females. The Musk Duck *Biziura lobata* of Australia is also promiscuous. The evidence comes mainly from birds in captivity, and more detailed observations on wild birds are needed. Harem polygyny may be involved.

Harriers. Polygyny is regular in the Hen Harrier *Circus cyaneus*, Montagu's Harrier *C. pygargus*, and probably Marsh Harrier *C. aeruginosus*. In the Hen Harrier as many as 7 females have been recorded breeding in an area occupied by a single male.

Game-birds. Several species of grouse (Tetraoninae) and the Great Argus *Argusianus argus* and Crested Argus *Rheinartia ocellata* (Phasianidae) have lek displays. In the Common Pheasant *Phasianus colchicus*, and probably many other pheasants with pronounced sexual dimorphism, the system is one of harem polygyny; the male contributes to the reproductive success of his mates by feeding them in the period before egg-laying, and they may benefit by nesting within his defended territory. Mating systems in the Phasianidae need further study, ranging as they do from monogamy (e.g. partridges) to lek systems; almost certainly there is wide variation in the development of polygyny, linked with the extent of the male's contribution to the reproductive effort of his mates. The Turkey *Meleagris gallopavo* (Meleagridae) has a system of harem polygyny in which the male apparently contributes nothing except genetic material.

Bustards. In the Great Bustard *Otis tarda* males display in leks and are either promiscuous or perhaps form temporary bonds with particular females; in either case they are polygynous. The Little Bustard *Tetrax tetrax* has been reported to be polygynous and monogamous; the Houbara *Chlamydotis undulata* is said to be monogamous. Mating systems in this family need much more study.

Waders. Several species that breed at high latitudes in the north are polygynous. In 4 species, the Ruff *Philomachus pugnax*, Great Snipe *Gallinago media*, Buff-breasted Sandpiper *Tryngites subruficollis*, and Pectoral Sandpiper *Calidris melanotos* the males are promiscuous, the first 3 of these displaying in leks or 'exploded leks' (see under LEK) to which the females come for mating. Harem polygyny is found in 2 species (Curlew Sandpiper *Calidris ferruginea* and White-rumped Sandpiper *C. fuscicollis*) and possibly a third (Sharp-tailed Sandpiper *C. acuminata*). The Eurasian Woodcock *Scolopax rusticola*, a woodland breeder, practises successive polygyny (see RODING).

Hummingbirds. Polygyny is probably general throughout the family; there is no convincing evidence for monogamy in any species. In the great majority of the species the males contribute nothing except genetic material to the reproductive effort of the females with which they mate. Lek displays occur in several species; in many others males display solitarily. In a few hummingbirds, however, resource-based mating systems occur. In the Anna Hummingbird *Calypte anna* and the Fiery-throated Hummingbird *Panterpe insignis* males are territorial over flower clumps rich in nectar, and allow access to these food sources to females with which they have mated, and possibly also to their young. Males of the Hairy Hermit *Glaucis hirsuta* hold territories along stretches of forest stream, within which up to 3 females may nest. In this case it seems that competition for specialized stream-side nest-sites is so strong that the help of the male is needed for effective defence of the nest against conspecifics.

Honeyguides. A resource-based mating system of a special kind is found in the Orange-rumped Honeyguide *Indicator xanthonotus* of the Himalayan foothills. Males defend the huge combs of the bee *Apis dorsata*, and feed on the wax. Females mate only with comb-holding males, and they and later their young are allowed access to the comb of the male with which they have mated. Casual observations suggest that some African honeyguides may have similar mating systems.

Lyrebird. Polygyny is apparently regular in the Superb Lyrebird *Menura novaehollandiae* of south-eastern Australia. It is not certain whether females form any sort of pair bond with the males with which they mate, but it is known that they may visit more than one displaying male before mating.

Cotingas and manakins. Many members of these 2 families are polygynous. The males display either in leks or solitarily, mating with the females that they attract to their display areas. Frugivory seems to be the main predisposing factor in the evolution of polygyny in this group. Thus in the related family Tyrannidae, most of whose members are insectivorous, monogamy is the general rule, but one of the more markedly frugivorous species, *Pipromorpha oleaginea*, has a lek system analogous to but less highly developed than the lek systems of cotingas and manakins.

Dippers. Polygyny appears to be regular in the American Dipper *Cinclus mexicanus*, and may be expected to occur in other species.

Wrens. Four northern species are regularly polygynous, but so far as known no tropical species are. In the European Wren *Troglodytes troglodytes*, polygyny is most prevalent in the habitats that are richest in food, and the same is probably true of the Marsh Wren *Cistothorus palustris* of North America. It seems that in this family polygyny is likely to develop when the food supply is rich enough for the female to be able to feed the young effectively single-handed; the male can then increase his reproductive output by acquiring more than one female and reducing the assistance that he gives to each of them.

Old World flycatchers. In the Pied Flycatcher *Ficedula hypoleuca* and Collared Flycatcher *F. collaris* a proportion of the males are bigamous. The adaptive basis of polygyny is probably essentially the same as in the wrens.

Old World warblers. Polygyny is regular in Cetti's Warbler *Cettia cetti* and the Great Reed Warbler *Acrocephalus arundinaceus*. In the former, the largest males tend to acquire most females. In the latter, males that occupy territories that are especially rich in food tend most often to be polygynous, and the adaptive basis seems to be the same as in the wrens.

Penduline tits. In the Eurasian species, *Remiz pendulinus*, males build a succession of nests, attracting a female to each one in turn. This system seems to be essentially similar to that of the weaver-birds dealt with below.

Buntings. In the Dickcissel *Spiza americana* a proportion of the males are bigamous. The Corn Bunting *Miliaria calandra* has also been claimed to be polygynous, but the evidence is conflicting.

American orioles etc (Icteridae). Two groups of species in this family, all colonial breeders, are regularly polygynous, the marsh-living blackbirds (*Agelaius*, *Euphagus*, *Xanthocephalus*, and probably other genera) and the tropical tree-nesting caciques (*Ostinops*, *Cacicus*, and related genera). In the former group, the main predisposing conditions seem to be that food is generally very plentiful in the best habitats and that a proportion of the males can occupy the best areas and exclude the other males (cf. the Marsh Wren, above, in which similar conditions obtain). The latter group of species are mainly frugivorous, and nest-colonies are in traditional (presumably safe) trees away from feeding areas. Males are much larger than females and take no part in nesting. Successful males may mate with several different females; whether they are promiscuous, as is usually thought, or dominate a part of the colony and mate with the females in that part, needs further investigation.

Weavers. Successive polygyny occurs in 3 colonially nesting genera, *Ploceus*, *Bubalornis* and *Euplectes*. Males build a succession of nests, displaying at each newly completed nest to attract a female and then building another as soon as the previous one is occupied. There is an evident correlation between polygyny and diet in this family; thus the polygynous species are all seed-eaters, while the insectivorous species are monogamous.

Australian magpies (Cracticidae). In *Gymnorhina tibicen*, a group breeder, a male may mate with one to several females in his group. Mating and other relationships within this and other group-breeding species are dealt with more fully under CO-OPERATIVE BREEDING.

Birds-of-paradise and bowerbirds. Polygyny is the rule in most members of these 2 families. Males display either solitarily or in leks and take no part in the nesting duties. As in the cotingas and manakins, a mainly frugivorous diet seems to be an important predisposing condition for the evolution of polygyny. D.W.S. (1)

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(See also references under LEK and MATING SYSTEM.)

POLYMORPHISM: term that was defined by Ford (1945) as the coexistence in one interbreeding population of two (dimorphism) or more distinct and genetically determined forms, the least abundant of which is present in numbers too great to be due solely to recurrent mutation. The frequency of the rarer form has been variously defined as 1–5% by subsequent authors. The commonest use of the term for ornithologists occurs in relation to distinct plumage colour variants (strictly polychromatism) which have a genetic basis and which are not merely sexual, seasonal or developmental plumage variations. Examples would be the dark and light colour morphs of the Arctic Skua *Stercorarius parasiticus* or the red and grey morphs of the Screech Owl *Otus asio*. In recent years, however, polymorphism has been investigated in birds and other organisms at the molecular level using electrophoresis and other techniques to detect discontinuous genetic variation in enzyme systems.

The essence of Ford's definition is that the morphs must firstly be phenotypically distinguishable with discontinuities in the phenotype, since polymorphism must not be used to include continuous or quasi-discontinuous variation. These discontinuities, however, need not be obvious to the eye, since enzyme polymorphism requires considerable biochemical manipulation for its detection. Secondly, the phenotypic variants must be genetically distinct and there should be some understanding of the genetic basis of the polymorphism. Minimally it should be demonstrated that there is allelic segregation at at least one gene locus.

The difference between discontinuous and continuous genetic variation, while easy to understand conceptually, is often difficult to distinguish in practice. Huxley (1955) considered clutch-size differences in birds to be an example of polymorphism, insofar as clutch-size is a meristic character and a clutch of 2 is phenotypically different from one of 3 eggs. However, as shown by Perrins and Jones (1974), the underlying genetic basis for clutch size variation is presumably polygenic, similar to most continuous phenotypic variation, with no clear correlation of particular genotypes with particular clutch sizes. CLUTCH-SIZE variation is clearly quasi-discontinuous variation.

Investigations into polymorphism in birds have fallen into 3 major categories: genetic, evolutionary and taxonomic.

Genetic studies have been carried out in an attempt to elucidate the genetic basis for the phenotypic discontinuities of polymorphism, but on relatively few species. Genetic differences between red and grey morphs of the Screech Owl have been ascribed to a single pair of alleles with red dominant to grey. Red-footed Boobies *Sula sula* on the Galapagos Islands have been classified into 3 morphs: Brown, Intermediate and White. In this case two codominant alleles at one locus was the simplest genetic explanation for the polymorphism, the intermediate plumage birds being heterozygous. A similar explanation could account for the polymorphism in Arctic Skuas. Lemmetyinen *et al* (1974) postulated 2 independently assorting pairs of alleles at each of 2 loci to account for the polymorphism in Arctic tern *Sterna paradisaea* chicks.

Thorneycroft (1966) showed a chromosomal basis for the plumage polymorphism in the White-throated Sparrow *Zonotrichia albicollis* and other chromosomal polymorphisms have been detected in species showing no detectable phenotypic variation.

The genetic tools available to the ornithologist studying polymorphism in a wild population of birds are limited. Since controlled crosses are usually not possible, it is necessary to use data from samples collected in the field where sample size often limits reliability of interpretation. Unless long term studies are carried out with marked birds, it is possible to use family data only if the polymorphism is visible in adult and young birds. Interpretation is also difficult if the genes controlling polymorphism do not obey the HARDY-WEINBERG equilibrium. If, for example, mating between the morphs is not random, it becomes difficult to predict the distribution of the morphs in the offspring of different types of matings. A genetic analysis of families of the dimorphic Lesser Snow Goose *Anser caerulescens* which did not rely on Hardy-Weinberg equilibrium, led to the postulation of a 2-allele, single gene explanation for the difference between the blue and white morphs of the snow goose, with the allele for blue coloration incompletely dominant over the allele for white.

Evolutionary studies in polymorphism have been concerned mainly with the question of natural selection. R.A. Fisher stressed that the presence of a stable polymorphism implies a selective balance between the morphs, with one genotype favoured in some circumstances, another genotype favoured in others. Various explanations have been put forward to explain the maintenance of polymorphism. These include: (a) heterozygote advantage (heterosis) where organisms carrying both alleles (heterozygotes) in a 2-allele polymorphism have a higher reproductive fitness than the homozygotes; (b) negative assortative mating, i.e. the tendency of one morph to choose the other morph as a mate; (c) frequency dependent selection, where the fitness of a morph varies with its frequency in the population, such that a morph has higher fitness than its alternate when rare and vice versa; and (d) balance of advantages due to temporal or spatial heterogeneity in the environment.

Huxley, following Dobzhansky's work with *Drosophila*, believed that heterozygote advantage was the primary explanation for the maintenance of polymorphism in birds; this has not been shown in the avian literature.

Negative assortative mating is the rule in the White-throated Sparrow with tan morphs usually mating with white morphs. It has also been documented in some populations of Arctic Skuas, but is not necessarily the mechanism whereby the polymorphism is maintained. Dark birds could be favoured where early breeding is advantageous, whereas light birds are favoured where late breeding is preferable. Neither of these explanations has been effectively demonstrated.

Apostatic selection is selection for variation for its own sake and is thought to be maintained by FREQUENCY DEPENDENT SELECTION, in that a given phenotype is favoured in direct proportion to its rarity through frequency dependent predator pressure. No avian prey species has been demonstrated to be polymorphic due to apostatic selection, but the hypothesis has been extended to include parasitic birds such as cuckoos and predators such as hawks and skuas. It has been argued that the hosts of parasitic cuckoos would be less likely to recognize and respond to a rare morph, which would be to the advantage of that morph. Paulson (1973) has hypothesized that the rarer morphs of a predator would be less familiar to a potential prey individual and thus have a greater chance for successful capture. This advantage should lead to balanced polymorphism and could explain the high frequency of polymorphism in hawks and skuas.

In contrast to the classic studies in Lepidoptera where selective differences between the morphs have been amply demonstrated, there are far fewer avian examples. The reasons for this are simple. Fitness differences between morphs would be very small or non-existent and to detect fitness differences over a range of temporal or spatial environments would require extremely large sample sizes. Thus, although Lemmetyinen *et al* (1974) postulated that grey morphs of the Arctic tern were favoured in areas dominated by grey rocks and brown morphs where the rocks were reddish or the soil sandy, they could detect no differences in reproductive fitness between the morphs in either environment. A notable example is the Lesser Snow Goose. An early study showed the blue morph increasing in frequency at the expense of the white morph. This was accounted for by higher nest predation and hunter pressure on the white phase birds. However, a later study of a different population and with a sample of several thousand birds over 10 years found no differences in reproductive fitness between the 2 morphs. All other measures of reproductive fitness at different stages of the life cycle also showed no differences.

An interesting case where disruptive selection pressure has been suggested to account for the dimorphism is the European Cuckoo *Cuculus canorus* where Voipio (1953) suggested mimicry of 2 common European raptors, the Kestrel *Falco tinnunculus* and the Sparrowhawk *Accipiter nisus*, the red morph resembling the former, the grey morph the latter. Similarity to the models, it was postulated, enables the Cuckoo to intimidate the host species.

Evolutionary studies have also centred around the question of assortative mating and mate choice. Many species of birds choose mates randomly with respect to morph. There is no evidence of assortative mating in Red-footed Boobies, Screech Owls, some populations of Arctic Skuas, New Zealand Fantails *Rhipidura fuliginosa*, and Ferruginous Hawks *Buteo regalis*. In White-throated Sparrows there is strong negative assortative mating. In some populations of Arctic Skuas, and Western Grebes *Aechmophorus occidentalis*, there is positive assortative mating. In Snow Geese there are elements of both positive and negative assortative mating. Only in Snow Geese has it been shown that the assortative mating is a consequence of mate choice based on morph appearance (Cooke 1978). In this species, a bird from a monomorphic family will generally choose a mate of the same morph as that of its family. By manipulation it has been shown that the choice of a mate is a function of learned experience during the pre-pairing period of the bird's life. This is important because it shows that a learned response can influence the genetic structure of a population, and thus the degree of mixed matings within the population. Kalmus and Maynard-Smith (1966) showed that in theory such a mechanism could lead to speciation of former morphs but only if 100% efficient. In Snow Geese, only 85% of the birds from monomorphic families choose a mate of that family colour. Two other notable examples of evolutionary studies of polymorphic birds are of interest. The Ruff *Philomachus pugnax* is a polygamous shorebird with males showing a considerable variety of breeding plumage morphs. The darker morphs have greater success at acquiring territories and attracting mates than the white morphs. The genetics of plumage colour in this species are obscure and the reasons for the maintenance of the white morphs are puzzling. A possible genetically based behavioural polymorphism in the Common Eider *Somateria mollissima* is described by Milne and Robertson (1965). The population consists of migratory and non-migratory birds, the 2 groups having different gene frequencies at a number of gene loci where enzyme polymorphism occurs.

Enzyme polymorphisms have been much studied in the hope of discovering more about the genetic structure of bird populations, both inter- and intra-specifically. Enzyme polymorphism as detected by electrophoresis is less frequent among birds than amongst most other taxa studied. Reasons for this are unclear.

The third area of interest in polymorphism is taxonomic and systematic. It has been pointed out that visible polymorphism in birds is restricted to relatively few families—Procellariidae, Ardeidae, Accipitridae, Falconidae, Stercorariidae and Cuculidae. Elsewhere it is scattered among one or two species within a family, e.g. Phalacrocoracidae, Anatidae, Phasianidae, Haematopodidae, Scolopacidae, Alcidae, Strigidae, Corvidae, Turdidae, Muscicapidae, Laniidae, Thraupidae and Estrildidae.

A well known observation related to polymorphism is the phenomenon of 'ratio-clines', where the proportion of the morphs differs in different parts of the range. A classical example is the Guillemot *Uria aalge*, where the frequency of the bridled morph increased with latitude from below 0.5% to over 50%. Attempts to relate this and other ratio-clines to differing environment conditions along the clines have seldom been successful. The selective pressures affecting the relative fitness of the morphs are obviously complex and gene flow along the clines must be taken into account. In addition, genetic drift and historical factors play a role. The Lesser Snow Geese which winter on the Gulf Coast of USA consist predominantly of blue morphs at the eastern end of the distribution and white morphs at the west. There is some historical evidence that the 2 morphs were formerly allopatric with blue morphs wintering in the Mississippi delta and the white morphs in Texas. The mixing of the morphs may be recent as a result of historical modification by man of traditional feeding areas by such policies as burning of marshes, and the cline may reflect a stage in the equilibrium of the morphs. Rockwell and Cooke (1977) showed that localized changes in the ratios of the morphs in time and space could be explained largely by gene flow between populations. Why the original difference occurred in the wintering distribution of the morphs is not answered.

In the early development of ideas on speciation, major mutations such as those found in polymorphic species were thought to be the origin of new species. Mayr (1970) has summarized the reasons why speciation is now thought to be mainly due to selection acting on genes affecting continuously variable characters differentially in different isolated subpopulations of an originally inter-breeding population. While this is clearly true and generally accepted, there are some interesting species groups where polymorphism may have represented a stage of their evolutionary history. In many taxa there are dark species, light species and polymorphic species consisting of both light and dark morphs (*Buteo*, *Anser* (*Chen*), *Phalacrocorax*, *Haematopus*, Ardeidae, *Falco*, *Sula*). In *Sula* for instance, most species are white but the Brown Booby *Sula leucogaster* is brown and the Red-footed Booby is dimorphic. Most *Anser* geese have a grey plumage, but the Ross Goose *Anser rossii* is white and the Lesser Snow Goose dimorphic. Perhaps the Brown Booby and Ross Goose have had a dimorphic period in their evolutionary past. In fact the Ross Goose is polymorphic in its gosling stage.

Often polymorphism has not been recognized taxonomically as such. For example, the Brown Jay *Cyanocorax morio* and the Sooty-capped Bush Tanager *Chlorosphingus pileatus*, both of which are dimorphic, were formerly each separated into 2 species. Presumably there are many examples of polymorphism as yet undiscovered, particularly in the tropics and in cases where there is a strong ratio-cline. If there is strong positive assortative mating among the morphs, this will appear similar to the hybridization between closely related species. Only a careful genetic analysis will elucidate the true taxonomic status. F.C.

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Perrins, C.M. & Jones, P.J. 1974. The inheritance of clutch size in the Great Tit (*Parus major* L.). Condor 76: 225–229.

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Thorneycroft, H.B. 1966. Chromosomal polymorphism in the White-throated Sparrow, *Zonotrichia albicollis* (Gmelin). Science 154: 1571–1572.

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POLYPHYLETIC: of more than one evolutionary ancestry; applied to an assemblage of species, and contrasted with MONOPHYLETIC.

POLYTOPIC: found in different places—applied to a form that has widely separated populations.

POLYTYPIC: term applied to a taxon that has more than one unit in the immediately subordinate category, e.g. a genus comprising 2 or more species, or a species divisible into subspecies—contrasted with MONOTYPIC.

POMATORHININI: see BABBLER.

POORWILL: substantive name of *Phalaenoptilus nuttallii* and *Nyctiphrynus* spp. (see NIGHTJAR; also WHIP-POOR-WILL).

POPULATION DYNAMICS: see AGE; ECOLOGY.

POPULATION INDEX: a measure of population level related to a base figure, usually 100 (see CENSUS).

PORPHYRIN PIGMENTS: see COLOUR.

PORTAL: term applied, especially, to a system of veins draining the abdominal portion of the alimentary tract and associated organs to the liver, but also to some other systems similarly leading into glandular organs (see VASCULAR SYSTEM).

POSTURAL FACILITATION: see FACILITATION, POSTURAL.

POSTURE: see COMFORT BEHAVIOUR; SIZE; SLEEP.

POTOO: substantive name of the species of Nyctibiidae (Caprimulgiformes, suborder Caprimulgi); in the plural, general term (alternatively 'tree-nighthawk') for the family. 'Potoo' is the creole name for one of the species; it was apparently used for the first time in ornithology by Gosse in *Birds of Jamaica* (1847).

Characteristics. Potoos are 23–50 cm in length, rather long-winged and long-tailed birds, with soft cryptic coloration of grey, white, buffish-brown and almost black. The sexes are alike. The downy nestlings are white with narrow dark shafts (*Nyctibius griseus*) or white barred all over with brown (*N. grandis*). The bill is small and terminally decurved with a projecting 'tooth' on the maxillary tomium. There is a huge mouth of which the inside is flesh coloured. The legs are very short. The eyes are very large; *N. griseus* has a bright yellow iris, *N. grandis* a dark brown one, but both species reflect bright orange at night. Their flight is silent.

Habitat. *N. griseus* and *N. grandis* inhabit open woodland and also cultivated land, e.g. coffee and citrus plantations.

Distribution. The family is confined to tropical Middle and South America. The family consists of a single genus, with 5 species. The Great

Common Potoo *Nyctibius griseus*. (*C.E.T.K.*).

Potoo *Nyctibius grandis* is much the largest (weights from Surinam: 5 males 450–624, mean 533 g; 7 females 504–604, mean 557 g). It has been recorded locally in Central America (records from Guatemala, Nicaragua and Panama) and is widespread in South America, south to Peru and Brazil. The best known species, the Common Potoo *N. griseus*, is considerably smaller (weights from Surinam: 4 males 146–167, mean 156 g; 2 females 149, 155 g). It has the widest distribution, occurring from southern Mexico east through Central America and throughout South America south to Argentina, and also on the islands of Jamaica, Hispaniola, Gonave, Trinidad and Tobago. The 3 other species are rare and their ranges are probably not fully known. The Long-tailed Potoo *N. aethereus* is rufous and has a long, markedly graduated tail with the central feathers pointed. It is recorded from Guyana, southern Venezuela, western Colombia, eastern Peru, Paraguay and Brazil. The White-winged Potoo *N. leucopterus* is distinguishable by its white, black-tipped inner wing-coverts, forming a broad white band on the wing. It is recorded from Venezuela, northern Colombia and the coastal region of Brazil in Bahia. The Rufous Potoo *N. bracteatus* is the smallest, and is most rufous with the tail feathers barred black and tipped with white. It is recorded from Guyana, Colombia east of the Andes, eastern Ecuador and eastern Peru.

Food. The recorded food of *N. griseus* consists of insects of several orders (Hemiptera, Orthoptera, Coleoptera, Isoptera, Lepidoptera), that of *N. grandis* of various Coleoptera.

Behaviour. Potoos are strictly nocturnal, solitary and arboreal, spending the day sitting in an upright attitude on a branch of a tree or the top of a stump (cf. FROGMOUTH). Head scratching is done indirectly (over the wing). The roost is often used for a long time at a stretch. The birds become active in the evening, especially on bright moonlight nights, catching flying insects. This they do in flight from an elevated perch after the fashion of flycatchers (Muscicapidae), returning with their prey to the observation point.

Voice. *N. griseus* has a strophe of plaintive, very melodious notes in an exactly descending scale. *N. grandis* has a rich vocabulary, including a guttural *Oorrooroooo*, also a barking *wow* in which the head is thrown back with the bill pointed upwards.

Breeding. The single egg is laid in a small depression on a tree stump or branch, sometimes quite near the ground, but occasionally at a great height. The bird incubates by sitting in an upright position on the egg. When it feels unobserved and is at ease, it incubates with the head withdrawn and the bill pointed forwards, the plumage fluffed and relaxed; on becoming alarmed, the whole bird stiffens and lengthens slowly upwards, the bill pointing straight up and partly open, the eye partly opened into a slit. It can be closely approached and even handled, but then the bird threatens by opening its large eyes, fluffing out its plumage and spreading its tail, snapping its bill and opening wide its huge mouth.

The eggs of this species are oval and white without much gloss and are sparsely marked with small lilac and brown spots. Eggs from Trinidad measure 41.5 × 32.0 mm, from Surinam 35.9 × 26.1 mm and from Brazil 36.2 × 29 mm. The only known egg of *N. grandis*, from Brazil, was similar and measured 52.1 × 38.3 mm. Eggs of *N. griseus* have been found in Costa Rica in December, in Colombia in January, in Trinidad in March, April, July and August, in Surinam in April, and in Brazil in November and December. An egg of *N. grandis* was found in Brazil in July, and a nestling in Surinam in June. A probable egg of *N. aethereus* was found in Paraguay in December. Skutch (1970) studied the nesting habits of *N. griseus* in Costa Rica. He found that both parents incubated, covering the egg continuously except for an interval not exceeding 15 min at daybreak and a longer interval of 45–95 min at the beginning of the night. The long nocturnal session and the even longer diurnal session appeared to be continuous and by different parents. They apparently never turned or even touched the egg in its precarious position.

The incubation period was at least 33 days. The newly hatched nestling rested from the first facing the supporting branch just as the parents did when incubating and brooding. During the first 2 weeks a parent brooded the nestling, but ceased nocturnal brooding when it was 19 days old and diurnal brooding when it was 25 days old, after which it was always alone. When 10 days old it was fed 15 times by both parents on a moonlight night between nightfall and dawn, and when 35 days old it was fed 10 meals. When being fed, the nestling uttered a hoarse buzz. At the age of 26 days it was first seen to rest on a branch above the nest; at 35 days it was well feathered. Its first short flight was seen when it was 47 days old, and on its 51st day it finally flew from the tree and was not seen again. From the laying of the egg to its departure at least 84 days elapsed.

F.H.

Borrero, H.A. 1970. A photographic study of the Potoo in Colombia. Living Bird 9: 257–263.

Haverschmidt, F. 1968. Birds of Surinam. Edinburgh.

Skutch, A.F. 1970. Life history of the Common Potoo. Living Bird 9: 265–280.

POTOYUNCO: a name for *Pelecanoides garnotii* (see PETREL).

POULT: a domestic chicken; sometimes applied to other species.

POULTRY: collective term for birds of domesticated species (as distinct from 'game') used for the table (see DOMESTICATION).

POWDER DOWN: feathers which produce a fine powder (see FEATHER; PLUMAGE).

PRAIRIE CHICKEN: substantive name of *Tympanuchus* spp. (see GROUSE).

PRATINCOLE: substantive name of the species of the subfamily Glareolinae (Charadriiformes, suborder Charadrii, family Glareolidae); in the plural, a general term for the subfamily. Pratincoles, like the closely related coursers (subfamily Cursoriinae; see COURSER), are an entirely Old World group found throughout Africa, southern Europe, Asia and Australasia.

Only 2 genera are currently recognized: *Glareola* with 7 species (*pratincola, nordmanni, maldivarum, ocularis, nuchalis, cinerea* and *lactea*) and *Stiltia* with one species (*isabella*). Australian Pratincole *Stiltia isabella* is structurally and behaviourally intermediate between the coursers and the pratincoles and, although it shows greater affinity with the pratincoles, it provides a clear evolutionary link between the 2 subfamilies.

Characteristics. Like most coursers, *Glareola* has a pectinated middle toe, but *Stiltia* does not. Members of the genus *Glareola* are characteristically short-legged and have short tails; *Stiltia* is long-legged, has a square tail and a dark belly-band, giving it the appearance of a courser. All the pratincoles have long wings (especially so in *Stiltia*), a black-and-white tail and rump pattern, plain brown or grey dorsal plumage, little or no sexual dimorphism, a black bill with a bright red or orange base, and a fairly well developed hind toe which is somewhat raised above ground level. Their front toes are much longer than those of the coursers. The long wings are an adaptation to catching flying insects on the wing, although pratincoles also feed on the ground. They measure 18–30 cm and weigh 80–100 g.

The Collared or Red-winged, Black-winged and Oriental Pratincoles (*Glareola pratincola, G. nordmanni* and *G. maldivarum*) have a narrow black collar bordering the yellowish throat; they are obviously closely related to each other and may be merely races of one species.

Habitat. All the *Glareola* species live near water, usually in the form of large rivers, but sometimes marshes or flooded rice paddies. *Stiltia* is less water-dependent and inhabits open semidesert or dry grasslands, although water is often available in the form of rivers, lakes or temporarily flooded hollows.

Distribution and movements. The Collared Pratincole has breeding populations from South Africa north to Europe and east to north-western India; all are migratory, but their movements have yet to be mapped out in detail. The Black-winged Pratincole breeds from south-eastern Europe to western Asia and migrates to Africa when not breeding. The Oriental Pratincole is an eastern Asian breeder, some populations of which migrate southward as far as Australia and rarely to New Zealand. The Madagascar Pratincole *G. ocularis* breeds on Madagascar and migrates in the non-breeding season (from about April to September) to East Africa.

The White-collared Pratincole *G. nuchalis* of tropical Africa, the Grey Pratincole *G. cinerea* of West Africa and the Little Pratincole *G. lactea* of India and southeastern Asia are all resident. They have less deeply forked tails, lack a black collar and are sometimes put in a separate genus, *Galachrysia*. The Australian Pratincole breeds in northern and central Australia (rarely as far south as Adelaide) and migrates in the southern winter northwards, part of the population remaining in northern Australia and the rest crossing the sea to Indonesia.

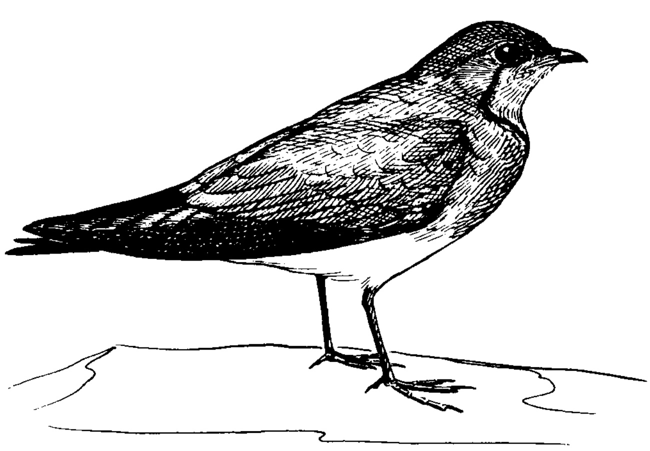
Food. All pratincoles feed entirely on insects caught on the wing or on the ground. The Australian Pratincole probably feeds mostly on the ground, chasing its prey with a swift run ending in a sudden turn with a wing outstretched, apparently to stop the prey from escaping further.

Behaviour. The pratincoles are all highly gregarious at all times, even when breeding. During migration they occur in flocks of several hundred birds. Like coursers, they are especially active in the evening when the flocks zig-zag to and fro with high-pitched calling. Flocks may wheel high in the air, and the riverine species often skim the surface of the water while feeding.

Voice. Pratincoles are particularly vocal in flight, although they also have contact calls given on the ground. The notes are high-pitched trilling or twittering in the genus *Glareola* and beautiful piping whistles in *Stiltia*. Alarm calls are somewhat harsher in tone. When inactive, pratincoles are mostly silent, often settling in a more or less close pack, all facing in the same direction and remaining motionless and inconspicuous.

Breeding. The *Glareola* species breed colonially near large rivers or marshes, sometimes on rocks in the middle of a river. Their nest is a mere scrape in the ground or a hollow on a rock. The eggs number 1–4 per clutch depending on the species (usually 2–3) and are well camouflaged with their bold irregular dark markings on a light yellowish background. Eggs of the Red-winged Pratincole in southern Africa are very dark—an adaptation to the birds' habit of often nesting on areas of burnt grassland. Their downy young are similarly blackish in colour.

The Australian Pratincole also nests in loose colonies, but on open stony semidesert in inland Australia. Like other pratincoles it nests near water, usually temporary pans flooded by recent rain, sometimes up to 2 km away. It makes no nest, laying its clutch of 2 eggs on a bare patch of soil among stones or gravel. The eggs resemble stones in colour and texture. The downy plumage of the chicks is pale buff with almost no markings, to match the light coloured clay substrate of the normal breeding habitat.



Collared or Red-winged Pratincole *Glareola pratincola*. (*C.E.T.K.*).

In all pratincoles both sexes incubate almost equally, with a nest-relief occurring every 1–2 hours. In very hot weather (when air temperatures exceed 35°C) the changeovers may be more frequent than this. Incubation is said to take 17–18 days in the Collared Pratincole and 21 days in the Australian Pratincole. The young leave the nest as soon as they are dry, and are led to the shelter of a shady shrub from which they emerge only to be fed by a parent arriving with an insect in its bill. The chicks obtain all their water from their food; like the adults they have a functional salt gland (see EXCRETION, EXTRARENAL) which removes excess sodium chloride and conserves water. The adults drink frequently. In very hot weather at least one species, the Little Pratincole, soaks its belly feathers at the nearest water and flies back to its nest to cool its eggs at each nest-relief which occurs about every half hour (see BELL-SOAKING).

Courtship in the pratincoles consists of elegant displays usually involving the wings and head-down body postures. Injury-feigning distraction displays are well developed in all species when they have eggs or young. G.L.M.

Maclean, G.L. 1976. A field study of the Australian Pratincole. Emu 76: 171–182.
Sterbetz, I. 1974. Die Brachschwalbe. Wittenberg.

PRE-ADAPTATION: see under ADAPTATION.

PRECOCIAL: active immediately after hatching (see YOUNG BIRD).

PRECOCIOUS FLIGHT: see FLIGHT, PRECOCIOUS.

PREDATION: the killing of members of one species by members of another species for food (see also FEEDING HABITS); the term is almost entirely confined to discussion of the effects of activities of predators upon the population of the prey species (see also ECOLOGY). A predation study demands a means of ascertaining the numbers in which a species is present in a given area, and the numbers killed within that locality by a known predator. The population may be measured directly or by a sampling method such as the LINCOLN INDEX; the second parameter demands that some visible and measurable traces of the slaughter remain: feathers, bones, skulls, elytra or wings of insects or even rifled dwelling places, as in the cases of the larvae of beetles of the genus *Pissodes* or of the moth *Ernarmonia conicolana*, whereof the ravaged and uninvaded wintering chambers can be distinguished.

In Holland, remnants at nests and plucking places were used to show that about half the deaths of all House Sparrows *Passer domesticus* in the area were due to the talons of Sparrowhawks *Accipiter nisus*. During a vole plague on the Scottish Border, pellets and stores at nesting sites showed that Short-eared Owls *Asio flammeus* were making inroads on the rodent population of not more than 0.05% per diem, and that the owls were, in fact, not in any way checking the plague. During an outbreak of *Archips fumiferana* in the spruce forests of Ontario, S.C. Kendeigh calculated that, at most, bird predation destroyed 5% of the larvae. There is one classic case of the effects of bird predation being immediately visible: during an outbreak of defoliating insects in Prussia in 1905, the woods of the Baron von Berlepsch, where the nesting of birds had been encouraged, were said to stand out 'among the surrounding woods like a green oasis' (see NEST SITES, MAN-MADE).

The incidence of bird predation may vary greatly from year to year in one locality, or within a single season between places very close together. In an area of rural Suffolk, England, 49 samples of marked *Helix aspersa* were released between the years 1956 and 1978. Of 1,009 snails released, 164 were recovered at the anvils of Song Thrushes *Turdus philomelos*, giving a minimal predation rate of 16%. In the 3 consecutive years 1956 to 1958 predation rates were 44%, 13% and 28%, while in 1963 (after a very severe winter) thrush predation was nil. At 2 sites within 200 m of one another predation rates in 1959 were 44% and 8%.

The effects of predation are not always adverse to the population level of the victim species. It has been demonstrated mathematically that if the principal cause of death in a species be the attacks of a pathogenic organism, and that if a predator tends to take weakly or sick specimens, the final result of the predation will be to increase the population of the prey species.

The effects of predation are not, of course, limited to alterations in the population levels of the prey species. Predation pressure is the effective agent in the evolution of cryptic adaptations of form and behaviour, as has been so clearly demonstrated in the relationship between Song Thrushes and the polymorphic snail *Cepea nemoralis*.

See photo PARENTAL CARE. P.H.T.H.

Gibb, J.A. 1958. Predation by tits and squirrels on the eucosmid moth *Enarmonia conicolana* (Hey.). J. Anim. Ecol. 27: 375–396.
Nicholson, A.J. 1936. The balance of animal populations. J. Anim. Ecol. 2: 131–178.
Rudebeck, G. 1950–1. The choice of prey and modes of hunting of predatory birds with special reference to their selection effect. Oikos 2: 65–88; 3: 200–231.
Sheppard, P.M. 1951. Fluctuations in the selective value of certain phenotypes in the polymorphic land snail *Cepea nemoralis* (L.). Heredity 5: 125–134.
Tinbergen, L. 1946. Der Sperwer al Roofijand van Zangvogels. Ardea 34: 1–213.

PREEN GLAND: see COMFORT BEHAVIOUR.

PREENING: see COMFORT BEHAVIOUR. See photos COMFORT BEHAVIOUR; FLIGHTLESSNESS.

PREFRONTAL: a paired bone of the SKULL.

PREMAXILLA: the main bone, on each side, of the upper jaw (see SKULL).

PREMIGRATORY RESTLESSNESS: marked behavioural changes in nocturnal migrants, particularly small passerines, which develop an additional activity rhythm during the hours of darkness, when they normally roost (see MIGRATION).

PRICKED: see WINGED.

PRICKLETAIL: *Siptornis striaticollis*, a South American furnariid (for family see OVENBIRD (1)).

PRIMARY: or 'primary feather', any one of the flight feathers borne on the manus (carpometacarpus and digital phalanges)—contrasted with the 'secondaries', borne on the forearm (see PLUMAGE; WING). The primaries are best numbered from the carpal joint outwards, but as the opposite practice is followed by some authors it is always desirable to say which is being used (cf. Ashmole *et al* 1961). In most non-passerine species there are—not counting a remicle, if present (see REMICLE)—10 primaries in normal individuals, but in grebes, except the flightless *Rollandia micropterum*, storks and flamingos, there are 11. In passerine birds, there are basically 10 primaries, but the 10th (outermost) is reduced to various extents in the different families, being vestigial in many and absent in the so-called nine-primaried Oscines (see PASSERIFORMES). (Stresemann 1963). See also MOULT; WING FORMULA.

Ashmole, N.P., Dorward, D.F. & Stonehouse, B. 1961. Numbering of primaries. Ibis 103a: 297–298.
Stresemann, E. 1963. Variations in the number of primaries. Condor 65: 449–459.

PRIMARY COVERTS: see TOPOGRAPHY.

PRIMITIVE: retaining characters (known or, often, presumed) of an ancestral form. Alternatively, and in general preferably, the term may be applied to characters that are similar to those of an ancestral form.

PRINIA: generic name commonly used as English substantive name of *Prinia* spp., alternatively 'long-tail' (see WARBLER (1) (Grass warblers)).

PRION: substantive name of *Pachyptila* spp. (see PETREL).

PRIONOPIDAE: a family of PASSERIFORMES suborder Oscines; HELMET-SHRIKE.

PRIORITY, LAW OF: see NOMENCLATURE.

PROAPOSEMATIC: see under APOSEMATIC.

PROCELLARIIDAE: see below.

PROCELLARIIFORMES: an order, alternatively 'Tubinares', comprising 4 families: Diomedeidae (Albatross), Procellariidae (Shearwater), Hydrobatidae (Petrel), Pelecanoididae (Diving Petrel). For general characteristics of the family see PETREL.

PROCRYPTIC: see under CRYPTIC.

PROEPISEMATIC: see under EPISEMATIC.

PROGESTERONE: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

PROKINESIS: the form of upper jaw mobility seen in the majority of birds (including all with holorhinal nostrils), in which rotation takes place about a region of flexible bone (zone elastica craniofacialis) at the junction of upper jaw and neurocranium. See SKULL.

PROLACTIN: see CROP, MILK; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

PROMEROPIDAE: a family of PASSERIFORMES, suborder Oscines; SUGARBIRD.

PROOTIC: a paired bone of the SKULL.

PROPATAGIUM: a membranous fold of skin along the anterior margin of the wing from shoulder to carpal joint (see MUSCULATURE; WING).

PROPRIOCEPTIVE: the senses involved when what is perceived is internal (sometimes termed 'interoceptive').

PROTECTION: see CONSERVATION.

PROTEIN METABOLISM: see ENERGETICS; METABOLISM; NUTRITION.

PROTOPTILE: term applied to the first of two nestling down plumages, in cases where there is such a sequence, the second then being called 'mesoptile' (see PLUMAGE).

PROTOZOA: see ENDOPARASITE.

PROVENTRICULUS: see ALIMENTARY SYSTEM; also, for stomach oil, under PETREL.

PROXIMAL: nearest to the centre of the body or to the point of attachment (e.g. of a limb); opposite of DISTAL.

PROXIMATE: applied to factors, in a system of causation, that immediately precede the effect; contrasted with ULTIMATE.

PRUNELLIDAE: a family of the PASSERIFORMES, suborder Oscines; ACCENTOR.

PSEUDAPOSEMATIC: see under APOSEMATIC.

PSEUDEPISEMATIC: see under EPISEMATIC.

PSEUDOCHELIDONINAE: see SWALLOW.

PSEUDONESTOR: alternative substantive name for the Maui Parrotbill *Pseudonestor xanthophrys*, one of the HAWAIIAN HONEYCREEPERS.

PSEUDOSCHIZORHINAL: see NARIS.

PSEUDOSUCHIA: see under FOSSIL BIRDS.

PSILOPAEDIC: with little or no down when hatched (see YOUNG BIRD).

PSITTACIDAE: see PSITTACIFORMES; PARROT.

PSITTACIFORMES: an order comprising only the family Psittacidae (see PARROT).

PSITTACOSIS: a virus disease, on occasion communicable to man, originally described as affecting parrots (Psittacidae) and allied birds but now known to affect widely different species (e.g. the Fulmar *Fulmarus glacialis*), as the result of infection by an identical or closely related virus, and therefore sometimes called 'ornithosis' (see DISEASE).

PSITTIROSTRINAE: see HAWAIIAN HONEYCREEPER.

PSITTRICHADINAE: see PARROT.

PSOPHIIDAE: see under GRUIFORMES; TRUMPETER.

PTARMIGAN: substantive name of *Lagopus* spp. other than *L. l. scoticus* and sometimes *L. lagopus*; used without qualification in Britain for *L. mutus*, elsewhere known as the Rock Ptarmigan; in the plural (sometimes unchanged), serves as a general term for the genus (see GROUSE).

PTEROCLETES; PTEROCLIDIDAE: see below.

PTEROCLIDIFORMES: an order, comprising the sole family Pteroclididae (see SANDGROUSE). In Wetmore's system treated as a suborder Pterocletes of the order Columbiformes, but other authors consider them more closely related to the Charadriiformes, particularly the COURSERS Glareolidae.

PTERODACTYL: see WINGS, COMPARATIVE ANATOMY OF.

PTERYGOID: a paired bone of the SKULL (see PALATE).

PTERYLA: (plural pterylae): an area of skin bearing contour feathers; a tract of contour feathers arranged in rows (see PTERYLOSIS).

PTERYLOGRAPHY: the study of feather tracts (see PTERYLOSIS).

PTERYLOSIS: the arrangement of contour feathers into orderly groupings (pterylae or feather tracts) on the skin; pterylae may also contain filoplumes, down, and/or powderdown among the contour feathers. The intervening spaces (apteria) are completely devoid of contour feathers, but may contain semiplumes, down, powderdown, or no feathers at all.

Except in a few species that have visible areas of bare skin (e.g. naked-headed vultures), the skin of birds appears to be fully and evenly covered by feathers. In reality, most birds have their feathers growing from relatively limited tracts. Land species usually have narrow pterylae, on about half of the skin area; the remainder of the body has essentially bare skin, overlain by the feathers that fan out from adjoining pterylae and cover the apteria. Waterbirds tend to have wider pterylae, and narrow apteria filled with down. Only in adult ratites, penguins Spheniscidae, and screamers Anhimidae are the contour feathers distributed uniformly over the body, but still arranged in discernible patterns (rows) and with at least a few small apteria in such areas as the ventral midline, the axillary region, or the head and neck; well-developed embryos of these birds show clearly defined pterylae and apteria. Pterylosis, therefore, is a basic feature of all birds—and is as uniquely avian as feathers themselves.

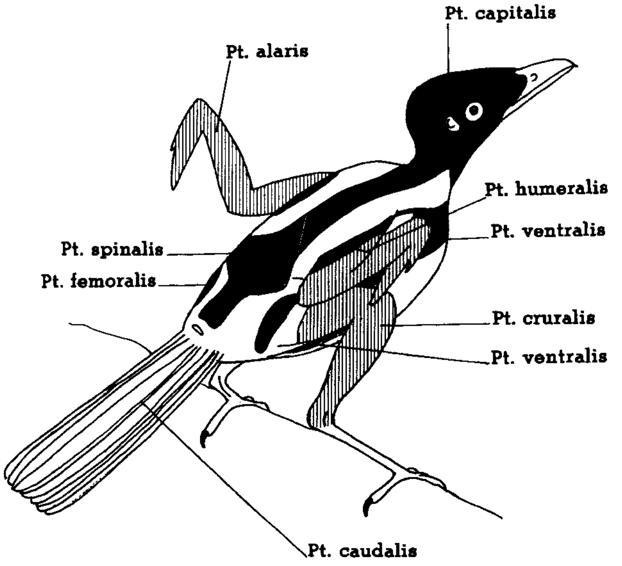


Fig. 1. A generalized passerine, showing the 8 major pterylae (feather tracts). (Redrawn by J. William Hardy from Ames, Heimerdinger & Warter 1968).

Use as a taxonomic character. The study of pterylosis (pterylography) has considerable potential for systematics studies. Although it is still in its infancy from the standpoint of the number of taxa studied, many different tract patterns are found to be indicative of relationships. The system seems to be evolutionarily conservative, and thus is most useful at the higher levels of classification (usually familial or above.) The only class-wide study of pterylography was made by its founder, C.L. Nitzsch (1867), in the early 19th century. His broad sampling of Aves, however, was just a beginning; since then morphologists have concentrated on describing the pterylae of additional species, studying them in finer detail, and applying their findings to systematics studies. The most significant differences of pterylae seem to lie in the number of feathers present and the internal patterns (arrangement of follicles into rows) in the major body tracts (spinal and ventral), and in the wings and tail.

Nomenclature. Most birds are feathered by discrete, easily visible, groupings of contour feathers. Whether each discernible patch is called a 'tract', or whether several related components should be classified together as a 'tract', is arguable. Following Nitzsch's concept of a bird's body being covered by a few large tracts, the 8 major pterylae may be termed:

1. *Pteryla capitalis*: the capital tract, that covers all surfaces of the head, often in many discrete subunits.
2. *Pteryla spinalis*: the spinal or dorsal tract, that extends, continuously or divided, narrow or broad, from the nape of the neck to the base of the tail and covers the dorsal neck, back, and rump. In passerines this tract typically is an uninterrupted band of feathering, narrow on the neck, broadly expanded over the back, and narrowing again on the rump.
3. *Pteryla ventralis*: the usually complex ventral tract, that covers the under surface from the neck to the cloaca. In passerines this takes the form of a substantial band of feathering on each side of the body from the upper breast to the flanks, then branching to a thin band that extends down either side of the abdomen to end at the cloaca. A broad median apterium, the site of the brood patch in many species, is enclosed by the 2 forks of this tract.
4. *Pteryla humeralis*: the humeral, scapular, or scapulohumeral tract, that covers the base of the wings and shoulders; commonly it is a relatively simple rectangular patch of feathers.
5. *Pteryla alaris*: the wing feathers (remiges) and their associated coverts.
6. *Pteryla femoralis*: the femoral tract, that covers the base of the legs, also usually with a simple rectangular grouping.
7. *Pteryla cruralis*: the often sparse crural tract, that covers the legs.
8. *Pteryla caudalis*: the tail (rectrices) and its coverts, and adjacent feathering of the uropygial gland and cloaca.

The tracts associated with appendages (humeral, alar, femoral, crural) are paired; the others are centred on the long axis of the body and have essentially perfect bilateral symmetry. In different species, genera, or families, the tracts may be well developed or merged, or subdivided to various degrees, leading to refinements of their terminologies. The apteria, being present only in the absence of, or between, pterylae, customarily are named by their location on the body or their relationship to adjacent pterylae.

Function. The adaptive significance of having feathers grouped into pterylae, with apteria in between, has never been satisfactorily explained. The answer probably involves many factors: the reduction of total feather weight; the reduced physiological drain by growing fewer feathers; the increased mobility of the limbs by having apteria under moving joints; and better thermoregulation through controlled heat exchange from bare skin. (See also FEATHER; FEATHERS NUMBER OF; PLUMAGE.) M.H.C.

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PTILOGONATIDAE: a family of PASSERIFORMES, suborder Oscines; SILKY-FLYCATCHER.

PTILOGONYS: generic name often used as substantive name of *Ptilogonys* spp. (see SILKY-FLYCATCHER).

PTILONORHYNCHIDAE: a family of the PASSERIFORMES, suborder Oscines (see BOWERBIRD).

PTILOPAEDIC: clad in down when hatched (see YOUNG BIRD).

PTILOPODY: the condition of having feathers on the tarsus and toes.

PTILOSIS: synonym of PLUMAGE.

PUAIOHI: *Phaeornis palmeri* of the Hawaiian Islands (for subfamily see THRUSH).

PUBIS: a paired bone (plural 'pubes') of the pelvic girdle, partly fused with the other elements (see SKELETON, POST-CRANIAL).

PUFF-BACK: substantive name of *Dryoscopus* spp. (see SHRIKE). There are also 'puff-back flycatchers' *Batis* spp. (for family see FLYCATCHER (1)).

PUFFBIRD: substantive name of some species of Bucconidae (Piciformes, suborder Galbulae); in the plural, general term for the family. This consists of 10 genera and 33 species of small or medium-sized arboreal birds (14–29 cm long) confined to continental tropical America.

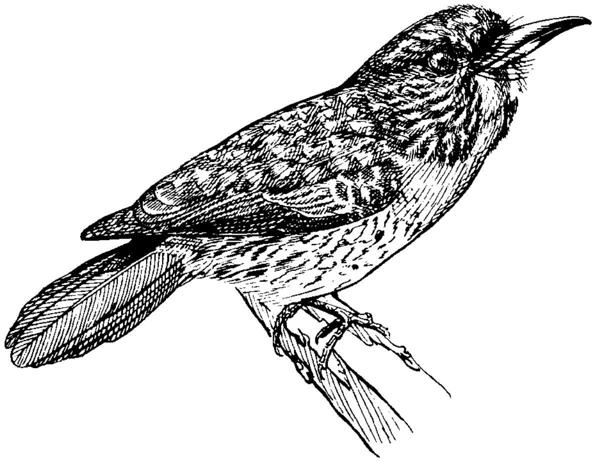
Characteristics, distribution and behaviour. The puffbirds are closely related to the jacamars (Galbulidae). Their large heads, abundant, lax, often dull-coloured plumage, and short tails make them appear stout and 'puffy', whence their name. The bill, of short or medium length, often notably stout, is decurved or hooked at the tip. The feet are zygodactylous, with two toes directed backward. The family is best represented in the Amazon Valley and Colombia, and is largely confined to warm lowlands. Its ancestors appear to have been much more widely distributed, and may have been the dominant small perching birds during the Eocene in North America, where at least 5 genera of the fossil family Primobucconidae have been found in deposits of this age in Wyoming.

One of the largest and most widespread extant members of the Bucconidae is the handsome, 25 cm long White-necked Puffbird *Notharchus macrorhynchus*, which ranges from southern Mexico to north-eastern Argentina. Both sexes are largely black on the dorsal surface. The forehead, nuchal collar, sides of the head, and under parts are white, with a broad black band across the breast. The thick, tapering bill is black.

Slightly smaller is the White-whiskered Puffbird, or Softwing, *Malacoptila panamensis*, which is found from southern Mexico to western Ecuador. The male is largely chestnut-brown and cinnamon, with the posterior under parts pale buff or whitish. Both above and below the female is more olive and greyish. Both sexes are liberally spotted and streaked with tawny and buff on the upper parts and streaked with brown and dusky on the breast and sides. Both sexes wear the long, slender, slightly curved, white malar tufts which are indicated by their name. Their large eyes are dull red.

Both the White-necked Puffbird and the White-whiskered Puffbird are found singly or in pairs, or sometimes in family groups of 3 or 4, but never in flocks. They rest motionless for long periods on a more or less exposed lookout perch at no great height, apparently lethargic but actually keeping a sharp watch for suitable food. By means of a surprisingly sudden dart, they snatch a caterpillar, winged insect, spider, or small lizard from a neighbouring bough, or sometimes they drop down to seize it amid low herbage. Then they carry it back to a perch and devour it at leisure.

A very different type of puffbird is the Swallow-wing *Chelidoptera tenebrosa*, widespread in tropical South America. This is a stout, large-headed bird about 15 cm in length. When folded, its long wings reach almost to the end of its short tail. Both sexes are largely blackish, with a patch of white on the lower back and rump. The abdomen is rufous-chestnut, which pales to white on the under tail coverts. The voyager along the Amazon and its great tributaries often sees these graceful birds perching in pairs on the topmost naked twigs of tall riverside trees, whence they make long, spectacular darts to snatch insects (including many winged ants) from the air, much in the fashion of some of the bigger American flycatchers (Tyrannidae).



White-whiskered Puffbird *Malacoptila panamensis*. (*C.E.T.K.*).

Because of their very plain attire, the 4 species of the genus *Monasa* are called 'nunbirds'. The Black-fronted Nunbird *M. nigrifrons* of the Amazon valley is about 29 cm long. In both sexes, the upper plumage, wings, and tail are dull black and the ventral surface is dark grey. The bill, which tapers from a broad base to a sharp point, is bright orange—whence the name 'pico de lacre' ('sealingwax bill') sometimes applied to birds of this genus. More gregarious than other puffbirds, nunbirds travel in small flocks, and at least one species breeds co-operatively.

The 6 small species of the genus *Nonnula* are known as 'nunlets'. Both sexes of the 14-cm-long Grey-cheeked Nunlet *N. frontalis* are plain brown above and ochraceous or tawny below. This species is found in the lowlands of Colombia and eastern Panama, and little is known of its habits.

Voice. Puffbirds show the same contrasts in voice as in plumage. The loudest utterance of the White-whiskered Puffbird is a high, thin whistle or 'peep'. The Swallow-wing has a weak, appealing whistle. The sociable nunbirds have a surprising range of utterances from soft, musical murmurs to far-carrying shouts. From 3 to 10 White-fronted Nunbirds *Monasa morphoeus*, often perching in a row on a high, horizontal branch or liana, join their almost soprano voices in a chorus that rings through the rain forest for 15–20 min. While calling, puffbirds often twitch their tails from side to side.

Breeding. The breeding habits of puffbirds are poorly known, but two main types of nests have been discovered: cavities which they carve in the hard, black, arboreal nests of termites, and burrows in the ground. Less frequent sites include hollow trees, holes made by woodpeckers, burrows made by small mammals, and oven-shaped nests of clay built by the Pale-legged Hornero *Furnarius leucopus*. Both sexes of the Black-breasted Puffbird *Notharchus pectoralis* take turns at digging with their bills into the side of a large, roughly globular termitary. Their narrow, horizontal tunnel expands at its inner end into a neatly rounded chamber, on the hard floor of which the eggs rest.

Burrows of the White-whiskered Puffbird have been found in the gently or at times steeply sloping, leaf-strewn ground in rain forest. From a round opening, the tunnel descends with a slight inclination for about 50 cm. At the lower end it widens into a chamber, which is lined on the bottom and sides with brown dead leaves. Around the opening of the burrow, which is flush with the ground, the birds arrange twigs, petioles, and the like to form a low collar, through which they enter and leave, and which makes the aperture less conspicuous. This feature is far more strongly developed in the Black Nunbird *Monasa atra* of northern South America, which above the entrance to its descending burrow in level ground raises a large pile of coarse dead sticks; the birds reach their burrow through a rounded tunnel that runs along the surface of the ground beneath the heap of sticks. Probably the chamber at the inner end is lined with dead leaves, like that of the White-fronted Nunbird, which, however, arranges only a low collar around the mouth of its 100–125 cm long burrow. The Swallow-wing, however, places no sticks or other material around the entrance to its burrow, which may be in a bank or in level ground. Like the tunnels of other puffbirds, those of the Swallow-wing are downwardly inclined and straight, but they are longer than those of other species, up to 200 cm in length. The eggs rest on a slight lining of dry grass.

Puffbirds lay 2 or 3, rarely 4, white, glossy eggs that resemble the eggs of woodpeckers. These are incubated by both parents, at least in the Black-breasted and the White-whiskered Puffbird. The latter incubates according to a simple but unusual schedule; the male sits continuously from early afternoon to the following dawn, then the female takes one long session of 5–8 h. The eggs are unattended for a half hour or more between these sessions. Black-breasted Puffbirds take shorter sessions, entering and leaving the nest a number of times in a day. The incubation period is unknown.

Newly hatched puffbirds are blind and perfectly naked, without natal down. The prominent callous pads on their heels are smooth, as in jacamars and motmots. The male White-whiskered Puffbird does all the brooding and his duller mate nearly all the feeding, an arrangement that may have some slight protective value. When only a day or two old, the blind nestlings move up the tunnel to take food from their mother at the burrow's mouth. This consists of large, badly mangled insects, with an occasional spider or small lizard, carried in the parent's bill, one item at a time. Waste is not removed from the burrow. After the father ceases to brood them by night, the nestlings, now with open eyes and becoming feathered, at nightfall somehow raise up the fragmented leaves from the bottom of the chamber to form a screen between themselves and the entrance tunnel. They leave the burrow at the age of 20–21 days, when they are well feathered and have 'whiskers' like their parents. Blind, naked nestlings of the White-fronted Nunbird toddle up to the mouth of their longer burrow to receive food from the 3 or 4 adults—parents plus helpers—who often attend them. After emerging at the age of about 30 days, juvenile nunbirds rise high into the trees. Soon they take their food in a spectacular manner, flying up from a distance to snatch it from an attendant's bill as they shoot past. This provides practice for nunbirds' habitual mode of foraging. A.F.S.

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PUFFIN: substantive name of *Fratercula* spp. (see AUK); used without qualification, in Britain, for the sole Atlantic species, *F. arctica*. See photo FLIGHT.

PUFFINOSIS: name given to a disease of the Manx Shearwater *Puffinus puffinus*, probably allied to psittacosis and sometimes causing heavy mortality among the young birds (see PSITTACOSIS).

PUFFLEG: substantive name of *Eriocnemis* spp. (for family see HUMMINGBIRD).

PUKEKO: native name for the Purple Gallinule *Porphyrio melanotus* of New Zealand, considered by some to be a race of *P. porphyrio* (for family see RAIL).

PULLET: an immature female domestic fowl (which may lay infertile eggs).

PULLUS: a nestling or chick prior to fledging. Most frequently used of ringed birds and of museum specimens, as an age-class term.

PULMONARY ARCH: see VASCULAR SYSTEM.

PUPIL: the opening in the iris of the eye (see VISION).

PURPLETUFT: substantive name of the 3 species of *Iodopleura*, a genus of small, somewhat swallow-like COTINGAS, the males of which have an erectile patch of bright violet feathers on either flank.

PYCNONOTIDAE: a family of the PASSERIFORMES, suborder Oscines; BULBUL.

PYGOPODES: formerly used as the name of an order which embraced the present Gaviiformes and Podicipediformes and originally also the Alcae.

PYGOSTYLE: the fused caudal portion of the vertebral column (see SKELETON, POST-CRANIAL).

PYLORIC ORIFICE: the exit of the gizzard into the duodenum (see ALIMENTARY SYSTEM).

PYRRHULOXIA: *Cardinalis sinuatus* (formerly *Pyrrhuloxia sinuatus*) (see CARDINAL-GROSBEAK).

PYRRHULOXIINAE: see CARDINAL-GROSBEAK.

PYTILIA: substantive name of the 3 species of *Pytilia*, an African genus of waxbills (see ESTRIDID FINCH).

Q

QUADRAT: a square of ground of any size used for sampling (see CENSUS).

QUADRATE: a paired bone of the SKULL.

QUADRATOJUGAL: a paired bone of the SKULL.

QUAIL: substantive name of species in two distinct groups of Phasianidae, the American quails of the subfamily Odontophorinae and the Old World quails *Coturnix* spp. etc. (the so-called 'bush-quails' of India are in fact dwarf partridges)—see PHEASANT. The arrival of migratory parties, still a familiar event in Mediterranean countries, is described in the Book of Numbers, 11, 31: 'And there went forth a wind from the Lord, and brought quails from the sea, and let them fall by the camp, as it were a day's journey on this side, and as it were a day's journey on the other side, round about the camp, and as it were two cubits high upon the face of the earth.'

QUAIL, BUSTARD- or BUTTON-: see BUTTONQUAIL.

QUAIL-DOVE: substantive name of *Geotrygon* spp. (see PIGEON).

QUAIL-FINCH: *Ortygospiza atricollis* (for family see ESTRILDID FINCH).

QUAIL-THRUSH: alternatively 'ground-thrush', substantive name of *Cinclosoma* spp. (see RAIL-BABBLER).

QUELEA: substantive name of the 4 species of *Quelea*, a genus of African weaverbirds one of which, the Red-billed Quelea *Q. quelea*, periodically becomes a serious agricultural pest (see QUELEA CONTROL; WEAVER).

QUELEA CONTROL: action taken against the Red-billed Quelea *Quelea quelea* (see WEAVER) to reduce the damage that this notorious pest causes to small-grain cereal crops in Africa.

The majority of small grain cereals in Africa, such as millet, sorghum and increasingly rice and wheat, are grown in the savanna regions. The savannas include extensive tracts of annual grasslands that produce vast quantities of seed, supporting very high densities of granivorous birds. Of these, Queleas are easily the most numerous, feeding in flocks numbering tens of thousands and whose roosts and breeding colonies frequently contain millions of individuals. Because of the similarity of their natural food of wild grass seeds to the grains of cultivated grasses grown by man, Queleas can cause extensive damage to cereal crops, though usually only when their preferred wild food is not readily available. Crop damage caused by this huge number of birds can be devastating, particularly to subsistence farmers who may regularly lose 30–50% of their crop and occasionally the whole crop. In many African countries either the national government or international agencies accept responsibility for trying to alleviate crop losses by maintaining Quelea control units. The effectiveness of the methods they use has been greatly improved by research into Quelea ecology and patterns of crop damage.

Quelea damage occurs at 3 main periods of the year:

1. From the middle to end of the rains as rain-fed cereals are ripening. Damage is usually caused by hordes of young birds newly fledged from local breeding colonies. Whereas adult Queleas may migrate elsewhere to rear another brood (see ITINERANT BREEDING) the young do not move far in the first few weeks of independence and often use the old colony as a roost so that any fields within foraging distance (10–15 km) will be subject to continuing depredations unless harvested.

2. In the dry season to irrigated crops. This time of year is one of increasing food shortage as the stock of dry grass seeds produced during the previous rains is gradually depleted. Quelea roosts and feeding flocks become even larger as the dry season progresses and food becomes increasingly patchily distributed. Irrigated crops ripening then are especially vulnerable.

3. To crops maturing in areas of early rainfall by Queleas on their 'early-rains' migration (see ITINERANT BREEDING).

Early control methods in all these situations centred around a strategy of permanent reduction of the Quelea population to a level where they would no longer be of economic importance. However, despite increasingly desperate attempts to eradicate the birds, using flame-throwers to destroy their nests, explosives placed in the roosts, and finally by aerial spraying of roosts and colonies with highly toxic organophosphorus contact poisons like parathion (in a single year an estimated 183 million Queleas were destroyed in South Africa alone), no long-term reduction of the population occurred. The long-distance migrations regularly undertaken by Queleas simply meant that other individuals invaded every year from outside the controlled area.

Destruction of birds on this scale does, however, result in a local population reduction, perhaps for long enough for a crop to be harvested without loss. Similarly, the destruction of nests removes the very real threat of damage to nearby fields by newly fledged young (though if the nesting bushes are simply chopped down the adults frequently continue feeding the young even at ground level). Such a strategy of 'immediate crop protection', which ignores birds not actually causing damage, is now carried out by aerial spraying from a helicopter or fixed-wing aircraft of fenthion, a more safely handled organophosphorus poison. The method is very hazardous, involving low-level flying often in the dark, may kill other species and poison livestock, and pollutes the environment (though fenthion degrades quickly). The chemical is applied at rates of 20–25 l/ha^{-1} of 20% active ingredient (4–5 kg/ha^{-1}) and often more. Lower dosages may inhibit the birds' feeding so that they die later of starvation but this is not attempted routinely.

Spraying is expensive, requires highly-skilled personnel and cannot be used over water or near villages and is often not worthwhile on small numbers of birds. In such situations traditional methods of bird scaring are often resorted to, such as banging gongs and throwing sticks. However, the net effect of this is to scare the birds from field to field, spreading the damage more evenly over all the plots (though a farmer unable to employ as many scarers as his neighbour is penalized), rather than reduce the overall damage. The point is that damage often occurs when the Queleas have no readily available alternative food source and birds that would otherwise starve are nearly impossible to keep off the crops. Likewise distasteful chemical repellents applied directly to the crop (e.g. methiocarb) may be effective enough when the neighbouring farmer cannot afford to use them, for the birds simply descend on his crop instead. However, their widespread use forces the starving birds to eat the contaminated grain. For the same reason acoustic scarers may be ineffective and the growing of 'bird-proof' varieties of cereal, e.g., 'goose-necked' sorghum or long-awned wheat, may only reduce crop losses where Queleas have an alternative choice of food, or can move elsewhere. Dissuasive methods may only work where damage is caused by birds already on migration; certainly large-scale killing has no long-term benefit in such a situation for the dead birds are immediately replaced by new arrivals.

The timing of Quelea migrations may be used to advantage in some regions, where the harvest may be gathered while the birds are elsewhere. In northern Botswana early crops (either early-planted or quick-maturing) may be harvested before Queleas returning on their 'breeding migration' produce young in local colonies. In Cameroun and Chad rice is grown in an area not normally inhabited by Queleas though they pass through on migration. There damage can be reduced if the vulnerable period of growth, when the grain is at the 'milky' or 'doughy' stage, can be timed to occur before the birds pass through on their southward 'early rains' migration. Normally, however, this dovetailing of the agricultural calendar with the Queleas' seasonal migration pattern cannot easily be done. In the near future Quelea control will continue to rely on large-scale destruction of birds, though it is to be hoped with a minimum of environmental pollution.

See photo COLONIALITY. P.J.J.

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QUEO: *Rhodinocichla rosea* (for family see TANAGER).

QUETZAL: *Pharomachrus mocinno*, often called Resplendent Quetzal and sometimes Resplendent Trogon (see TROGON); also the substantive name of other *Pharomachrus* spp.

QUILL: the calamus of a feather, or the calamus and rachis together; more loosely used for the feather itself, especially a remex or rectrix (see FEATHER).

QUINTOCUBITALISM: or 'eutaxis' (see WING).

R

RACE: used synonymously with SUBSPECIES. The term 'race' is preferred by some, as indicating the geographical basis of subspecific differentiation and perhaps suggesting a more flexible concept. On the other hand, 'subspecies' is the official term in the International Code of Zoological Nomenclature (1984)—see NOMENCLATURE.

RACHIS: sometimes 'rhachis', the distal portion of the shaft of a feather, bearing the vane (see FEATHER).

RACING PIGEON: see HOMING PIGEON.

RACKET; RACQUET: a terminal broadening of the vane of a feather, characteristic of (especially) certain of the rectrices in some species; the subterminal portion of the rachis of such a feather may be devoid of barbs or carry a relatively narrow vane.

RACKETTAIL: substantive name of *Discosura longicauda* and *Ocreatus underwoodii* (for family see HUMMINGBIRD); and of *Tanysiptera* spp. (see KINGFISHER).

RADAR: makes possible the detection and mapping of simultaneous bird movements over wide areas, and of bird movements that cannot be detected visually—at night, at high altitudes, within and above clouds. Since its start in the late 1950s, radar ornithology has developed into several different branches and has greatly expanded knowledge of the timing and course of bird MIGRATION.

The principles of 'RADAR' (RAdio Detection And Ranging) involve transmission of pulses, usually 0.1–5 μs long, of radio waves, normally 3–25 cm wavelength, and reception of the reflected signal. Radio waves propagate with the speed of light, and the range to the target can be determined from the time taken for the echo to return. The azimuth and, for radars with a vertically narrow beam, elevation of the radar antenna give the direction to the target. The resolving power of the radar is dependent on pulse duration and beam width, while maximum detection range is determined by transmitting power, receiver sensitivity, gain of aerial and echoing area of the target. The inverse square spreading rule applies to both outgoing and reflected radio waves, with the result that maximum range is proportional to the fourth power root of echoing area. As a consequence, radar can detect small targets, like birds, bats and insects, at surprisingly long distances—maximum range of a target 1/10,000 the echoing area of another, is 1/10 the maximum range of the larger target. Echo information from radars with horizontally rotating beams normally are displayed on a plan position indicator (PPI), and with vertically nodding beams on a range height indicator (RHI).

Two principal types of radars have been used as tools in ornithology—fan-beam surveillance and pencil-beam search/tracking radars. The former is most suitable for obtaining a broad view of bird movements over large volumes of air space, while the latter provides height data, and, when operated in a tracking mode, gives detailed and continuous information for individual birds or bird flocks about flight speed, height and direction. Doppler radar has also been used for recording bird flight speeds.

The radar echoing area of a bird depends on the ratio of the size of the bird to the radar wavelength. When this ratio is high, optical scattering from the bird of radio waves occurs, and the echoing area is effectively that of a sphere of water equal to the mass of the bird, or about half the silhouette area of an equally-sized metal sphere. This applies to most bird species when registered by X-band (wavelength 3 cm) radars. For ratios smaller than one, Rayleigh-type scattering of the radar waves occurs, and the echoing area becomes disproportionately small. As a consequence, L-band (wavelength about 25 cm) radars are poor for detection of small birds. For bird sizes similar to the radar wavelength, echoing areas fluctuate, due to interference scattering, and may be as high as four times that of the water sphere or as small as one-quarter of the water sphere. These fluctuations occur when an S-band (wavelength 10 cm) radar is used to detect small and medium-sized birds. The echoing area of a bird is not constant but varies greatly with direction from which the bird is observed. Detailed analysis of modulations in the reflected radar signal, signature analysis, reveals the wing-beat pattern of flying birds, in terms of flapping frequency, duration of flapping and non-flapping periods. Characteristic echo signatures can be used for species identification.

The first extensive radar studies of bird migration, in the years just before and after 1960, were carried out by Ernst Sutter in Switzerland, David Lack in Great Britain, and William H. Drury, J.A. Keith and Ian C.T. Nisbet in the United States. Lack mapped migration across the North Sea at all times of the year, and initiated analysis of many of the behavioural and ecological problems in bird migration pursued in later radar studies. Extensive radar investigations of bird migration have since been carried out in further areas in and around Great Britain, e.g., Shetland, the Hebrides and the English Channel, in many regions of the United States, Canada and the West Indies, in Scandinavia, and in Switzerland, where migration over both the lowlands and the Alps has been studied by surveillance as well as tracking radars. Marine radars

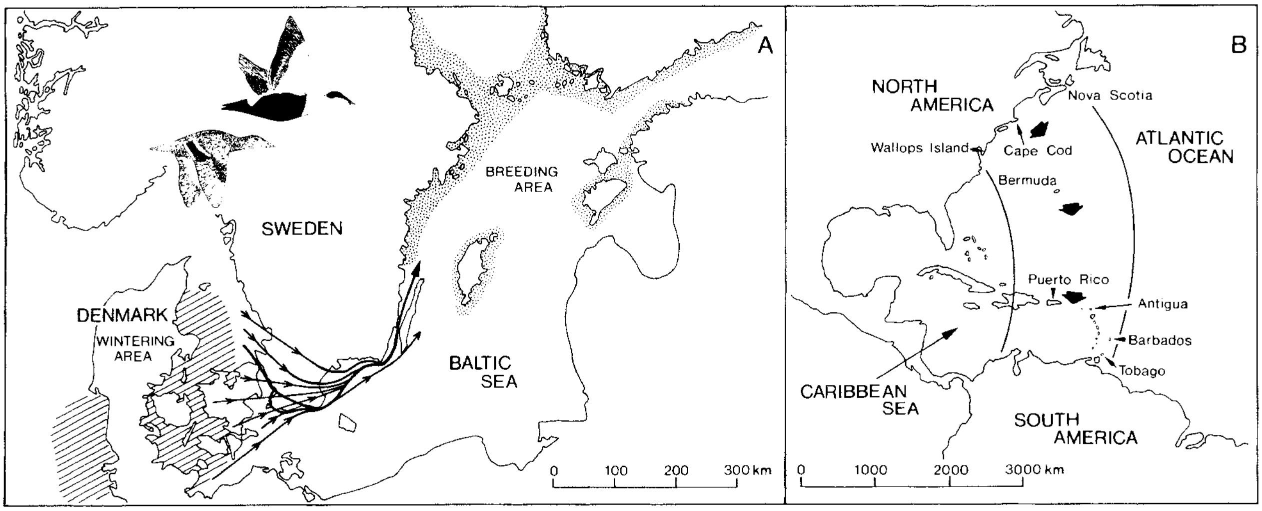

Fig. 1. Examples of migratory routes mapped in radar studies.
(A) Spring migration of the Baltic Sea Eider *Somateria mollissima* population. (From Alerstam, Bauer & Roos 1974. Ibis 116).
(B) Long-distance autumn migration across the western North Atlantic Ocean (Williams & Williams, 1978, in ref. 4, below).

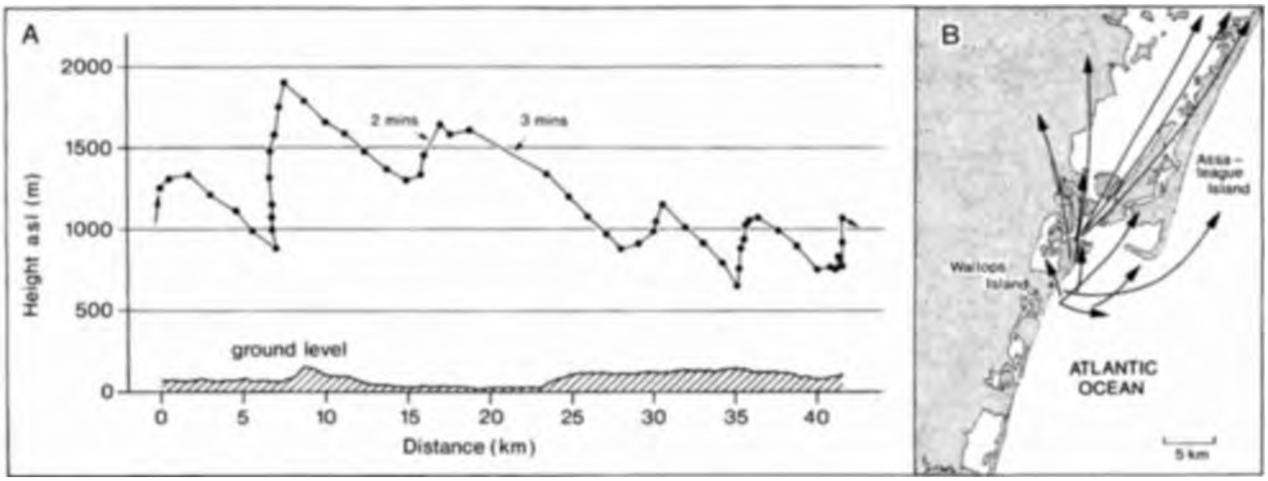

Fig. 2. Examples of radar tracks of migrating bird flocks or individuals. (A) Height versus horizontal flight distance in a flock of Cranes *Grus grus* on soaring migration in south Sweden. (From Pennycuick, Alerstam & Larrson 1979. Ornis Scand. 10).

(B) Flight paths of White-throated Sparrows *Zonotrichia albicollis* released aloft on clear spring nights. (From Emlen & Demong 1978, in ref. 4, below).

have been used for monitoring bird migration across the Mediterranean Sea and the western North Atlantic Ocean. So far radar has only been used in one tropical country (Ghana) and not yet in the Southern Hemisphere.

Main ornithological research issues analysed in radar studies are the following:

(1) **Mapping** of geographical patterns of bird migration or bird roosting movements. High-power surveillance L-band radars permit effective mapping of routes of migrating birds up to 100–200 km from the radar station. Echo-type and speed can be used for distinguishing a few broad categories of birds. More detailed identification is not usually possible, except for a few distinctive behaviour patterns (e.g., Starling *Sturnus vulgaris* roosts, aerial roosting Swifts *Apus apus*) and diurnal bird movements if radar recording is combined with simultaneous field observations from a network of sites, or from an aircraft. Under such premises, radar studies may provide a detailed picture of the migratory pattern of a single species, as exemplified in Figure 1A for the spring migration of the Baltic Sea Eider *Somateria mollissima* population. Widening the perspective from the short-distance Eider migration to routes about 10 times as long, Figure 1B demonstrates a migratory pathway across the western North Atlantic Ocean, documented by observations from radars at places indicated in the figure, and from radars on board ships. This pathway is regularly used by passerines and shorebirds on autumn migration, flying non-stop for 60–100 hours over the open ocean, with median heights at Puerto Rico/Antigua often as high as 4,000–5,000 m, top heights close to 7,000 m.

(2) **Population monitoring.** Combined radar and field observations, providing data on numbers of echoes from migrating bird flocks and mean flock sizes, respectively, can be used for estimating population sizes. By way of example, the Baltic Sea Eider population is estimated in this way at 750,000 birds, an estimate later confirmed by aircraft censuses of breeding birds in the countries concerned.

(3) **Migratory intensity** in relation to weather. Radar has provided extensive evidence that following winds and absence of precipitation are key factors associated with dense broad-front migration. Radar investigations of points (1), (2) and (3) are often embodied in bird hazard to aircraft studies.

(4) **Flight strategies of birds.** Detailed tracking radar data on, e.g., flight speed, altitude and wing-beat pattern are used for testing theories about mechanics and aerodynamics of bird flight, including gliding and soaring theory. Figure 2A shows, as an example, a minute-by-minute radar record of height versus distance along the migratory direction of a flock of Cranes *Grus grus*. The Cranes use soaring migration, gaining height by circling in thermals and gliding between thermals towards their goal. Radar studies demonstrate that migrating birds select altitudes with favourable winds. The majority of migrants regularly fly below 1,000 m, while maximum heights have been noted from 6,000 to above 8,000 m.

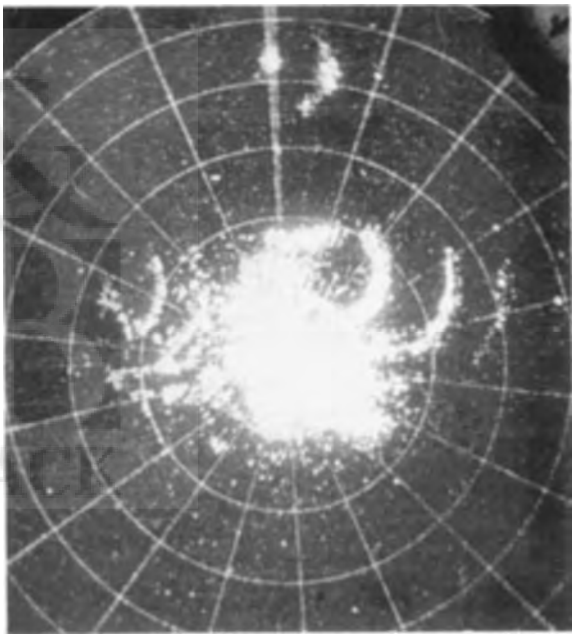

Fig. 3. Waves and arcs of echo which are caused by departures of birds on migration from known roosts have been recorded, both by day and by night. Fig. 3 is a plan-position photograph taken at 06.39 on 5 March 1958, within one minute of sunrise. Arcs of echo are spreading from three separate points on the display at the same time. In each case the sector of arc recorded is that moving eastward from its source, a standard direction of migration at this season. The most clearly-defined arcs are those to the northeast of the radar. Two are strongly evident, separated by a distance of 8 km, and a fainter third 6 km farther ahead. In all, 7 waves of echo spread out from this point, the first leaving the roost at 06.20, 20 minutes before sunrise, and the last at 06.46, 6 minutes after sunrise. (*Photo*: *W. G. Harper*)

(5) **Orientation of migrating birds.** Radar observations show that in some instances migrants compensate completely for wind drift over land and coastal areas, in other instances they are drifted to some degree by wind, and over the open sea they fail to compensate completely for wind drift. Explanations of these results are as yet only speculative. Experiments with small migrants, carried aloft in a box beneath a balloon, released and tracked by radar, demonstrate that the birds are well-oriented in clear nights and when horizon glow from the setting sun is visible, but not so in overcast nights. Radar tracks of individual White-throated Sparrows *Zonotrichia albicollis*, experimentally released

under clear spring nights, with the birds most often flying off in their normal migratory direction, are shown in Figure 2B. T.A.

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RADIALE: one of the proximal carpal bones (see SKELETON, POSTCRANIAL; WING).

RADIATION (1): in the evolutionary sense, divergence of forms of common ancestry, with increasing dissimilarity as a result of differences in adaptation—the antithesis of convergence (see ADAPTATION; CONVERGENCE; see also EVOLUTION; NATURAL SELECTION; SPECIATION).

RADIATION (2): in the distributional sense, geographical spread of a species or group of related species from the area in which the particular species or the ancestral species of the group (e.g. family) was originally evolved as a separate entity (see DISTRIBUTION, GEOGRAPHICAL; RANGE CHANGES; see also SPECIATION).

RADIATION (3): in the physical sense, with only incidental application in ornithology, emission of ionizing rays—to which birds or other organisms may become exposed.

RADIO TELEMETRY: see RADIO TRACKING AND BIOTELEMETRY.

RADIO TRACKING AND BIOTELEMETRY: the remote monitoring of an animal's location by wireless is called radio tracking and remote monitoring of its physiology (e.g. heart rate) is termed biotelemetry. Radio telemetry involves a battery powered transmitter which emits low-powered signals via a transmitting antenna. These signals are received by another, directionally sensitive antenna which connects to a receiver. Ideally, the directional properties of the receiving antenna allow bearings to be taken on the animal's position from two places and the point at which these bearings intersect marks the animal's location. Biotelemetry and radio tracking should not be undertaken lightly; they are expensive, time-consuming and often, frustrating; but can lead to answers to biological questions which are otherwise unobtainable (e.g., location of sleep sites used by elusive nocturnal birds). Described here are practical aspects of selecting, building and using telemetry equipment.

The history of radio telemetry effectively began in the early 1960s. Early circuits were simple, robust, adaptable to both loop and whip antennae and could be packaged to fit most birds and mammals. A similar circuit (Fig. 1) was developed to capitalize on the more useful features of these circuits. Using this transmitter design, the writer has successfully tracked many species of birds. If a resistive device is incorporated in the circuit at R_T (150–400 K) physiological and environmental parameters can be measured by pulse interval modulation. For instance, a 200-K thermistor (at 25°C) may be substituted to measure linear temperatures between 31° and 45°C, accurate to 0.1°C. This temperature transmitter has been used to measure 24 h egg and body temperatures of incubating gulls (*Larus argentatus* and *L. fuscus*). Other environmental parameters such as light level (R_T = photoresistor), presence of moisture, and pressure (if a strain gauge is substituted for R_T) can also be measured.

If the circuit of Fig. 1 is built with subminiature components, it weighs as little as 1.0 g and operates for 7–10 days using a 0.3 g mercury hearing aid battery. This transmitter has been field-tested on birds as small as Great Tits *Parus major* weighing approximately 20 g and effective tracking ranges are up to 100 m in thick forest and 500 m line of sight.

Powerful multistage transmitters are required for long-range tracking (3–10 km). By pulsing the transmitter 2 or 3 times every few seconds, individual animals can be recognized, much as the alphabet and numbers are recognized through Morse Code transmission.

Pulse interval modulation allows activity and mortality sensing. An easily built two-stage activity-sensitive radio-tracking transmitter is shown in Fig. 2. The values given result in a pulse rate of 60 min^{-1} when the mercury switch is shorted. Opening the contacts of the mercury switch results in a doubling of the rate. Changes in pulse rate caused by opening and closing the switch allow movement to be detected. The sensitivity of the device to particular movements usually depends on where the transmitter is fitted to the animal and hence how it moves relative to the plane of animal movement. Unambiguous distinction can be made between inactive resting, sporadic and continuous activity.

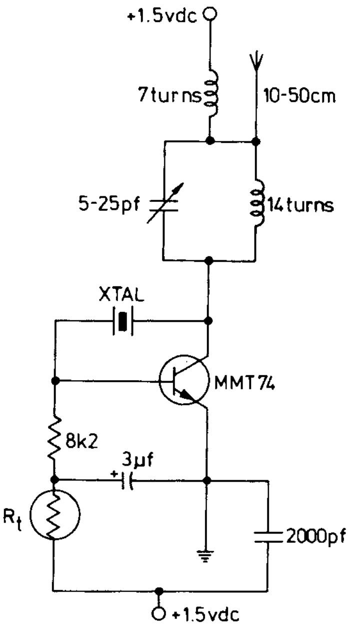

Fig. 1. A miniature, crystal controlled transmitter.

Batteries. A compromise between battery weight, increased transmitter life and range limits the use of many transmitters. Battery failures either through self-deterioration or penetration by moisture have been the commonest causes of transmitter failure (followed by poor-quality transmitter crystals). Recently, advances have been made using solar cells, where benefits were obviously only to studies of diurnal birds unless rechargeable batteries were incorporated into the solar transmitter.

Encapsulation and attachment. Transmitter components should be encapsulated in light-weight, durable and waterproof materials. Components should be coated in beeswax which increases waterproofing and facilitates the removal and replacement of batteries. As a general rule, the total package (transmitter, battery, antenna, harness and encapsulation), should weigh less than 3–5% of the animal's body weight.

Radio harnesses for birds include chest packs attached by a loop antenna that circles the bird's body, backpacks attached by harness loops under the wings with a whip antenna trailing down the bird's back and tail-mounted either on imped or natural feathers (see Amlaner and Macdonald 1980, for review). Swanson and Keuchle (1976) mounted a transmitter above a duck's bill using a nasal pin. Their transmitter included a switch so positioned that it changed the pulse rate depending on whether the duck's head was up, or down as when feeding.

Welfare. It is imperative for both humanitarian and scientific reasons that the transmitter does not hamper or damage the animal in any way. Boag (1972) found that Red Grouse *Lagopus lagopus scoticus* wearing transmitters fed less than those without. Sargeant, Swanson and Doty (1973) suggested that fitting a radio pack to a Blue-winged Teal *Anas discors* contributed to its being preyed on by Mink *Mustela vison* (see Siegfried *et al* 1977). Comparisons can be made between observations on the same animal before and after radio tagging, but some effects may be very subtle, e.g., on long-term reproductive potential. Kenward (1977) found no difference in weight loss or dispersion tendency of Goshawks *Accipiter gentilis* wearing transmitters from those wearing leg rings and noted that the hourly rate of bringing prey to the nest was the same for a Sparrowhawk *Accipiter nisus* before and after being fitted with a transmitter. Amlaner, Sibly and McCleery (1970) conducted a detailed study of the survival and hatching success of Herring Gulls carrying

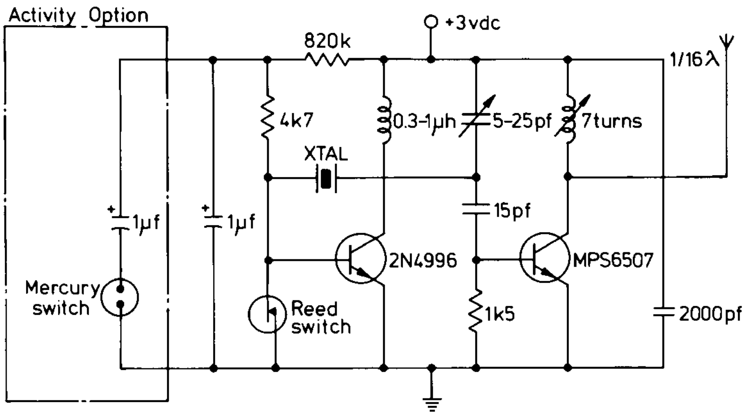

Fig. 2. A two stage transmitter for use in long range radio tracking studies. It includes a mercury switch whose movement enables the animal's activity to be monitored through changes in 'bleep' rate.

dummy transmitters weighing between 10–50 g and found that wearing heavier transmitters decreased survival of the offspring.

Basic radio tracking. Tester (1971) suggested three categories of error all of which could act together to frustrate the tracker's ability accurately to locate his quarry: error inherent in the receiving equipment and its operation, error resulting from the animal moving while bearings are being taken, errors resulting from anomalies such as reflection and refraction of the signal creating false bearings.

Although not commonly stressed in the literature, the radio tracker's subjective 'feel' for the radio landscape of his study area is widely acknowledged as an important facet of accurate radio tracking. The following suggestions help to minimize the risks of both movement and topographical error. Take consecutive bearings with as little delay as possible. For direction finding it is easier to detect the difference between signal and silence (i.e., null) than between signal and louder signal. Know the individual features of the landscape well, and how they affect radio signals. If errors are suspected, take several alternative bearings; at least three are necessary to detect movement errors. When radio tracking from a car it is helpful to continue listening to the signal while travelling between reception sites so that fluctuations in signal strength along the route can be noted in the context of the landscape. Bearings and the derived radio locations should be ranked in terms of their accuracy, depending on both the width of the null points and the variation of successive bearings that do not intersect at the same spot.

Conclusion. Radio tracking is an invaluable addition to the biologist's skills and fieldcraft, and has contributed to diverse studies (reviewed by Macdonald 1978). Just as this technique has revolutionized studies of elusive species during the past decade or so, now people look to the possibility of transmitting and receiving additional information, through biotelemetry, as the next methodological advance (Amlaner 1978; Amlaner and Macdonald 1980). C.J.A.

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RADIUS: a bone of the forelimb (see SKELETON, POST-CRANIAL; WING); also a barbule in the vane of a feather (see FEATHER).

RAFT: a closely-packed flock of birds on water.

RAIL: substantive name of many species of Rallidae (Gruiformes, suborder Grues); in the plural, general term for the family. The rails constitute a homogeneous and cosmopolitan family.

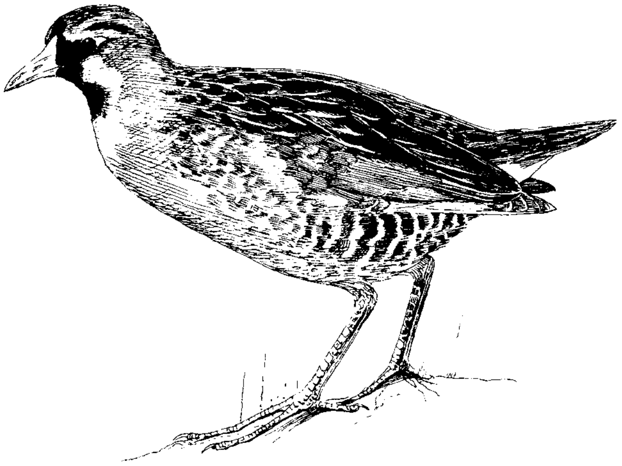
Characteristics. Rails are small- to medium-sized birds (20–65 cm long) with the body laterally compressed, with moderate to long legs and toes, short rounded wings of 10 or 11, rarely 8 or 9 primaries, and a short and soft tail usually of 12 rectrices (rarely as few as 6 feathers, sometimes almost non-existent). The bill varies from long and curved to short and conical. The plumage is of loose texture and the flight feathers are moulted simultaneously. The sexes often differ in size, the males being larger, but rarely differ in coloration. The plumage varies from nearly black or greenish-blue (but even deep purple) to olive-brown, buffish, or chestnut, sometimes with dark streaks and with white bars or spots.

Habitat. Although some forms prefer dry plains, Rails are mainly ground-dwelling water and swamp birds (see SWIMMING AND DIVING), well adapted to living in dense vegetation.

Distribution. Rails are found in all continents north to the Arctic Circle and south to the islands of the sub-Antarctic Convergence. Some 129 species are or were known, contained in 18 genera. Five genera are monotypic. The typical genus includes the Water Rail *Rallus aquaticus*, the only member of this genus with a Palearctic distribution; it is distinguished by a long red bill. It occurs from Great Britain and Iceland, discontinuously, to eastern Asia; migrants often fall victims to striking against lighthouses and powerlines. North American representatives are the larger Clapper Rail *R. longirostris* and King Rail *R. elegans*, inhabiting salt and freshwater marshes. The smaller and warmly brown-tinged Virginia Rail *R. limicola* is found in marshes of the Western Hemisphere. Widely spread over the southern part of Africa is the Cape Rail *R. caerulescens*, very similar to the Water Rail but with uniform dark brown upper parts. In south-eastern Asia, from southern China and India to the Philippines and Sulawesi, the Blue-breasted Banded Rail *R. striatus* is found; in India this species, with its rufous crown and hind neck and its dark brown upperparts barred with white, is one of the most familiar water birds. Rather similar, but smaller and with the back black-streaked olive-brown, is the Slate-breasted or Lewin's Water Rail *R. pectoralis*, occurring in Australia, Flores, and the mountains of New Guinea. In the same area and distributed also over the lesser Sunda Islands, Sulawesi, and the Philippines, is the beautiful Banded Rail *R. philippensis*, characterized by a rufous pectoral band and a grey eye-stripe. More restricted in distribution is the Barred Rail *R. torquatus*, inhabiting the Philippines, Sulawesi, and New Guinea. The head is blackish with a broad white line under the eye. Of the 13 other species included in this genus, there are 3 in South America and 1 in Madagascar, while the other 6 are or were inhabitants of small islands; of these last, one species still survives on Guam, but the others, known from Tahiti, Wake Island, and the Chatham Islands, are extinct.

Of the 2 known species of island woodrails the one formerly occurring on New Caledonia, *Rallus lafresnayanus*, is extremely rare, but a tiny population (18 birds in 1972) of the other, *R. sylvestris*, is still found on Lord Howe Island; these forms are more forest than swamp birds. Another peculiar form is the still common Inaccessible Island Rail *Atlantisia rogersi*, a very small, flightless, dark rail with degenerate hairlike plumage; it lives in the tussock grass which covers the island. Representatives of the banded crakes *Rallina* spp. are distributed from India to northern Australia. All have warm rufous heads and breasts, the abdomen more or less clearly banded black and white; they are shy and retiring birds, living in marshes or along streams in dense undergrowth.

Of the woodrails *Aramides* spp. of Middle and South America, eastern Indonesia and northern Australia 11 subspecies are known. They are large rails with stout bills, generally olive-brown upperparts, grey breast, and black hind parts; when flushed they take wing reluctantly. The wekas *Gallirallus* are restricted to New Zealand. They occur from sea level to well up in the mountains in different habitats. They are brownish in colour and the wings are rudimentary. Not unlike in general appearance, but with a more conical bill and red legs, is the Nkulengu Rail *Himantornis haematopus*, living in the forests of West and Central Africa. Here also occurs the Grey-throated Rail *Canirallus oculeus*, with chestnut neck and breast, olive upper parts and white spots on the almost black



Sora Rail *Porzana carolina*. (*C.J.F.C.*).

wing feathers.

The Corncrake or Landrail *Crex crex* is distributed over most of Europe and well into central Asia; its favourite habitat is grassland. In winter it migrates into Africa and may erupt occasionally into other southern latitudes.

One of the larger genera is *Porzana*, with a world-wide distribution and comprising some 21 species, one extinct (*palmeri*). Of these the Spotted Crake *P. porzana*, the Little Crake *P. parva*, and Baillon's Crake *P. pusilla*, are European birds which also range over part of middle Asia. Baillon's Crake has a peculiar discontinuous distribution, being also known from the southern part of Africa and from Australia and New Zealand. A widespread North American species is the Sora *P. carolina*, in winter reaching northern South America and accidentally occurring in Great Britain. Ranging from the Philippines to Australia, New Zealand, and many Pacific islands is the Spotless Crake *P. tabuensis*, a dark leaden-grey species with dark brown upper parts. Other species occur in South and Central America (3), in eastern and south-eastern Asia (3), in Australia and Oceania (2), and in Madagascar (1). In some species there is a slight difference in plumage between the sexes. In Africa the Black Rail *Porzana flavirostra*, with a yellow bill, is one of the commonest species.

Restricted to America are 11 species of *Laterallus*; of these the only one known in North America is the American Black Rail *L. jamaicensis*, a small bird with white spots and streaks on the upper parts, frequenting grassy inland swamps and brackish coastal marshes. Diminutive in size are the pygmy rails *Coturnicops* spp. (here taken to include *Sarothura*); the 13 species occur from Africa to the Western Hemisphere and Japan. They show a well-marked sexual dimorphism, and are exceedingly secretive in habits. Six species of *Amaurornis* are distributed from India to the Solomon Islands; except for the White-breasted Waterhen *A. phoenicurus*, they are dull grey and olive-brown.

The large Watercock *Gallicrex cinerea* has a reddish frontal shield projecting backwards in a horn; it is found over a wide area from southern to eastern Asia, and migrants reach the Greater Sunda Islands. The Moorhen or Waterhen or in America Common Gallinule *Gallinula chloropus* is distributed over much of the world, being found in all continents except Australia and having colonized many oceanic islands. In Australia, New Guinea, and eastern Indonesia it is replaced by the closely related Dusky Moorhen *G. tenebrosa*. In Africa occurs the small Lesser Moorhen *G. angulata*. The moorhen of Tristan da Cunha, *Gallinula* ('*Porphyriornis*') *nesiotis nesiotis*, was hardly able to fly and is now extinct; but another subspecies, *G. n. comeri*, is still not uncommon on Gough Island. The widespread (American) Purple Gallinule *Porphyrula martinica* has relatives in Africa and South America, *alleni* and *flavirostris*.

A large species is the (Old World) Purple Gallinule or Swamphen *Porphyrio porphyrio*, with a discontinuous distribution from southern Europe through southern Asia to Australia, New Zealand, and islands in the Pacific, and also occurring in Africa and Madagascar. It is azure or greenish-blue below, brown or almost black above, and has a stout and conical bill; all populations are now generally considered as belonging to 3 species, including the flightless Takahe *Porphyrio* ('*Notornis*') *mantelli* from New Zealand, thought to have become extinct but rediscovered in recent years in some inaccessible valleys in the mountains on South Island.

The Coot *Fulica atra* has lobed toes and a white frontal shield and is found over the greater part of Europe, Asia, and Australia, as is the American representative *F. americana* over the greater part of the Americas. Of the remaining 7 species, one is African and all others are Central and South American in distribution. Of these the Giant Coot *F. gigantea* and the Horned Coot *F. cornuta* breed in the high mountain lakes of the Andes; the latter species has the remarkable habit of using stones for building its nest.

Food. The diet is varied—mainly animal, but some species prefer vegetable food. The robbing of eggs and young of other birds is known.

Behaviour. Rails walk with bobbing heads and flirting tails possibly correlated with acuity of vision, as in other walking birds such as pigeons. Some of them are good flyers, covering long distances during migration; but in others, living on oceanic islands, the power of flight has been reduced, and in these cases the introduction of rats or other predators can at once endanger the existence of the species. The majority of the species have secretive habits and many are nocturnal, so that our knowledge of the life of many forms is still scanty.

Voice. At dusk and during the night rails may make themselves conspicuous by their specific loud calls and harsh repetitive squeals or monotonous notes like knocking pebbles together.

Breeding. Nests are well concealed; the clutch-size ranges from 1–14 eggs, sometimes due to more than one female laying *in situ*. The ground colour varies from near white to ochreous or brownish buff, often with reddish, greyish-brown, or black specks, spots, or blotches. The eggs may be incubated by both sexes for from 2½ to nearly 4 weeks. The nestlings are covered with black or dark brown down; they leave the nest soon after hatching and are cared for by both parents, sometimes also by young of an earlier brood. They become independent in up to 8 weeks.

See photo INCUBATION. S.D.R.

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RAIL-BABBLER: substantive name of some species of the subfamily Orthonychinae (Cinclosomatinae) of the family Timaliidae (Passeriformes, suborder Oscines); in the plural, general term for the subfamily. Within it are placed provisionally a small number of insectivorous species which all occur, except one, in the Australian–Papuan region and are all essentially terrestrial in their habits. They have thickset bodies and short bills, generally with small heads and thin necks. Their legs are fairly long, their tails broad and their plumage soft and fluffy. There are many uncertainties about their taxonomic relationship; they do not seem to be closely related to one another, and they may even belong to entirely different groups. These uncertainties are reflected in current Australian field-guides. Thus the logrunners or chowchillas (*Orthonyx*, 2 species), the quail-thrushes (*Cinclosoma*, 5 species) and the whipbirds and wedgebills (*Psophodes*, 4 species, although wedgebills were formerly in *Sphenostoma*) are either placed in a family of their own (Orthonychidae) or else, as here, absorbed into the babblers (Timaliidae); so are the scrub-robins (*Drymodes*, 2 species) which in the field-guides are placed in the thrushes (Turdidae). Also in this grouping are here included the genera *Eupetes* (4 species), *Melampitta* (2 species) and the monotypic genera *Androphobus* and *Ifrita*.

The provisional nature of the classification adopted here for these groups must be stressed. Recent evidence from DNA hybridization indicates that these and other Australian passerine birds of uncertain affinities are all the result of evolutionary radiation of ancestral Australian endemic stocks, and that the resemblance of some of them to babblers, thrushes and other passerine groups is attributable to convergence (Sibley and Ahlquist 1982).

Characteristics. The logrunners have robust legs and feet and a specialized tail in which the shafts of the feathers are modified at the tip into stiff spines, used to help prop up the birds while they feed. The sexes in both species may be distinguished through the colour of the throat, white in the male and chestnut in the female. The Northern Logrunner *Orthonyx spaldingi* (length *c.* 25 cm) is much larger and is more cleanly marked black and white than the Southern Logrunner *O. temminckii* (length *c.* 18 cm) which is mottled brown above. The 2 *Melampitta* species are black all over and also differ in size (18 cm and 29 cm respectively). They are active birds which cock their short tails and nervously flutter their wings as they move through the vegetation. The whipbirds and wedgebills (length 20–27 cm) are noted for their erectile crests. They are, in general, dull drab birds in which the sexes are the same, although the whipbirds do have a prominent white patch or streak on the throat.

The quail-thrushes (length 20–30 cm) are distinctively and boldly marked, particularly the males which are larger than the females. Males have two patterns of black and white on the underparts and these are used to determine the limits of the various species. The colour of the upperparts is variable in species living in dry habitats and matches the colours of the local soils. The white tips of the dark tail feathers are conspicuous in flight, which occurs in short bursts, is low and fast, and terminates with the bird running at the flying speed. The young of all species are spotted.

The sexes are alike in the scrub-robins (length 19–20 cm). One notable distinction between the 2 species is the colour of the mantle; this is grey in the Southern Scrub-robin *Drymodes brunneopygia* and reddish-brown in the Northern Scrub-robin *D. superciliaris*. They habitually cock their tails at about 45°, and raise and lower them, and flick their wings nervously whilst moving through the undergrowth.

In marked contrast to the rest of the group, the *Eupetes* species (length 20–30 cm) are brightly coloured blue, chestnut, or reddish, have rather long necks and their young are unspotted. The Green-backed Babbler *Androphobus viridis* is unique in having a dark olive-green mantle and so is the Blue-capped Babbler *Ifrita kowaldi* in having a shiny blue crown with a black patch in the centre.

Habitats, distribution and movements. The logrunners are mainly confined to rain-forests along the eastern coastal belt of Australia, but the Southern Logrunner surprisingly turns up again in New Guinea. The 4 species of Australian quail-thrushes are found on stony ground, particularly on ridges where there is plenty of cover, and live in open forests. The Ajax Quail-Thrush *Cinclosoma ajax* is found throughout the lowlands of south-east and south New Guinea but only locally in the west.

Whipbirds and wedgebills are confined to Australia. Three are dry country species whilst the Eastern Whipbird *Psophodes olivaceus* is found in dense thicket in or near the wet forests along the east coast. The 2 scrub-robins also occupy quite different habitats, the Northern Scrub-robin in forests in New Guinea and north-eastern Australia and the Southern Scrub-robin in dry country outside the forests in a number of localities in southern Australia.

All the *Eupetes* species are forest birds; 3 are found in New Guinea and the other, the Malaysian Rail-babbler *E. macrocercus*, occurs on the Malaysian Peninsula, Sumatra, Borneo and the Natuna islands. The remaining genera, *Melampitta*, *Ifrita* and *Androphobus* are found in mountain forests in New Guinea, the majority are rare and *Androphobus* is only found on the Snow and Weyland Mountains.

Food. Insects of one kind or other are the main diet of the majority of the rail-babblers but fruit has been found in the stomachs of some *Melampitta* and *Eupetes* species. The logrunners clear leaves from the soil by rapid scratching, throwing debris aside, and use both feet to excavate for food. The distinctive bare patches that remain on the forest floor give the birds' presence away. The Blue-capped Babbler is unique in the group, feeding at all levels of the forest, often reaching the tree-tops as it searches the moss-covered trees in a treecreeper-like manner.

Behaviour. Little or no information is available for the majority in this grouping. The logrunners, whipbirds and wedgebills and quail-thrushes move in pairs or small parties, but are sometimes solitary. The quail-thrushes are particularly shy and secretive, and freeze when disturbed or burst up from cover like quails.

Voice. Quail-thrushes and logrunners announce their presence by their loud, penetrating contact calls, especially at dawn and dusk. The quail-thrushes also have territorial songs and use song posts that may be as high as 6 m. The Northern Logrunner is an accomplished mimic and is said to drown the song of other birds with its oft-repeated *chow chowchilla*. The remarkable whipcrack call of the Eastern Whipbird is an antiphonal duet. The other whipbird and 2 wedgebills also duet but not the Chiming Wedgebill *Psophodes occidentalis*. The song patterns of scrub-robins have similarities to those of the quail-thrushes.

Breeding. Most members of the group nest near or on the ground. Logrunners build globular nests made from sticks, ferns, fibrous leaves, mosses, etc., and these may be placed on a bank, against a stone or log. Whipbirds and wedgebills use similar materials but the nest is cup-shaped and placed 1–2 m high in bracken, shrub or sapling. The quail-thrushes and some, possibly all, *Eupetes* species line a depression in the ground with grass, leaves and rootlets, often sheltered by an overhanging rock. In contrast, the Green-backed Babbler places its nest as high as 4 m above the ground.

Known clutch-sizes are 2–3 (whipbirds and quail-thrushes), 1–2 (*Eupetes* and logrunners) and one egg (Blue-capped Babbler). The eggs vary from white to pinkish buff, blue-white or blue-green and are, in the majority of species, marked with brown, black, reddish or purplish-grey spots or blotches. Pure white eggs are laid by logrunners and the Blue-capped Babbler. Incubation and fledging periods appear to be unknown.

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RAIL, BENSCH'S: misnomer for the Monias *Monias benschi* (see MESITE).

RAIN BATHING: see COMFORT BEHAVIOUR.

RAIN-BIRD: name variously applied in different parts of the world (usually because the birds, when particularly noisy, are supposed to predict rain), e.g., to the Green Woodpecker *Picus viridis* in Britain (see WOODPECKER), the Grey Currawong *Strepera versicolor* in Australia (see CURRAWONG), the White-browed Coucal *Centropus superciliosus* in parts of Africa and other members of the Cuculidae in the New World and Australia (see CUCKOO), and Peale's Petrel *Pterodroma inexpectata* in New Zealand (see PETREL); also 'rain-goose' to the Red-throated Diver *Gavia stellata* in Orkney (see DIVER), and 'rain-quail' (because abundant in some parts in the rainy season) to *Coturnix coromandelica* in India (see under PHEASANT).

RAINBOW-BIRD: Australian name, alternatively Rainbow Bee-eater, of *Merops ornatus* (see BEE-EATER).

RAIN-FOREST: a tropical environment characteristic of areas where there are both high temperatures and heavy rainfall, the latter spread throughout the year; seasonal heavy rains (monsoon) produce a different result. In most parts of the world the true rain-forest has little undergrowth and consists mainly of trees rising unbranched for 30–50 m and then spreading to form part of a 'canopy' that is continuous for great distances, broken only—except temporarily for accidental reasons—by vertical rock faces and the courses of large streams. The avifauna is richer in species than that of any other habitat.

During the second half of the 20th century the rain-forests of the world began to suffer massive destruction with the prospect that only vestiges would be left by the end of the century. Campaigns to 'save the rain-forest' have figured largely in the programmes of the World Wildlife Fund and other conservation organizations.

RAIN-POSTURE: special anti-rain attitude adopted by birds of many families (both passerine and non-passerine), especially those frequenting open habitats and tropical areas subject to seasonal downpours, typically while perching with little or no shelter in heavy rain; the near-vertical stance with head retracted and feathers tightly sleeked against the contours of the body helps to drain the water off and minimize its wetting effects.

RALLIDAE: see under GRUIFORMES; RAIL.

RAMI, MANDIBULAR: (plural of 'ramus'), the two halves of the lower mandible, separated by soft tissue near the base but uniting distally in the gonys (see BILL).

RAMPHASTIDAE: see under PICIFORMES; TOUCAN.

RAMUS: a barb of a feather (see FEATHER); also in the sense shown under RAMI, MANDIBULAR.

RANGE CHANGES: the enlargement or contraction of, in particular, the breeding area of a species. It is clear from the fossil record that fundamental changes in bird distribution patterns have followed major planetary climatic cycles: hence in the warm Tertiary Period (20–40 million years ago) such tropical families as the turacos (Musophagidae), barbets (Capitonidae) and trogons (Trogonidae) extended into what is now Europe; while at the other extreme large parts of Eurasia must have had very impoverished avifaunas at the height of each Pleistocene glaciation. Recent changes have been less profound, but a good many have been detected in the short period (about 300 years) that ornithologists have been documenting bird distributions (see DISTRIBUTION, GEOGRAPHICAL).

Range expansions. The common occurrence of range expansion (geographical radiation) in the past can be inferred from the present extensive distributions of many species, on the presumption that each of these has spread from a more limited area in which speciation took place; the point has all the more validity when a species has begun to fragment into morphologically distinguishable populations (becoming SUBSPECIES), showing that some factor or factors have interrupted the even gene flow that kept the original population homogeneous. Past geographical radiation has led to such anomalies as the Old World larks (Alaudidae) having a Nearctic representative (*Eremophila alpestris*), and the New World family of wrens (Troglodytidae) sharing one species (*T. troglodytes*) with Eurasia. Such theoretical considerations apart, range expansion has visibly occurred, in various species and to a substantial extent, within the period of detailed ornithological recording.

Within the historical period gradual range expansions have been more common than abrupt ones, even after excluding cases where expansion has been a consequence of recovery from an earlier catastrophic decline. Doubtless a variety of reasons have caused this gradual spread. Thus the northward expansions shown by a variety of temperate zone species in northern Europe (including Iceland) in the 1920s and 1930s were clearly correlated with simultaneous climatic amelioration, and few of these gains were lost when this phase ended in the 1940s/1950s (with a subsequent lowering of mean spring temperatures in northern Europe). Since 1950 there has been an increased tendency for boreal species to nest further south in Scandinavia and especially in Scotland. Two (perhaps interacting) mechanisms have been suggested: the evolution of blocking anticyclones over Scandinavia in spring which induce some migrants to settle and breed further south than normal, and the adoption of new breeding areas following the acquisition of wintering grounds closer to the area to be colonized (exemplified in Scotland by Shore Lark *Eremophila alpestris* and Lapland Bunting *Calcarius lapponicus*).

The range expansion of a species over a continental area may (on occasion) be quite rapid, and a particularly remarkable instance has been the spread of the Collared Dove *Streptopelia decaocto* from the Balkans to the Atlantic within 30 years. In this case, and in those of the marked northward spread in western Europe of Cetti's Warbler *Cettia cetti* and Serin *Serinus serinus*, it is tempting to postulate genetic changes that conferred wider habitat and/or climatic tolerances. No range expansion can succeed unless the new territory invaded provides suitable conditions, whether through environmental improvements within the area, or through the colonizing species adapting to new conditions—as when the typically alpine Dotterel *Eudromias morinellus* nests below sea level in Dutch polders, and the cliff-nesting Kittiwake *Rissa tridactyla* breeds on sand dunes (regularly in Denmark).

Another important circumstance leading to range expansion is that of long-distance migrants breeding in their wintering areas; it may be relevant that most such cases involve species having delayed maturity, and therefore not infrequently oversummering within their respective winter ranges. An analysis of elements in the Afrotropical avifauna of European origin showed a continuum from long-established and well-differentiated taxa, through established breeders little or not at all morphologically distinguishable from European populations, to northern migrants nesting only irregularly in Africa. (In contrast, there have been only a few, marginal, cases of Afrotropical species extending into North Africa or southern Europe.) This phenomenon of 'migration suspension' can also be inferred to have occurred in the New World, where a number of migratory species have given rise to resident insular races in the Caribbean, on Galapagos, and elsewhere.

An abrupt range expansion occurs when a species colonizes an island (more rarely a continent) where it does not normally occur even as a migrant; and there are few, even oceanic, islands which do not have their own endemic land-birds as consequences of invasions in the past. Perhaps because the number of ecological niches on islands is restricted, and liable to be filled through speciation by the ancestral colonizer, there are few modern examples of successful abrupt range expansion. One conspicuous exception concerns the invasion-type movements across the Tasman Sea from Australia, whereby New Zealand has gained breeding populations of Silvereye *Zosterops lateralis* (since 1856), Grey Teal *Anas gibberifrons* (probably since the late 19th century), Spur-winged Plover *Vanellus miles* (since about 1932), White-faced Heron *Ardea novaehollandiae* (since 1941), Royal Spoonbill *Platalea regia* (since 1950, still rare), Coot *Fulica atra* (since 1954), Black-fronted Dotterel *Charadrius melanops* and Welcome Swallow *Hirundo neoxena* (both from 1958). Moreover, during the 1970s there were New Zealand breeding records for Masked Wood Swallow *Artamus personatus* (1972 only), and for Australian Dabchick *Tachybaptus novaehollandiae* and Hoary-headed Grebe *Podiceps poliocephalus* (both of which seem to be in process of establishing themselves). There are also now frequent records of the Cattle Egret *Bubulcus ibis* and even reports of breeding. Cases elsewhere include two high-latitude colonizations: of Greenland by the Fieldfare *Turdus pilaris* (in 1937, following an invasion during a period of climatic amelioration), and of South Georgia by the Speckled Teal *Anas flavirostris* (population discovered in 1971).

Certain irregular irruptions, especially those occurring in spring, may lead to breeding in new areas, although not usually to permanent establishment therein (see IRRUPTION). On the other hand, some overseas invasions—possibly accidental in origin—may result in successful colonization simply because suitable conditions were already present in the new area, inaccessible until the ocean barrier was passed. Moreover, artificially introduced species may be able to spread rapidly for the same reason, especially if the newcomer happens to be more versatile than potential native competitors; such secondary range expansion has been seen with the Starling *Sturnus vulgaris* in America, and in a variety of European passerines liberated in man-modified habitats in Australia and New Zealand. Among natural but accidental colonizations, the classic example is the spectacular spread by the Cattle Egret *Bubulcus ibis* in the New World, where since about 1930 it has extended its range explosively both northwards and southwards; it is presumed that the colonizers reached South America from Africa via St Helena and St Paul's Rocks, where there have been recent sightings to show that transatlantic vagrancy by the species is continuing. In the opposite direction it spread via New Guinea to Western Australia, with frequent sightings in the 1950s. The first record from New Zealand was in 1963.

The circumstances of range expansion among sea birds are obviously somewhat different, in that their often wide non-breeding ranges may include many potential new breeding sites. It seems likely that, in these birds, range expansion stems from population pressure within established colonies; in the cases of gulls, at least, new food sources from man's waste products and new safe roosts on artificial reservoirs appear to have been important factors. The expansion potential of seabirds is demonstrated in Britain and Ireland by the remarkable spread of the Fulmar *Fulmarus glacialis* (confined to St Kilda until 1878) and Kittiwake, by the establishment of new Gannet *Sula bassana* colonies, and by the adoption of nest sites on roof tops and other buildings in towns and cities by several species of gull.

Despite a variety of Nearctic vagrants reaching Europe annually, there has been only one known instance of nesting—of Spotted Sandpiper *Actitis macularia* in Scotland—excluding two instances of Black Duck *Anas rubripes* hybridizing with Mallard *A. platyrhynchos* in England.

Range contractions. With the exception of populations endemic to small islands, for which unchecked decline will result in extinction (see EXTINCT BIRDS), declines most often manifest themselves in reduced densities that are not necessarily reflected (at least initially) in contractions of gross distributions. Where declines and contractions of range occur, the ultimate factors may be natural (often climatic) or unnatural (usually through human impact). In either category, species with restricted habitat requirements are the most vulnerable.

Climatic amelioration in North Atlantic regions in the 1920s and 1930s enabled various temperate species to expand northwards (see above), but also resulted in contractions for some arctic species at the southern periphery of their range; instances include Brünnich's Guillemot *Uria* *lomvia* and Little Auk *Alle alle* in Iceland, and Ivory Gull *Pagophila eburnea* in Svalbard. When this warming phase ended by the 1950s, expansion by temperate birds slowed down and some early gains were lost, for example by Starlings in northern Fenno–Scandia. In Britain, modern contractions by certain insectivorous summer migrants, such as Wryneck *Jynx torquilla* and Red-backed Shrike *Lanius collurio*, may have been exacerbated by change towards cooler and wetter spring weather. At the other climatic extreme, increased aridity has resulted in an enlargement of southern deserts to the detriment of some resident species: Ostriches *Struthio camelus* formerly occurred much further north in Africa (also in the Middle East); while reduced Sahelian rainfall has also affected the survival of various European-breeding trans-Saharan migrants crossing or wintering in this zone. Short-term, traumatic weather factors (such as an unusually severe winter) generally have only a temporary effect, but can be serious in island situations: it may have been a hurricane which exterminated the remnant population of Grand Cayman Thrush *Turdus ravidus*. Special cases include contraction following hybridization with a more successful (dominant) congener—Mexican Duck *Anas (platyrhynchos) diazi* and Black Duck with Mallard in North America—or through BROOD-PARASITISM affecting breeding success in a small population—as in Kirtland's Warbler *Dendroica kirtlandii* in Michigan; such instances are generally preceded by declines through (especially) habitat loss, leaving small populations more vulnerable to other pressures.

The more worrying cases of range contraction observed this century are those attributed, directly or indirectly, to man's interventions. By far the more important factor has been habitat loss, especially through wetland drainage and deforestation, and it has affected tropical and temperate species alike. Changed agricultural practices have also made their impact in various ways. Thus more intensive land use has caused contractions affecting bustards (Otididae) and Demoiselle Cranes *Anthropoides virgo* on the steppes of the USSR and Prairie Chickens *Tympanuchus cupido* on the North American equivalent; changed hay-cropping regimes (following mechanization) have reduced the European population of Corncrakes *Crex crex*; pesticide usage has hit raptors especially; while greater care of livestock has been one cause for declines of vultures in southern Europe. When habitat loss is coupled with overhunting, the total impact is serious; classic cases include Eskimo Curlew *Numenius borealis*, Wild Turkey *Meleagris gallopavo*, the extinct Passenger Pigeon *Ectopistes migratorius* and various Asian cranes (Gruidae). Trapping for AVICULTURE is thought to have contributed to reductions among certain Australian parakeets (Psittacidae) and Asian pheasants (Phasianidae). Restricted populations have also proved vulnerable to the impact of alien species, especially mammals, introduced by man, whether through habitat destruction, e.g., by pigs and goats, or through direct predation on ground-nesting birds. Introduced disease has been suggested as a factor in a Hawaiian study, though it has not been established that this applies to larger land masses. R.W.H.

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RANK: see BIOSTATISTICS.

RAPHIDAE: see under COLUMBIFORMES; DODO.

RAPTOR: term used in much the same senses as BIRD-OF-PREY.

RATIO-CLINE: a geographically continuous change in the ratio in which different morphs are present within a species that is dimorphic or polymorphic in appearance or behaviour (see POLYMORPHISM).

RATITAE: see below.

RATITE: having a flat, raft-like sternum, i.e., without a keel; the converse of 'carinate' (see SKELETON, POST-CRANIAL). The structure is especially characteristic of the orders of flightless running birds, mainly of large size, formerly grouped together as the 'Ratitae' and still loosely referred to collectively as the 'ratites' (see EARLY EVOLUTION OF BIRDS). A more or less ratite condition of the sternum is also found in some flightless species in other orders (see FLIGHTLESSNESS).

A family based on the fossil genus *Eleutherornis* is referred to the Struthioniformes, and one based on *Dromornis* to the Casuariiformes (see FOSSIL BIRDS). Further, the Tinamiformes (Tinamidae) of the Neotropical Region, although flying and carinate, are considered to be closely related to the 'ratites' (see TINAMOU).

The living or geologically recent ratites are all comprised in the order STRUTHIONIFORMES.

RAVEN: substantive name of some large species of Corvidae; used without qualification, in Britain, for *Corvus corax* (see CROW (1)).

RAYADITO: substantive name of the 2 species of *Aphrastura*, a South American furnariid genus (for family see OVENBIRD (1)).

RAZORBILL: *Alca torda* (see AUK).

RECENT BIRDS: those forms that either exist at the present day or at least survived into geologically recent times.

RECESSIVE: see GENETICS.

RECOGNITION: a term that was originally applied to human behaviour but requires a new definition when applied to animal behaviour. The prefix 're' implies a learning process which allows the subject to identify an object as something that it has met before, and to distinguish it from other things. It has nevertheless been shown (R.A. Hinde) that a Canary *Serinus canaria* will 'recognize' nest material as something to build a nest with (its behaviour shows that it identifies it and distinguishes it from other objects) when it has never before seen such material. Similarly, we speak of 'sex recognition', 'species recognition', and so on, when responses are confined to certain classes of objects, irrespective of the way in which this specificity of the response developed—whether it is 'innate' or has to be acquired. 'Recognition' is therefore usually taken to mean identification and distinction of an object or a class of objects among the multitude of external things that an animal is likely to encounter. It is not an absolute achievement; the range of objects identified and grouped together may vary from very wide (sex recognition) to very narrow (individual recognition); it never is so wide that it comprises all things; it probably never is so narrow as to be just one unique thing—even the best human observer may find it difficult to distinguish between identical twins. The width of the range is adapted in such a way as to make 'errors' in the natural situation sufficiently rare to avoid frequent miscarriages. 'Recognition', therefore, is an expression referring to what could be called the 'degree of specific releasability' of a response, and it has to be studied by an analysis of the stimulus situation evoking the response. This response is not (as often in human beings) a verbal one, but it has to be a recognizable movement.

In this sense, birds can be said to recognize a very great number of things. The range is usually wide in responses to food; a Song Thrush *Turdus philomelos* recognizes red berries as a class (and perhaps distinguishes between several kinds), and also snails and earthworms. The range is extremely narrow in all cases of individual recognition. There is a graded series between these two extremes.

Recognition is often achieved in a series of steps, viz., when the response is really a chain of separate reactions, each elicited by different stimuli provided by the same object. Thus the first response of a female Red-necked Phalarope *Phalaropus lobatus* to a prospective mate is often misdirected; she may approach birds of several other species (Purple Sandpiper *Calidris maritima*; Lapland Bunting *Calcarius lapponicus*; Ringed Plover *Charadrius hiaticula*). After this initial approach, however, the next response is shown only to Red-necked Phalaropes, while the other birds are ignored. Yet this second response is still the same to males and females and only the third step shows sex recognition, for it is then that females are chased and males are accepted. This seems to be a very general method of achieving specificity of response in spite of the relatively unspecific nature of each stimulus situation (see SIGN STIMULUS).

In many examples recognition is not dependent on previous conditioning; the female Canary's recognition of nest material has already been mentioned; similarly, a young Herring Gull *Larus argentatus* responds 'innately' to the adults' alarm calls. But song-birds refusing to eat wasps or their mimics have had to learn to recognize them as obnoxious, and a goose *Anser* sp. learns to recognize its fellow geese, first as representatives of a species, and later as individuals (see LEARNING; BEHAVIOUR, DEVELOPMENT OF). In symbiotic relationships in the widest sense (including intra-specific as well as inter-specific relationships), recognition has been enhanced by specializations both on the sensory side (responsiveness to special stimuli) and on the effector side (by the development of unambiguous releasers (see RELEASER)); a striking example of the latter is the specificity of song, and of signals that keep a flock of birds together. Highly specific releaser-response relationships seem to have been developed in connection with reproductive isolation between sympatric species (see SPECIATION; also ISOLATING MECHANISM; COLORATION, ADAPTIVE). N.T.

RECOGNITION, INDIVIDUAL: the ability of individual birds to recognize particular familiar individuals of the same species. To show that one bird recognizes another it is necessary to demonstrate that it behaves differently towards the familiar individual than towards other conspecifics, and that the response is not solely due to recognition of a particular site or context.

Individual recognition of offspring by parents has been demonstrated in many species of colonial seabirds, including penguins (Adélie *Pygoscelis adeliae*, Yellow-eyed *Megadyptes antipodes* and King Penguin *Aptenodytes patagonicus*), terns (Arctic *Sterna paradisaea*), gulls (Black-headed *Larus ridibundus* and Herring Gull *L. argentatus*) and Guillemots (*Uria aalge*), where parents bring food to their own chick in the midst of the colony even if it has strayed away from the nest site. Correspondingly, offspring of some seabirds, including guillemots, several species of gulls, and Wandering Albatross *Diomedea exulans* are able to recognize their parents and run towards them but not towards other adults that land nearby. In most species, recognition develops gradually during the early growth of the offspring (although auditory recognition may develop before hatching) resulting in the offspring becoming 'imprinted' on their parents. It is usually before adequate recognition has developed, when the chicks are very young, that in some species, parents may adopt strange chicks. Recognition may continue after the young have fledged in cases where parental care continues.

Species where individual recognition of offspring by parents has not been established during the nestling period include Black-browed *Diomedea melanophrys* and Grey-headed Albatross *D. chrysostoma*, Gannet *Sula bassana*, Kittiwake *Rissa tridactyla*, and Puffin *Fratercula arctica*; and many passerines, for example Robins *Erithacus rubecula* and Pied Flycatchers *Ficedula hypoleuca*. This could be due to the small chance that the young will stray from the nest site or that the parents will mistakenly feed strange chicks.

Mutual recognition between monogamous partners has been documented in a wide variety of species including Gannets, Bewick's Swans *Cygnus columbianus bewickii*, Herring Gulls, Flickers *Colaptes auratus*, Jackdaws *Corvus monedula* and American Goldfinches *Spinus tristis*, where individuals begin greeting displays when their partner appears at a distance. In some species recognition is observed even when partners have been separated for several months.

Recognition by territory owners of neighbouring territory holders occurs in several passerine species where individuals show a stronger aggressive response to strangers than to neighbours. Evidence that birds recognize unrelated flock members is less abundant, although experiments showing an increased aggressive response of domestic hens to strangers introduced into a small stable flock indicate recognition.

How individuals recognize each other is not always clear. In experiments showing recognition of neighbouring territory holders, individual birds were distinguishing differences in the songs (not the positions) of their neighbours from others. In particular, pitch and detailed phrase morphology have been found to be important in individual recognition in some species. However, among songbirds, it is not yet clear whether individual recognition can occur in species with large song repertoires. Auditory cues are also used by offspring guillemots, ducks (Wood Duck *Aix sponsa*), and domestic chicks even before hatching, and by partners of pairs in American Goldfinches. Recognition by visual cues has seldom been demonstrated directly. But Guillemots *Uria aalge*, whose eggs show great variation, and Ostriches *Struthio camelus* are able to recognize their own eggs (see AUK; OSTRICH).

Observations of birds recognizing their parents, mates and other flock members at a distance, in the absence of audible vocalizations, have been described for Gannets, Pintails *Anas acuta*, Herring Gulls, and Marsh Tits *Parus palustris*. Whether in these cases the birds are distinguishing particular physical characteristics or idiosyncratic behaviour is not clear. At closer range, experimental evidence suggests that the precise cues involved are mainly on the head: artificial changes in appearance of the head, neck and comb in chickens were most successful in preventing recognition by flockmates. In wild Bewick's Swans, individuals sometimes peck their mates when the latter are feeding with their heads below the water, but when the mate brings its head up a greeting immediately occurs, often with no audible vocalization. Despite the scarcity of evidence, the use of visual cues in individual recognition seems likely to be widespread in view of the exceptional visual acuity of birds and the extent to which they communicate visually. D.K.S.

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RECORDING: ultra-quiet song (see BEHAVIOUR, DEVELOPMENT OF (*Subsong*)); also, of course, the human activities of mechanically registering and reproducing bird or other sounds, and, more generally, the keeping of regular notes and observations.

RECOVERY: see MARKING.

RECTRIX (RECTRICES): a main tail feather (see TAIL).

RECTUM: the large intestine (see ALIMENTARY SYSTEM).

RECURVED-BILL: *Megaxenops parnaguae*; sometimes applied also to *Xenops* spp. (see OVENBIRD (1)).

RECURVIROSTRIDAE: see under CHARADRIIFORMES. The family comprises the avocets and stilts (see under AVOCET).

REDBILL: name in South Africa for *Anas erythrorhyncha*, otherwise Red-billed Pintail (see DUCK).

REDBREAST: alternative name of the Robin *Erithacus rubecula* (see THRUSH).

REDHEAD: *Aythya americana* (see DUCK).

REDIRECTION: the direction of a behaviour response at other than the normal object. As a rule, animal behaviour is directed at certain parts of, or objects in, the environment—food-pecking is directed at food, attack is directed at a rival, and so on—and this is made possible by steering (as distinct from merely releasing or inhibiting) mechanisms; but in certain circumstances a response is directed at an object other than that normally drawing the response. Such responses to abnormal objects can be classed in two categories. On the one hand, when an animal is very hungry it may peck at inedible or inadequate objects not normally aimed at; a sexually deprived animal may copulate with substitute partners sometimes very unlike the normal partner; and a broody bird may sit on objects very dissimilar to eggs. These responses have in common that they are directed at a substitute object in the absence of the adequate object, and that the adequate object is preferred as soon as it is present. On the other hand, when a man scolds his subordinate after he has himself been rebuked by his superior, or kicks a chair in anger although the fellow human who aroused his anger is there, we speak of a redirected attack; and such redirected attacks are common in birds. They occur when an individual is provoked to attack another individual, but cannot do so because it is either afraid of its attacker or is inhibited in some other way, for instance by personal 'love' for its sex partner. A redirected attack may be aimed at a third bird happening to be near, or it may be as extreme as table-banging by an angry human; thus a male Herring Gull *Larus argentatus* regularly pecks violently into the ground when facing a rival near the territory's boundary. It seems likely that such redirected attacks have also contributed to the 'raw material' from which signal movements have evolved (see DISPLACEMENT ACTIVITY; RELEASER). They are often followed by displacement activities, and can probably determine which particular displacement activity will be shown by providing stimuli that facilitate one particular movement. N.T.

REDPOLL: substantive name of 2 *Carduelis* spp.; used without qualification, in Britain, for *C. flammea* (see FINCH). See photo NEST BUILDING.

REDSHANK: substantive name of *Tringa totanus*, for which it is used in Britain without qualification, and one congener (see SANDPIPER). See photo COPULATION.

REDSTART (1): substantive name of *Phoenicurus* spp.; used without qualification, in Britain, for *P. phoenicurus* (see THRUSH).

REDSTART (2): substantive name, in North America, of species of *Setophaga* and *Myioborus* (see WARBLER (2)).

REDTHROAT: *Sericornis brunneus* (see WARBLER, AUSTRALIAN).

RED TIDE: the bloom of a single-celled organism in the sea, its large numbers often imparting a rusty-red coloration. In temperate waters the organism is usually *Gonyaulax tamarensis*, which, when at high densities, produces an extremely powerful nerve poison to which birds and mammals are very sensitive. Frequent red tides are recorded from the west coast of North America. The first major outbreak in Europe this century occurred in 1968, killing 80% of the breeding shags *Phalacrocorax aristotelis* on the Farne Islands (NE England) in a few days, and many other species being affected. Since then, blooms have been recorded from Norway to Spain. Red tides in tropical waters are caused by a different organism which does not produce a toxin but which de-oxygenates the water, killing large numbers of fish, but few seabirds. J.C.C.

REDUCTION-DIVISION: meiosis (see CELL; GENETICS).

REDWING: *Turdus iliacus* (see THRUSH); in North America sometimes applied to the Redwinged Blackbird *Agelaius phoeniceus* (see ORIOLE (2)); in Africa applied to *Francolinus levaillantii* (see PHEASANT).

REED-FINCH: substantive name of *Donacospiza albifrons*, a South American finch (for family see BUNTING).

REED-HAUNTER: substantive name of *Limnornis curvirostris* and *Limnoctites rectirostris* (for family see OVENBIRD (1)).

REEDHEN: substantive name sometimes applied to gallinules of the genus *Porphyrula* (for family see RAIL).

REEDLING: alternative name for the Bearded Tit *Panurus biarmicus* (see under PARROTBILL).

REELING: see CHURRING.

REEVE: see RUFF.

REFLEX: 'an innate relatively simple and stereotyped response involving the central nervous system and occurring very shortly after the stimulus which evokes it; it specifically involves a part only of the organism, though the whole may be affected, and is usually a response to localized sensory stimuli' (Thorpe 1951)—see FIXED ACTION PATTERN; also LEARNING.

REFRACTORY PERIOD: see penultimate paragraph of ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

REFUGE: see CONSERVATION.

REGENT-BIRD: Regent Bowerbird *Sericulus chrysocephalus* (see BOWERBIRD).

REGION, ZOOGEOGRAPHICAL: or faunal region, see DISTRIBUTION, GEOGRAPHICAL.

REGULIDAE: a family recognized by some authors, but here merged in the subfamily Sylviinae of the Muscicapidae (see WARBLER (1)).

REGURGITATION: ejection of partially digested food from the gizzard, as food for young; ejection of PELLETS; ejection of stomach oil by young birds, e.g., Fulmar *Fulmarus glacialis*, under threat from an intruder (see ODOUR). See photo PARENTAL CARE.

REINFORCEMENT: see LEARNING.

REJUNGENT SPECIES: see RING-SPECIES.

RELEASER: term originally given a precise and unambiguous definition by Lorenz in 1935 but since applied in two very different senses. In the original sense, a releaser is not a stimulus, but a type of effector device (in the widest sense—either a structure, or a movement, or a scent, or a call) with a very specific function, namely that of providing stimuli which release (or inhibit) a response or a set of responses in another animal of the same species. The concept became necessary when it was pointed out that there are structures, movements, sounds, and so on which can be shown to provide such stimuli, for which no other function can be found, and which are obviously well suited to the broadcasting of stimuli. Thus, the red colour of the breast feathers of a Robin *Erithacus rubecula*, the brightly coloured wing specula of ducks (Anatidae), the red patch on the lower mandible of a Herring Gull *Larus argentatus*, the nest-showing ceremonies of various male birds (Wren *Troglodytes troglodytes*; Kestrel *Falco tinnunculus*; Black-headed Gull *Larus ridibundus*; Redstart *Phoenicurus phoenicurus*; Pied Flycatcher *Ficedula hypoleuca*), the head-tossing movements of female gulls (Larinae), the song of male song-birds, alarm calls, and many more, all provide stimuli releasing or directing more or less specific responses in fellow members of the species, and are therefore called releasers. The 'rodent-run' and other distraction displays of waders (Charadrii) and other birds lure predators away from the brood (see DISTRACTION BEHAVIOUR); these activities, like the hissing of the Great Tit *Parus major* and Wryneck *Jynx torquilla*, aposematic coloration, and the luring flight of honeyguides (Indicatoridae), subserve interspecific communication; the term releaser can of course be applied to them as well.

While the word is not important, provided that it is used consistently, the distinction between the two concepts (releaser and stimulus) is essential. The difference between the concept of releaser and that of sign stimulus, to which the word 'releaser' is often applied, is to be found in the adaptedness of the releaser as a signalling device (see SIGN STIMULUS). A pike *Esox lucius*, snapping at a piece of shiny metal dragged through the water, is responding to a sign stimulus normally provided by its prey. Yet the silvery shine of, for example, a roach has certainly not developed as a means to enable the roach to be captured by a pike; if anything, the pike has helped to exert selection pressure against such conspicuousness. The red spot on the bill of the Herring Gull, on the contrary, must have been favoured by selection pressure, since it helps in eliciting the chick's begging, which in turn stimulates its parent to feed it; and song, by attracting females, facilitates pair formation and as such is favoured by selection. The argument is particularly convincing in those cases where releasers have developed in spite of the dangers to which they expose their bearers in other contexts, especially when they make them more vulnerable to attack by predators.

Thus the term 'releaser' is intended to characterize a category of effector by its exclusive or main function, just as the term 'wing' is used to name any organ which provides lift and propulsion in flight, even although a wing may also be used as, for instance, a weapon in fighting.

Many releasers, such as alarm calls, have been shown literally to release a response. Others, such as the head-flagging in gulls and other 'appeasement gestures', stop a response (see DISPLAY); others again, such as the song of male song-birds, release and also direct the movements of other birds (in this case, repulsion of males and attraction of females). For this reason, the term 'signalling device' is perhaps preferable. The latter example also shows that one feature may have more than one function. The second function need not be that of signalling, and its demands may even conflict with those of the releaser function; the most obvious examples of such conflicting demands are procryptic birds that have at the same time conspicuously coloured structures; such species have reached a compromize by concealing the bright colours so long as they are not actually needed.

Comparative studies sometimes enable one to make a guess at the origin of releasers, and it is probable that they are secondary specializations of organs and movements primarily adapted to other functions, selection pressure having favoured simplicity, conspicuousness, and unambiguity; and this seems in accord with the known properties of the sensory functions through which they exert their effect (see SIGN STIMULUS). Evolution being a slow and gradual process involving a very large number of extremely small steps, it is evident that the distinction between organs which are obvious, highly specialized releasers (such as the wings of a male Argus Pheasant *Argusianus argus*) and those that are not yet, or no longer, or not exclusively releasers cannot be sharp. This is of course true of every category of organ.

The function of an alleged releaser is often suggested by observations but can be experimentally tested in experiments with dummies. N.T.

Lorenz, K. 1935. Der Kumpan in der Umwelt des Vogels. J. Orn. 83: 137–213, 289–413.

RELICT (or RELIC): term applied to isolated (sometimes discontinuous) populations that appear to represent a former much wider distribution.

REMEX: a main flight feather; the remiges are classed as primary and secondary (see PLUMAGE; PRIMARY; WING).

REMICLE: term properly restricted to a small feather found on the wing in some species, attached to the second phalanx of digit II. Most authors have considered it to be a vestigial primary remex, but Stresemann believes it to have been a covert to the terminal claw possessed by ancestral forms (see under PRIMARY).

REMIGES: plural of REMEX.

REMIZIDAE: family of PASSERIFORMES suborder Oscines; PENDULINE TIT.

RENAL FUNCTION: see EXCRETION, EXTRARENAL.

REPELLENTS, CHEMICAL: man has probably tried to protect his crops with chemical repellents of some kind ever since he first tilled the soil. Concoctions of plants which, at least to humans, have pungent odours or an unpleasant taste feature in countless 'cottage' remedies for the prevention of bird damage and this folklore extends to the use of foul-smelling animal oils, faeces and urine, all of which may be used as ingredients in traditional repellent formulations. It is understandable that people should use such materials in an attempt to repel animals; we find them unpleasant, therefore other species having similar sensory systems will also find them unpleasant. This reasoning finds support in the fact that some animal species themselves employ chemical repellents in defence; skunks (*Mephitis*) are legendary in this respect but there are many less well-known examples including some birds. For example, Fulmars *Fulmarus glacialis* defend the nest site by squirting intruders with a foul-smelling liquid regurgitated from their crops and Eiders *Somateria mollissima* cover their eggs with faeces before leaving the nest unattended. However, these mechanisms have probably evolved for use against predatory mammals, rather than birds, and confirmation of the practical value of chemical repellents against birds is hard to find.

Since any repellent effect is first dependent on the bird perceiving the stimulus, it is pertinent to consider what we know about the chemical senses of birds. By far the most important of these are the senses of SMELL (olfaction) and TASTE (gustation) and, although normally regarded as separate functions, they are so closely related as to be, at times, indistinguishable. Consider a bird approaching a potential food source. The olfactory system will be the first of the chemical senses to receive stimulation; the question is 'Do birds have a functional sense of smell?' This has been a subject of controversy ever since Darwin and Audubon addressed themselves to the problem and is not fully resolved yet. On present evidence it seems fair to conclude that the olfactory mechanism is functional in most birds but only a few species exhibit odour-related behaviour in connection with food. If most birds disregard olfactory cues then in practice it will prove impossible to manipulate their behaviour via this channel of communication. Clearly this would not be true for those few species that do seek food by smell, e.g., the Kiwis *Apteryx* and honeyguides *Indicator*; their food-finding would be vulnerable to disruption by the introduction of false or masking odours. But these species are not pests and, unless future research reveals otherwise, we should regard the birds that eat our crops as unresponsive to odours. Hence the development of olfactory repellents seems unlikely.

If odours will not repel birds then perhaps flavours can be used to better effect. Nobody seriously doubts that birds can taste but nevertheless the role of gustation in food selection remains obscure. As in mammals, the sensory receptors for the perception of flavours are the 'taste buds', consisting of clusters of cells lying in cavities in the epithelium of the tongue, but whereas mammals typically have many thousands of taste buds few birds have more than a hundred. It is tempting to conclude that birds are correspondingly less sensitive to flavours than mammals but this is not necessarily so; for instance it has been shown (Duncan 1963) that pigeons can discriminate between substances that are tasteless to man. It is logical to assume that an animal possessing a functional sense of taste will utilize that sense in the selection of food, yet there is little evidence that birds do so. Englemann (1940) concluded that hens select grains on the basis of shape, and to a lesser extent colour; taste played little or no part. Much of the experimental work done since then, often in connection with the search for chemical repellents, points to the conclusion that taste *per se* is not very important to birds and suggests that a substance is unlikely to qualify as a bird repellent simply because it has an unpleasant flavour. However, taste stimuli rarely occur in isolation; certainly the ingestion of food represents a complex sensory experience, involving visceral, tactile, olfactory and thermal information in addition to that concerned with flavour. In consequence, behaviour that gives every appearance of being taste-orientated may be controlled by other factors.

Some authorities refer to a specific 'chemical sense' in birds and regard the many unspecialized nerve endings as receptor organs. If such a sense exists, it remains ill-defined and there is little to indicate how it functions. It is certainly true that in some cases chemical stimulation may result in pain, or other disturbing sensations, and animals quickly learn to avoid situations that give rise to such unpleasant experiences. This is known as 'conditioned aversion' and typically follows sub-lethal poisoning by a toxic food. The phenomenon often occurs in connection with poison baiting for rodent control when the condition is known as 'bait shyness'. In those circumstances it is a highly undesirable response, because it reduces the consumption of bait and hence the kill, but it is exactly the response we endeavour to achieve with repellents. Some chemicals, e.g., lithium chloride and certain carbamate compounds, seem to possess properties conducive to the establishment of aversive associations of this type and which can result in a dramatic avoidance of further contact with the chemical. One such compound, methiocarb, is now widely used in the USA and elsewhere as a bird repellent (Rogers 1980). Despite being highly poisonous few, if any, casualties occur because birds are repelled before they have time to ingest a lethal dose. Nevertheless, there are obvious risks associated with the use of such chemicals and it is open to question whether very toxic substances qualify to be called 'repellents'.

Chemical defence mechanisms evolved by insects against bird predators usually involve cardiac glycosides which have a specific action on the vertebrate heart. They also have side-effects, one of which is to stimulate vomiting, and since the emetic dose is about half the lethal dose this functions as a safety factor and normally prevents retention of a lethal dose. Brower (1969) has pointed out that in such a mechanism there are 3 levels at which repellency can occur; basic gastronomic rejection, brought about by the effect of the poison, and subsequently rejection by recognition of flavour or appearance as a conditioned response. It has been suggested that such aversive conditioning could be applied to predator–prey problems involving large raptors (Brett *et al* 1976). These experiments are a stimulating advance in repellent research although confirmation of success in practical application is still awaited.

Another mechanism of repellency is that of behaviour-modifying chemicals. There is no evidence for the existence in birds of any mechanism analogous to that of pheromones in insects, but chemicals have been used to modify behaviour in a different way. Birds display great panic following the ingestion of the compound, 2,4-animopyridine, possibly because they suffer pain and partial paralysis. Affected birds tend to utter distress calls and fly in spirals; conspecifics hearing the calls, and observing the strange behaviour, usually flee. Thus, for gregarious species, large flocks may be scared away by the aberrant behaviour induced in a few individuals. A bait containing 1% or 2% of treated particles is used and in this way sufficient can be laid to prove attractive whilst ensuring that relatively few birds are affected. It is sometimes argued that such a method is a useful conservation tool, since it avoids mass destruction, but many people consider the technique to be inhumane and its use is prohibited in many countries, including Britain.

Yet another approach to repellency is to consider feeding mechanisms and exploration of this is just beginning. It is obvious that any particular species of animal accepts as food only a narrow spectrum of potentially nutritious items. In other words, they are selective and this implies the existence of a mechanism of discrimination which results in acceptance or rejection. If these mechanisms can be elucidated they may mark a significant step toward the discovery of really effective repellents.

E.N.W.

Brett, L.P., Hawkins, W.G. & Carein, J. 1976. Prey–Lithium aversions III: Buteo hawks. Behavioral Biology 17: 87–98.

Brower, L.P. 1969. Ecological chemistry. Scientific American 220(2): 22–29.

Duncan, C.J. 1963. The response of the feral pigeon when offered the active ingredients of commercial repellents in solution. Annals of Applied Biology 51: 127–134.

Englemann, C. 1940. Versuche über die Beliebtheit einiger Getreidearten beim Huhn. Zeitschrift für vergleichende Physiologie 27: 525–544.

Rogers, J.G. 1980. Conditioned taste aversion: its role in bird damage control. *In* Wright, E.N., Inglis, I.R. & Feare, C.J. (eds.). Bird Problems in Agriculture. British Crop Protection Council Symposia Series Monograph 23.

REPRODUCTIVE ISOLATION: a situation in which intrinsic factors wholly or largely prevent interbreeding between closely related species, or populations of a species (see ECOLOGICAL ISOLATION; ISOLATING MECHANISM; SPECIATION). It is to be distinguished from geographical or ecological isolation, where extrinsic circumstances prevent contact between populations that might otherwise be fully capable of interbreeding.

REPRODUCTIVE RATE: see CLUTCH-SIZE (Reproductive rates and other reproductive tactics); ECOLOGY.

REPRODUCTIVE SYSTEM: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

REPTILIAN ANCESTRY: see EARLY EVOLUTION OF BIRDS.

RESERVE, NATURE: see CONSERVATION.

RESIDENT: remaining throughout the year in the area under reference, the term being applied to a species, subspecies, population, or individual bird as the context requires; in another usage the term means breeding in the area, a distinction being then drawn between 'permanent resident' and 'summer resident' (='summer visitor')—see MIGRATION.

RESONANCE: setting up vibrations that increase the volume of a sound (see SYRINX; also MECHANICAL SOUNDS).

RESPIRATORY SYSTEM: in general, this system in birds is differentiated into the rigid lungs for gas exchange and into the air sacs, which act as bellows for their ventilation. This differentiation is based on the subdivision of the avian body cavity by septa (Duncker 1979). The unique avian respiratory system is characterized by the highest gas exchange capacity in vertebrates, and in its development it is necessarily based on the incubation in an egg.

Each of the two symmetrical lungs fills one of the cavities which are situated in the dorsal portion of the rigid thoracic cage. Each pleural cavity (Fig. 1) is lined medially by the vertebral column and its ventral processes, dorso-laterally by the flat transverse vertebral processes and by the ribs and their musculature. Dorsally, the ribs arch through the pleural cavity, making deep incisions into the lung. Ventrally, the pleural cavity is lined by the horizontal septum, which originates from the ventral margin of the vertebral column or its ventral processes, and is inserted, descending slightly ventrally, on to the ribs. At this lateral margin the horizontal septum contains the costoseptal muscles, which dilate during inspiration and contract during expiration (Fedde *et al* 1964). The actions of these muscles compensate for the slight volume changes of the pleural cavity, which are minimal due to their dorsal position in the rigid rib cage. Thus, the avian lung maintains a constant volume during the respiratory cycle, in contrast to reptilian and mammalian lungs which are inflated and deflated by the respiratory movements.

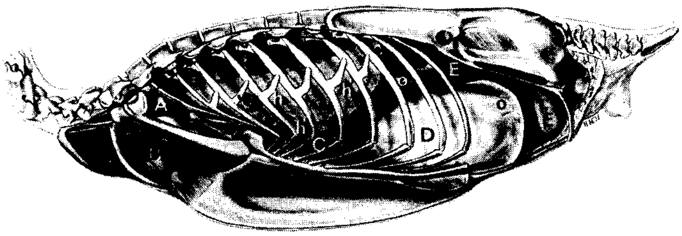

Fig. 1. Drawing of a preparation of a Mallard duck *Anas platyrhynchos*, left side from lateral. Thoracic and abdominal wall musculature has been removed and the lung is extirpated out of the pleural cavity. Horizontal septum (h) with Mm. costoseptales (h′), oblique septum (o). Cervical (A), clavicular (B), cranial (C) and caudal (D) thoracic, and abdominal (E) air sacs. (From Duncker 1971).

The volume changes of the respiratory movements act only on the air sacs, which ventilate the rigid bronchial system of the lung. The air sacs are situated in the subpulmonal cavity (Duncker 1979) beneath the lung and its horizontal septum. The symmetrical subpulmonal cavities are cranially united and together with the air sacs fill the thorax cranial to the heart, often protruding into the lower neck. Lateral and caudal to the heart, the subpulmonal cavity with the air sacs occupies the space on each side between the body wall and the intestines, separated medially from the intestines by the oblique septum. This septum originates from the vertebral column and cranially from the lateral pericardial wall; it is inserted ventrally near the lateral margin of the sternum. The subpulmonal cavity extends further caudally than the lung; and varies in extent among the different avian families. Only the most caudal air sac invades the peritoneal cavity and spreads dorsally around the intestines (Fig. 1).

The air sacs are thin-walled and in addition to filling the subpulmonal cavity and the dorsal peritoneal cavity, protrude in the form of diverticula between different organs: between the kidneys and the synsacrum, around the articulations of the bones of the trunk and the neck including the shoulder and hip joint; they also invade the bones of the trunk, the vertebral column and the proximal bones of the wing and leg. Additionally, they invade the vertebral canal between the vertebral bodies and the dura mater in the thoracic and lower neck region. This pneumatization is found in the majority of birds, independent of their body size, but varying in extent; it is generally reduced or lacking only in some birds which swim under water. It has no function in connection with respiration.

Upper air ways. The air enters through the external nares at the upper bill into the nasal cavities. The location, form and direction of the external nares are highly variable, e.g. near the tip of the bill in kiwis, at the base of the bill in most species. The air passes through the nasal cavities and/or the oral cavity, which function in warming and humidifying the air, and in olfactory control. This passage over the mucosal surfaces is important, especially in small species, as an aid to effective heat and water balance by re-utilization of the expired air (Schmidt-Nielsen *et al* 1970).

The slit-like opening of the glottis at the base of the tongue, which is controlled by muscles, regulates the in- and out-flow of air. There are no vocal chords as in mammals; the sound production in birds is restricted to the SYRINX. The glottis opens into the larynx, which leads into the trachea. The avian trachea is, in contrast to mammals, totally surrounded by tracheal rings, which ossify in many species. Externally, the trachea is accompanied over its length by the tracheal muscles.

The lower trachea enters the cranial thoracic aperture, where it is surrounded by the clavicular air sac, which incorporates also the bifurcation of the trachea. In some birds, especially in penguins, the trachea is double-tubed, starting more or less distant from the larynx. Starting at the bifurcation, the two extrapulmonary primary bronchi run

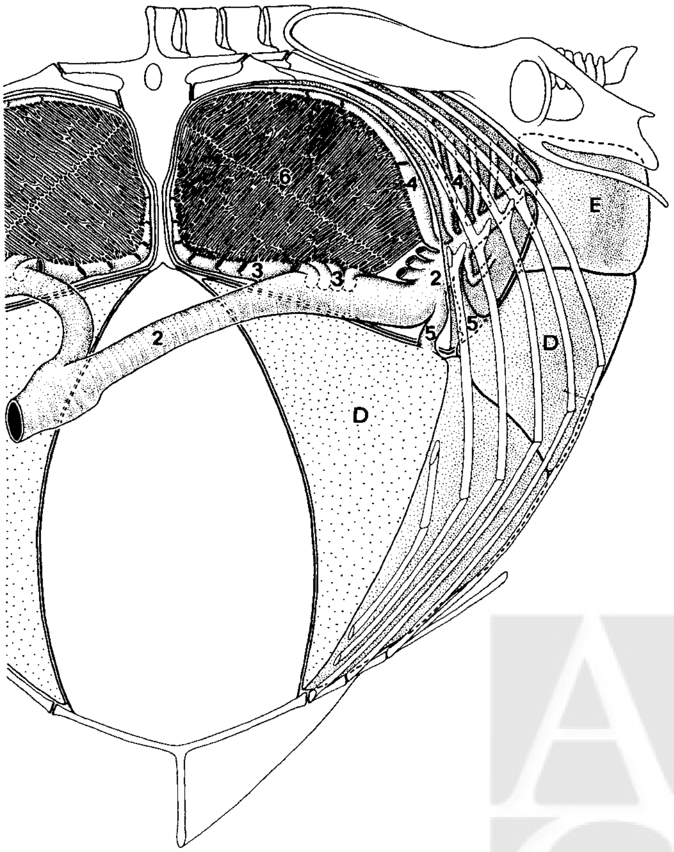

Fig. 2. Schematic cross section of the trunk of a White Stork *Ciconia ciconia*, view from cranial on to the caudal part of the trunk, out of which only the primary bronchus (2) projects. The lung with medioventrobronchi (3), mediodorsobronchi (4), lateroventrobronchi (5) and parabronchi (6) above the horizontal septum; beneath it, between body wall and oblique septum, the air sacs (D, E). Between both oblique septa space for the intestines. (From Duncker 1971).

toward the lung hilus. They are surrounded by C-shaped bronchial cartilages, which also protect the first short part of the intrapulmonary primary bronchus. Then the cartilages disappear completely; the further primary bronchus and all other bronchi of the avian lung are free of cartilage. The respiratory epithelium of the trachea and primary bronchi contain glands consisting of goblet cells, varying in number depending on the species and on the size of the bird. Goblet cells are responsible for the final humidification of the air (Menuam and Richards 1975).

Lungs. The lungs (Fig. 4) are not lobed and adhere to the walls of the pleural cavities. They are fixed and rigid in form and are constant in volume during all respiratory phases. The primary bronchus enters the lung hilus through the horizontal septum at the ventral lung surface together with the pulmonary vessels. The primary bronchus gives off immediately on its dorso-medial side the first set of secondary bronchi (the 4 medioventrobronchi) (Fig. 2), which spread over the ventral lung surface. The primary bronchus continues on its course to the dorsolateral lung surface, at or near which it bends caudally. It then runs in a dorsally curved course to the caudal lung margin, giving off the second set of secondary bronchi (the 7 to 10 mediodorsobronchi) which spread out at the laterodorsal surface of the lung. Opposite the mediodorsobronchi, the 4 or 5 lateroventrobronchi originate, spreading out between the primary bronchus and the horizontal septum. At the caudal lung margin the primary bronchus terminates in the abdominal air sac.

From the internal surfaces of these 3 sets of secondary bronchi the parabronchi originate (Figs. 2, 3). The parabronchi of the medioventrobronchi anastomose with those of the mediodorso- and lateroventrobronchi in the planum anastomoticum, situated medially in the lung. The cranial air sacs are connected to the medioventrobronchi, the caudal air sacs to the first lateroventrobronchus and to the terminal primary bronchus (Fig. 3). This system makes up the paleopulmo (Duncker 1971), which is present in all birds. Between the posterior primary bronchus and the air sac ostia of the caudal air sacs an additional connection is formed via a parabronchial network (Fig. 5), the neopulmo (Duncker 1971). The neopulmo is absent in penguins and emus; it is found in all other birds and is most highly developed in galliform and song birds.

The paleopulmo. The 4 medioventrobronchi (Figs. 2, 3, 4) originate dorsomedially from the entering primary bronchus, one directly behind the other. The first bends cranially, the others medially: they dilate and ramify, spreading over and occupying the ventral surface of the lung directly above the horizontal septum. The first medioventrobronchus, with its numerous branches lying side by side, occupies the cranial third of the ventral lung surface and terminates cranially, bending on to the dorsolateral lung surface, medially on to the lower medial surface. The second medioventrobronchus continues, with its branches, along the ventral covering of the lung surface, followed by the third medioventrobronchus which reaches the mediocaudal edge of the lung. The terminal branches of both medioventrobronchi curve onto the lower medial surface. The fourth medioventrobronchus joins the third on its lateral side, in most species with only a few branches or none at all. Only the lateral part of the ventral lung surface caudal to the lung hilus is not occupied by medioventrobronchial branches, but rather by paleopulmonic parabronchi. A branch of the first medioventrobronchus penetrates the horizontal septum cranial to the lung and opens into the cervical air sac. The third medioventrobronchus, directly after its origin, gives off a short, wide stem, which bifurcates through the horizontal septum directly medial to the lung hilus and opens into the clavicular and into the cranial thoracic air sacs. The region lateral to the hilus contains the lateral ostia into the clavicular and cranial thoracic air sacs. This region is supplied by a large lateral branch of both the first and second medioventrobronchus and in many species also by a lateral branch of the fourth medioventrobronchus (Fig. 3). However, in most species these ostia are not directly connected to the medioventrobronchus branches, but via the parabronchial net.

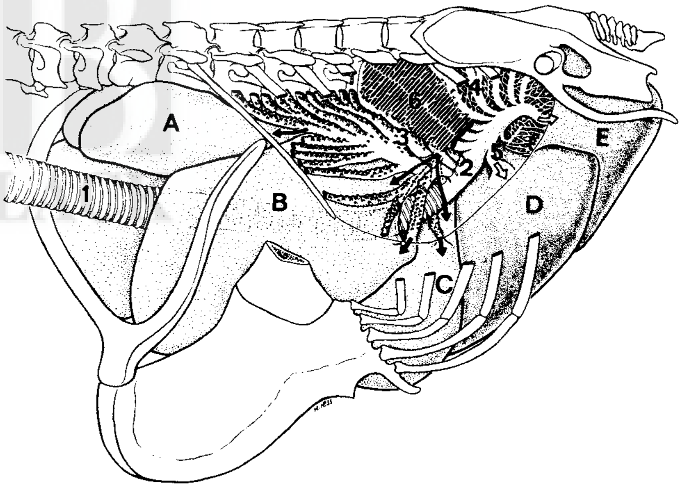

Fig. 3. Semi-schematic drawing of the lung and air sacs of the Stork. Trachea (1), primary bronchus (2), medioventrobronchi (3), mediodorsobronchi (4), lateroventrobronchi (5), parabronchi (6). Connections of the cranial air sac group indicated by black arrows: cervical (A) to the first medioventrobronchus, clavicular (B) and cranial thoracic (C) air sacs to the third medioventrobronchus and to the lateral ostia. Connections of the caudal air sac group are indicated by white arrows: caudal thoracic (D) and abdominal (E) air sacs to the lateroventrobronchus and caudal primary bronchus. (From Duncker 1972).

The 7 to 10 mediodorsobronchi (Figs. 2, 3, 4) originate dorsally from the primary bronchus, starting at that point where it bends caudally. The first 3 or 4 mediodorsobronchi originate directly one behind the other, their openings being separated from each other by only a thin membrane, whereas the distances between the openings of the succeeding mediodorsobronchi increase. All mediodorsobronchial openings are directed caudally, and the first 3 or 4 one above the other (Fig. 4). After their

Fig. 4. Drawing of the left lung of a Mute Swan *Cygnus olor*, from lateral. The lateral part of the lung has been removed to (1) expose primary bronchus (2), medioventro- (3), mediodorso- (4), lateroventrobronchi (5) and parabronchi (6). Ostia into the caudal thoracic (D′) and abdominal (E′) air sacs. The surface of the lung between the secondary bronchi is covered by thin-walled air bubbles (9). (From Duncker 1972).

initial cranial course, the mediodorsobronchi bend dorsomedially, except for the first and the last, which bend mediocaudally. They spread over the dorsolateral surface of the lung, directly beneath the thoracic wall. The first mediodorsobronchus ramifies into a large number of branches and supplies a broad area at the cranial lung surface, including the ventral part of the lung surface lateral to the lung hilus. The remaining mediodorsobronchi have a decreasing number of branches, and the last one, none at all. They supply areas of decreasing extent, which lie exclusively dorsal to the primary bronchus. In most species the neighbouring branches join each other directly, covering the entire dorsolateral surface. Their terminal branches end at a greater distance from the cranial margin of the lung, but mediodorsally they curve onto the medial surface. The mediodorsobronchi do not have any air sac connections.

The 2 to 5 lateroventrobronchi (Figs. 2, 3, 4) originate from the primary bronchus opposite the middle mediodorsobronchi. Their openings are directed caudally similarly to those of the mediodorsobronchi, and after their initial cranial course they bend ventrally and caudally. The first lateroventrobronchus is usually large, has no branches, and does not give off parabronchi into the paleopulmo. It connects to the caudal thoracic air sac via a funnel-shaped opening, penetrating the horizontal septum near the lateral lung margin between the lung hilus and the caudal lung margin. The next one to 4 smaller lateroventrobronchi regularly do not have ramifications. They occupy the space between the primary bronchus and the horizontal septum, giving off parabronchi medially. The lateroventrobronchi mark the lateral border of the paleopulmo, lying at the lateral lung surface in birds that lack a neopulmo.

The parabronchi of the paleopulmo (Figs. 2, 3) originate (1) from the entire internal surfaces of the medioventrobronchi and their terminal branches, and (2) from the entire internal surfaces of the mediodorso- and lateroventrobronchi and their terminal branches. Directly after their origin, they are interconnected with the neighbouring parabronchi by short ramifications. In most species they then run without further ramifications straight toward the medial planum anastomoticum. There, each parabronchus is connected with 2 or 3 parabronchi of the opposite side. Thus, the medioventrobronchi on one side are connected to the mediodorso- and lateroventrobronchi on the other side. The first and second medioventrobronchi and their lateral branches receive parabronchi from the first and second mediodorsobronchi and their lateral branches. The third and fourth medioventrobronchi receive parabronchi from all the succeeding mediodorsobronchi, the fourth medioventrobronchus also from the small lateroventrobronchi. These latter parabronchi lie directly at the ventral lung surface upon the horizontal septum, lateral to the fourth medioventrobronchus.

The neopulmo. Only in a few groups, such as penguins and emus, does the paleopulmo make up the entire lung. In cormorants and storks, there is a small additional network of parabronchi, the neopulmo (Fig. 5). It connects the caudal primary bronchus with the ostia of the caudal air sacs. The neopulmo becomes larger in more highly developed birds such as ducks, gulls and pigeons, and it achieves its highest development in plovers and sandpipers and in galliform birds (Fig. 5). The neopulmo never exceeds 20% of the total lung volume. The neopulmonal parabronchi possess the same species-specific structure as those of the paleopulmo, but they are richly interconnected over their entire length, lacking long unramified sections.

The neopulmonal parabronchi (Fig. 5) originate from the lateral side of the primary bronchus, starting cranially at the origin of the first mediodorsobronchus, and also from the lateral sides of the large and the succeeding smaller lateroventrobronchi. In species with a more highly developed neopulmo, parabronchi originate also from the initial parts of the mediodorsobronchi and run toward the ostia of the caudal thoracic and the abdominal air sacs, entering the ostia laterally, often forming a separate funnel-shaped opening or a collecting saccobronchus. In a larger neopulmo, multiple layers of interconnected parabronchi occupy the lateral part of the lung and displace the primary bronchus, together with the origins of the mediodorso- and latero-ventrobronchi, medially into the lung.

In a large neopulmo, an increasing number of neopulmonal parabronchi connect with the abdominal air sac, whereas in the primary bronchus the diameter terminally decreases. Thus, in galliform and song birds the primary bronchus is functionally substituted by the neopulmonal network, its entrance into the abdominal air sac being reduced

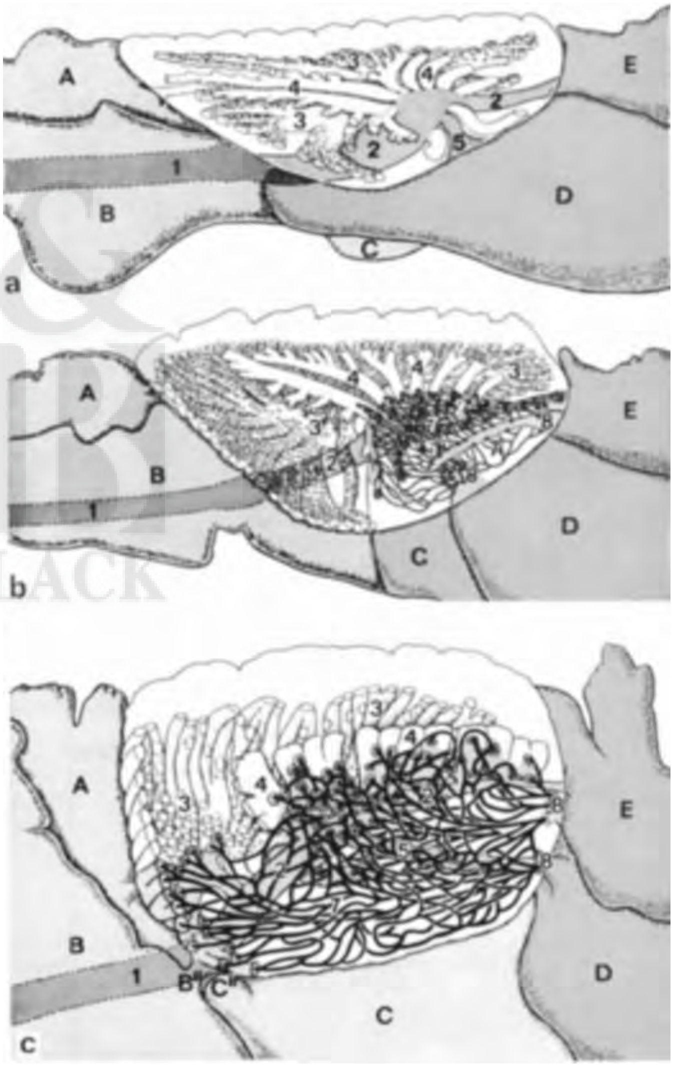

Fig. 5. Semi-schematic drawing of the paleopulmo and neopulmo. (a) King Penguin *Aptenodytes patagonicus*, without a neopulmo, (b) Mallard *Anas platyrhynchos* with a medium-sized neopulmo, (c) Domestic Fowl *Gallus domesticus* with a highly developed neopulmo. Trachea (1), primary bronchus (2), medioventro- (3), mediodorso- (4), lateroventrobronchi (5), neopulmonal parabronchi (7), saccobronchi (8), cervical (A), clavicular (B), cranial (C) and caudal thoracic (D), abdominal (E) air sacs with their ostia. (From Duncker 1971).

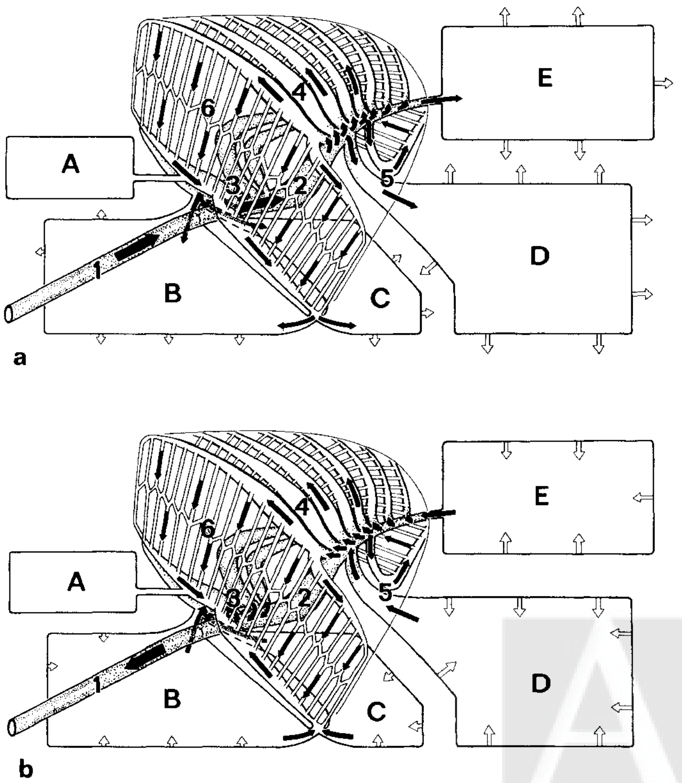

Fig. 6. Diagram of the paleopulmo and its air sac connections, (a) inspiratory phase, (b) expiratory phase. The black arrows indicate the direction of air flow during the respiratory phases; the white arrows express the air sac dilatation or compression. Trachea (1), primary bronchus (2), medioventro- (3), mediodorso- (4), lateroventrobronchi (5) and parabronchi (6). Cervical (A), clavicular (B), cranial (C), caudal thoracic (D), and abdominal (E) air sacs. (From Duncker 1974).

to a diameter smaller than a parabronchus. However, the large lateroventrobronchus, connecting with the caudal thoracic air sac, is never reduced in its diameter. Its ostium is laterally enlarged by the development of the neopulmonal ostium, or it is displaced toward the medial ventral lung surface, and a separate neopulmonal ostium occupies the lateral lung margin. A large neopulmo also expands into the lung region lateral to the hilus, replacing the lateral branch of the first mediodorsobronchus. Thus, the neopulmo receives direct connections to the lateral ostia of the clavicular and cranial thoracic air sacs.

The parabronchus (Fig. 8) is the functional unit of the avian lung, being unique among vertebrates. It consists of a long hollow tube, through the lumen of which the air flows. The parabronchial lumen is surrounded by a zone of hollow chambers, the atria, through which the air diffuses into the surrounding broad mantle of exchange tissue. The exchange tissue is made up of a blood–capillary/air–capillary meshwork, which is supplied by arterioles and venules running in the interparabronchial septa between the neighbouring parabronchi. The parabronchial lumen is surrounded by circular bundles of smooth muscle cells, which are interconnected by oblique strands, or by a more hexagonal arrangement of these bundles, varying in different species. Between the bundles, openings from the lumen into the atria are separated by thin membranes (Fig. 8), which carry only a few capillaries to supply the muscles. Around the muscle bundles and in these membranes a loose network of elastic fibres is found, whereas in the mantle of exchange tissue there are no elastic fibres. Thereby, the diameter of the parabronchial lumen can be changed by the interaction of smooth muscle bundles and elastic fibres without altering the volume of the exchange tissue.

From the outside of each atrium a few infundibula invade the parabronchial mantle, giving rise to a great number of air capillaries. These are air-filled tubes lined by a very thin epithelium and in their diameter (5 μm–14 μm, species-specific) similar to blood capillaries. The air capillaries intrude between the numerous blood capillaries and fuse around them to form a sponge-like three-dimensional net (Fig. 8). The blood capillaries, originating from interparabronchial arterioles, run slightly curved, but mostly without interconnections, from outside the parabronchi toward its lumen. Here, beneath the atria, they collect into small venules which bring the blood back into the interparabronchial venules. This intermingled meshwork of blood and air capillaries makes up the large surface at which the gas exchange between blood and air takes place (Fig. 9).

The basic structure of the parabronchus varies only to an astonishingly limited degree in different bird species, even with extreme differences in body size, taxonomic position and flying ability. The diameter of parabronchi varies from maximally 2 mm in ostriches, swans and turkeys to minimally 0.5 mm in some small song-birds and hummingbirds. In the latter and other advanced flyers, the atrial zone may be reduced or lacking, whereas the basic parabronchial form is found in poor flyers. The anatomical constancy is due to the fact that exchange of gas in the air capillaries takes place only by diffusion, so that a thickness in these capillaries of more than 0.5 mm is ineffective. Based on certain physical laws stating that the surface tension of the wet phase of the air capillary boundary against air strongly increases with the reduction of the diameter of the air-conducting structure, the volume constancy of the lung and the

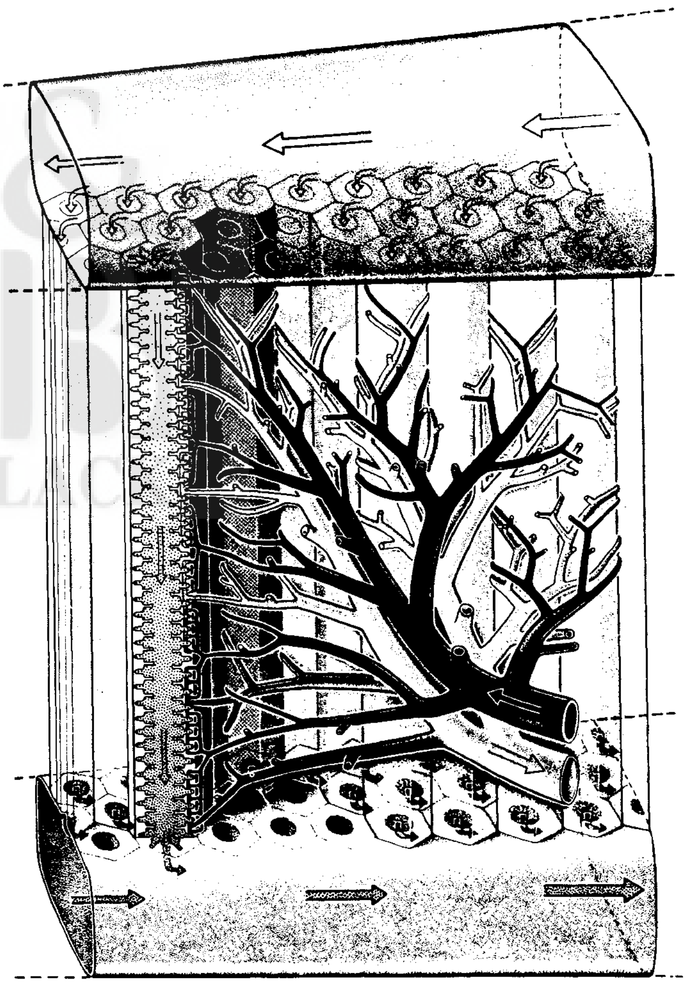

Fig. 7. Scheme of the vascular system of paleopulmonal parabronchi. The inspired air (white arrows) flows through a mediodorsobronchus (above) into the parabronchi, where the gas exchange takes place. The end expiratory air leaves the parabronchi (below) via a medioventrobronchus (densely stippled arrows). The venous blood flows through the pulmonary artery (dark) to all levels of the parabronchus, the arterial blood mixed from all parabronchial levels leaves the lung through the pulmonary vein (light). (From Duncker 1974).

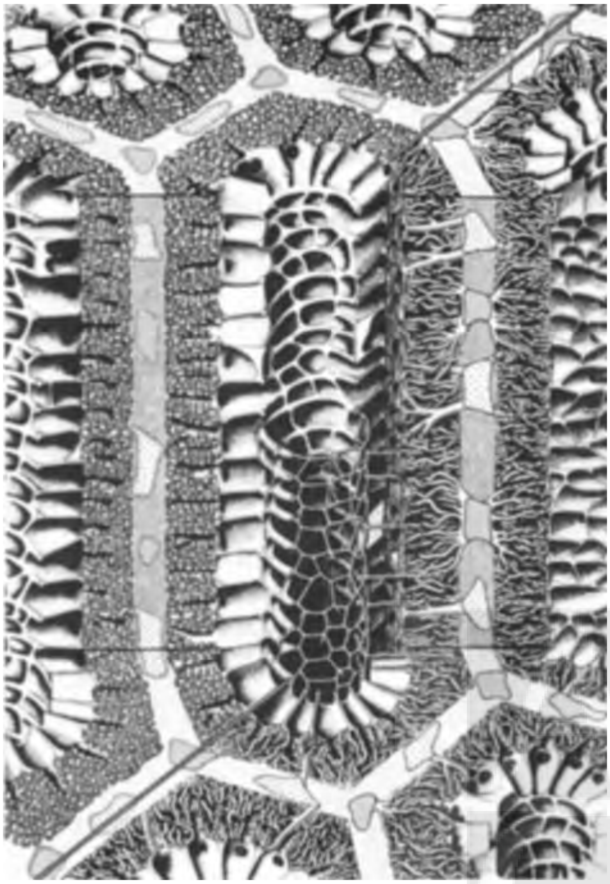

Fig. 8. Drawing of a parabronchus. On the left side: the atria with departing infundibula, which give off the air capillaries, making up a three-dimensional meshwork around the blood capillaries. On the right side: in the interparabronchial septa, arterioles (dense stippling) give off blood capillaries, which run toward the lumen where they collect to venules (light stippling); the latter penetrate the parabronchial mantle into the interparabronchial veins. The septa of the atria and their smooth muscle bundles are supplied by a loose capillary network. (From Duncker 1974).

rigid structure of the parabronchial mantle were a necessary precondition for the evolution of small tiny gas exchange structures, which have simultaneously allowed an enormous increase in the exchange surfaces.

The vascular system. The pulmonary artery enters the lung hilus cranial to the primary bronchus. It ramifies between medioventro- and mediodorsobronchi among the parabronchi so that its branches reach all parts of the parabronchi by the shortest distances (Fig. 7). A long parabronchus, connecting the medioventro- to the mediodorsobronchi, is equally supplied over its entire length with arterioles. The numerous venules of a parabronchus are collected into branches of the pulmonary vein, which run in the neighbourhood of the branches of the pulmonary artery. The pulmonary vein leaves the lung hilus caudal to the primary bronchus. The parabronchi of the neopulmo receive their vascular supply from caudal branches of the pulmonary artery and vein; a large neopulmo receives a separate, lateral branch of both vessels (see also VASCULAR SYSTEM).

Air sacs. Air sacs are large, extremely thin-walled extensions of bronchi, which expand beyond their penetration of the horizontal septum beneath the lung, filling the subpulmonal cavity or the dorsal peritoneal cavity. Their poor vascularization by the systemic circulation excludes participation in gas exchange and determines their function as bellows for ventilation. In the basic arrangement, a total of 9 air sacs exist, which can be separated into two functional groups: (1) the cranial air sacs, including the paired cervical, the unpaired clavicular and the paired cranial thoracic sacs (Figs. 1, 3, 5), are all connected to the medioventrobronchi; (2) the caudal group of air sacs consists of the paired caudal thoracic and the paired abdominal air sacs (Figs. 1, 2, 3, 5). The latter are directly connected to the primary bronchus, which terminates in the abdominal air sac ostium. The caudal thoracic sac is connected to the large lateroventrobronchus, and thus it is also connected to the caudal primary bronchus. The cranial group of air sacs occupies the space in the subpulmonal cavity in front of and lateral to the pericardium. The caudal thoracic air sac occupies the caudal part of the subpulmonal cavity, whereas the abdominal sac invades the dorsal peritoneal cavity. An abdominal air sac located in the peritoneal cavity is lacking only in kiwis. Their air sac, in which the primary bronchus terminates, lies in the subpulmonal cavity as the most caudal one.

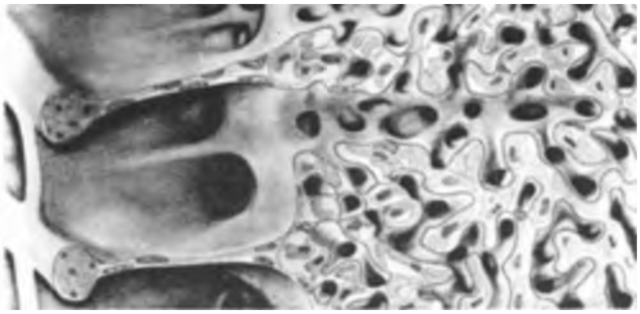

Fig. 9. Three-dimensional drawing of the wall of a parabronchus. At the left, atria are seen, separated by thin septa, from which a few infundibula originate. At the right, one infundibulum in longitudinal section is shown, giving origin to numerous air capillaries which cross-link and interlace, making up a three-dimensional meshwork around the blood capillaries. (From Duncker 1974).

The paired cervical air sac (Fig. 3) is connected by a branch to the first medioventrobronchus which penetrates the horizontal septum cranial to the lung hilus. The air sac extends cranially into the lower neck region, below the ventral neck musculature, adjacent and dorsal to the oesophagus. Lateral to the oesophagus the cervical air sac joins the dorsal part of the clavicular sac to form a separating membrane. By reduction of this membrane the cervical sac can fuse with the clavicular sac, as in turkeys or hummingbirds. The cervical air sac gives off pneumatic diverticula into the adjacent vertebral bodies, and a larger diverticulum between the rib cage and the cranial part of the scapula and the shoulder joint.

The clavicular air sac (Fig. 3), unpaired due to the early fusion of embryonic paired sacs during development, is connected to both lungs by a short stem of the third medioventrobronchus, medial to the lung hilus, and via the ostium at the lung margin lateral to the hilus. It fills the most cranial part of the thoracic cavity in front of the pericardium and beneath the lung and bulges through the cranial thoracic aperture under the skin and muscles cranial to the thorax. The clavicular air sac expands laterally to the pericardium where it joins the cranial thoracic air sac to form a separating membrane. In a large number of families the clavicular air sac extends ventrally and caudally between the pericardium and the sternum, most often as a narrow diverticulum up to the middle of the sternum. However, in hummingbirds and song-birds the clavicular air sac extends up to the caudal margin of the sternum. In contrast to all other air sacs, the clavicular sac surrounds several structures, which run through the cranial thoracic aperture: the oesophagus, the trachea with syrinx and extrapulmonary primary bronchi, the tracheal muscles, the subclavian artery and parts of the brachial plexus. The carotid artery, the jugular vein, the accompanying endocrine glands, and the vagus nerve run in the membrane separating the clavicular and cervical air sacs. In addition to numerous diverticula for the pneumatization of the adjacent bones, the clavicular air sac gives off large diverticula between the scapula and the rib cage, and also into the axilla and around the shoulder joint.

The paired cranial thoracic air sac (Fig. 3) is connected to the third medioventrobronchus medial to the lung hilus and to the ostium at the lung margin lateral to the hilus, very similar to the clavicular sac. This air sac is bordered dorsally by the horizontal septum and medially by the pericardial wall and the oblique septum, and laterally by the thoracic wall. Caudally, the air sac is separated from the caudal thoracic air sac by a membrane, which originates out of the joined walls of both air sacs. The cranial air sac in the majority of birds is smaller than the caudal thoracic sac, but in pigeons and galliform birds it is larger. An extreme situation arises in turkeys, in which the caudal thoracic air sac is lacking and the cranial thoracic air sac occupies the entire caudal subpulmonal cavity. In hummingbirds and song-birds the cranial thoracic air sac retains the original position, but is fused with the clavicular sac. In these species the cranial group of air sacs is represented by only one sac, which possesses all the ostia of the fused 5 sacs. The adjacent bones are supplied with pneumatic diverticula from this air sac, whether fused or not.

The paired caudal thoracic air sac (Figs. 2, 3, 5) is bordered dorsally by the caudal part of the horizontal septum, which contains the ostium of the lateroventrobronchus. Into this ostium the parabronchi of the neopulmo or its saccobronchus open laterally. Medially, the caudal thoracic sac is bordered by the oblique septum, laterally by the thoracic wall. The caudal extension of this air sac varies largely in different families and thereby also its volume. The caudal thoracic air sac is large in most birds, but relatively small in pigeons and galliform birds. In the turkey, the connections of the missing caudal thoracic air sac to the lateroventrobronchus and to the neopulmo are incorporated into the ostium of the abdominal air sac.

The abdominal air sac (Figs. 2, 3, 5) is connected to the caudal primary bronchus, which at the caudal lung margin penetrates the united, dorsal, perpendicular portion of the horizontal and oblique septa and opens into the funnel-shaped air sac ostium. The abdominal air sac is the only one (with the exception of the kiwi) which is not situated in the subpulmonal cavity, but spreads out in the dorsal peritoneal cavity lateral to the dorsal mesentery. The air sac wall adheres to the dorsal body wall over a varying wide oval area, so that the cranial parts of the kidney and the testes are covered, but not the left ovary. From the margins of this area of adhesion the very thin walls of the abdominal air sac hang freely movable into the peritoneal cavity. The dimensions of the air sac walls are limited in penguins, ostriches and rheas, but in most other birds are so wide that the thin walls are regularly folded up between intestinal loops. Air sac diverticula protrude from the dorsal area of adhesion between kidney and synsacrum, into the synsacrum and the femur, and around the hip joint.

The ostia of the air sacs and their connecting bronchi are to some extent structurally different. The ostia into the cranial air sacs are rigidly extended into the horizontal septum; the connecting medioventrobronchi are not able to vary their diameter. The ostia into the caudal thoracic and abdominal air sacs are also rigidly extended into the horizontal septum or in the septum at the caudal lung margin. However, the connecting lateroventrobronchus and the terminal primary bronchus possess a well-developed circular musculature. In contrast to the medioventrobronchi, which are poor in musculature and rigidly stretched, these connecting bronchi can vary their diameter, and thus they may contribute to the regulation of air flow into and out of these air sacs.

The ventilation of the lung is caused by the volume changes produced by the respiratory movements, which act only on the air sacs. The measured pressure changes are the same in all air sacs. During inspiration, fresh air flows directly through the primary bronchus and the large lateroventrobronchus into the caudal air sacs (Fig. 6a). In contrast, the cranial air sacs receive an inflow of air only via the richly interconnected medioventrobronchi. Thus, a pressure gradient to the mediodorsobronchi is developed, causing the air to flow from the primary bronchus through the mediodorsobronchi via the parabronchi and through the medioventrobronchi into the cranial air sacs. They therefore receive only expiratory air. During expiration, the air from the caudal air sacs is forced into the openings of the mediodorsobronchi, which are situated one above the other (Fig. 6b). This air flows through the parabronchi and through the medioventrobronchi, where it is joined by air from the cranial air sacs, leaving the lung through the primary bronchus. Thus, the air flows unidirectionally during inspiration and expiration through the paleopulmonal parabronchi (Scheid 1979, 1982) which is a consequence of the arrangement of the secondary bronchi and the orientation of their origins and their air sac connections.

In contrast to this unidirectional ventilation of the paleopulmo, the neopulmonal parabronchi are ventilated in directions altering with the respiratory phase, due to the fact that this parabronchial net lies in the direct connection between the primary bronchus and the caudal air sacs.

The gas exchange in the long parabronchi, whether ventilated unidirectionally or otherwise, is physiologically unique and much more efficient than in mammalian alveoli. The venous blood perfuses equally all capillaries over the entire length of the parabronchus (Fig. 7). In the proximal portion of the parabronchus the blood exchanges with fresh air, whereas in the more distal parts it exchanges with increasingly deoxygenated air, up to the terminal part of the parabronchus where the venous blood comes into equilibrium with the fully exchanged (end-expiratory) air. The gas content of the blood, varying in composition at the various parabronchial levels, has a lower CO_2 partial pressure than the end-expiratory air, and under hypoxic conditions, e.g. during flight at high altitudes (Scheid 1979, 1982), also has a higher O_2 partial pressure than the expired air. This so-called cross-current exchange system is responsible for the high physiological efficiency of the avian lung.

Contrary to earlier belief, the movements of birds due to flight are totally independent of respiratory movements, and they do not even support respiration. The two activities are anatomically independent of each other. The large flight muscles originate solely from the broad sternum, the coracoid, the clavicula and their membranes, but not from the rib cage (the respiratory apparatus), from which the movements of the flight apparatus are isolated by loose connective tissue and air sac diverticula. The respiratory movements are produced only by the muscles of the ribs and their uncinate processes, which give them a more effective leverage, and by the muscles of the abdominal wall (Duncker 1971). The separation of flight and respiratory movements has been proven by recording wing beats and breaths, which are found in different relationships to one another, varying from 3:2 to 5:1 in most species investigated. Only in the crow *Corvus* and the pigeon a 1:1 synchrony occurs (Berger and Hart 1974), which was the reason for the statement that flight and respiratory movements were coupled.

Ontogenetic development. Because of its structural peculiarities the avian lung/air sac system requires special developmental conditions. At the beginning of the second half of the incubation period, the lung fuses with the walls of the pleural cavity. Only the air sacs, which develop at the same time, can be inflated in the embryo. A few days before the end of the incubation period, the lung is fully developed together with all secondary bronchi and parabronchi. At this time air capillaries sprout from the atria into the parabronchial wall between the developing blood capillaries. The parabronchi and their developing air capillaries are full of pulmonary fluid. One to three days before hatching, the embryo ingests the amniotic fluid and the rest of the albumen, and breaks the membrane to the air space inside the egg. At this time regular respiratory movements start, and the embryo breathes air, thereby starting ventilation of the lungs and air sacs, and also of the parabronchi. During this time the gas exchange of the embryo is carried out by the chorio-allantoic membrane, but after ventilation has started the pulmonary fluid gets resorbed from the developing air capillaries. Thus, the gas exchange is increasingly taken over by the growing blood–capillary/air–capillary network, until at the end of this process, the embryo hatches. The air capillaries cannot be inflated because of their high surface tension and the rigid construction of the lung; moreover, they cannot suddenly be emptied of pulmonary fluid at the moment of birth. Therefore, birds require one to three days before hatching for their lungs to develop full functional status, during which time an overlap of the gas exchange process by the chorio-allantoic membrane and the air ventilation of the lungs occurs; this is only possible in a hard-shelled egg. Thus, the phylogenetic development of viviparity, which would have a number of biological benefits also for birds, was denied avian species by the structural peculiarities of their respiratory system (Duncker 1971, 1978) (see also DEVELOPMENT, EMBRYONIC). H.-R.D.

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RESTLESSNESS, PRE-MIGRATORY: see PRE-MIGRATORY RESTLESSNESS.

RETICULATE: term applied to a podotheca consisting of small scales, the divisions between which form a fine network (see LEG).

RETINA: part of the eye (see VISION).

RETRAP: see MARKING; TRAPPING.

REVERSE MIGRATION: a phenomenon in which birds fly in a direction opposite to that which they would be expected to take during a particular migration (see WEATHER AND BIRDS (Reverse migration)).

RHABDORNITHIDAE: family of PASSERIFORMES, suborder Oscines; CREEPER, PHILIPPINE.

RHACHIS: see RACHIS.

RHAMPHOTHECA: the horny covering of the bill, the upper and lower parts of it being sometimes separately designated rhinotheca and gnathotheca (see BILL).

RHEA: substantive name of the 2 species of Rheidae (Struthioniformes, suborder Rheae); in the plural, general term for the family. The group is restricted to the campo region of South America, where the birds are called 'Ema' or 'Nhandu' (Nandu). They are large running ratites, showing a general resemblance to the Ostrich *Struthio camelus* of Africa. The Ostrich, Cassowaries *Casuarius*, Emu *Dromaius novaehollandiae* and rheas are considered to be of monophyletic origin.

Characteristics. The Greater Rhea (or Common Nandu) *Rhea americana*, to which the following account refers, stands about 1.5 m high and weighs 20–25 kg or more. The normal coloration is not conspicuous, but white individuals are not uncommon. The sexes are similar, but the males are slightly taller.

Each foot has 3 well-formed toes, and the birds are fine runners. When alarmed they run with their necks stretched almost horizontally, and they can double at right angles to their course. At the same time they lift one of their wings, with a sail-like or ballooning effect. When there is enough cover they crouch down to conceal themselves. Although the wings are bigger in proportion than those of other ratites, they are useless for flying; they cover the upper part of the rump like a cloak when they are at rest. Unlike those of the Ostrich, the feathers have little commercial value; they are used in South America as dusters. Rectrices are absent. Rheas love to bathe and they are able to swim.

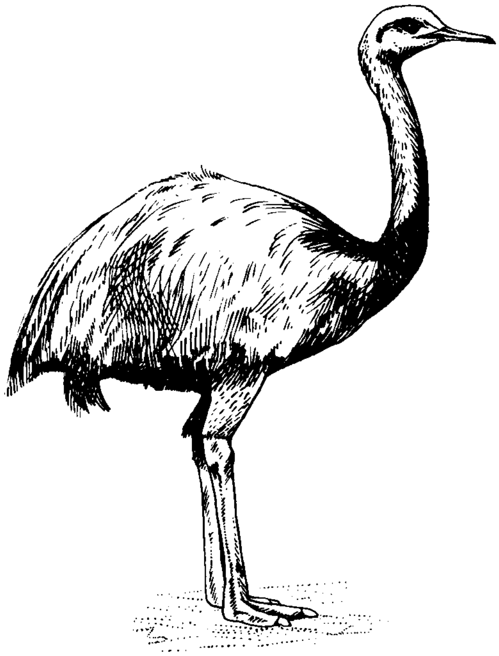
Habitat. Generally the species prefers country with taller vegetation to pure grasslands, with the breeding territory near a swamp or river if possible.

Distribution. *Rhea americana* is found from north-eastern Brazil to central Argentina. The other species, in a closely related genus, is Darwin's Rhea *Pterocnemia pennata*, occurring from Patagonia to the high plateaux of the Andes in southern Peru. It is somewhat smaller; the plumage shows white spots on a brownish background.

Food. Rheas feed on tender leaves, roots, seeds, and the like, also eating many insects, especially grasshoppers, and small vertebrates.

Behaviour and voice. The birds live in flocks; except in the breeding periods these groups consist of 20–30 individuals, at times considerably more. Occasionally they mix with herds of the Bush Deer *Dorcelaphus bezoarticus*, both species keeping a sharp look-out. In regions where they are not hunted they also mix with grazing cattle. Old male birds are solitary.

At the beginning of the breeding period the older males chase away the young ones and fight with their rivals by twisting their necks together, biting, and kicking. The male displays in front of 3–8 females: he runs to and fro, stands in front of them, pulls his neck in, jerks his wings and then spreads them away from his body so that the feathers flutter in the breeze. He frequently lets out a kind of low roar which sounds more like the voice of some wild beast than of a bird. At the same time he stretches his neck straight upwards, the inflated oesophagus serving as a sounding board. The Rhea also produces other sounds; the syrinx is better developed than in the Ostrich.



Greater Rhea *Rhea americana*. (*M.Y.*)

Breeding. At a dry spot protected by bushes, the victorious male prepares a shallow hollow in the ground by ripping away the grass with his bill; frequently he uses an already existing depression and often works at a number of spots. Finally, he lines the hollow with some dry vegetable matter. Some of the nests are surrounded by an open zone partly prepared by the birds themselves biting off the grass; this zone occasionally serves to protect the nest against campo fires.

The male then leads the females to the nest, showing his strikingly light-coloured rump. Frequently they have already started laying, dropping their eggs in various spots; but now they concentrate on the definite nest. It may happen that 6 females, one after another, each lay an egg in the nest and then leave together. Even females that belong to a different flock will join in and, consequently, the clutch may increase rapidly. Each female lays an egg every 2 or 3 days up to a total of 11–18. Otherwise they do not bother with the nest.

After there are a certain number of eggs in the nest the male begins to incubate. From then on he defends the nest by stretching out his neck and moving it in a snake-like fashion accompanied by hissing and snapping. Females who want to lay more eggs in the nest must behave submissively to reduce the male's aggression before they are allowed to do so. More eggs are also laid in the vicinity; the male rolls into the nest, with his bill, those eggs nearest it. Depending on circumstances, the clutch is complete with from 13 to 20–30 eggs; but clutches with more than twice that number of eggs have been found (e.g. 80). The number of eggs which go to waste is even larger. The measurements of the eggs vary considerably, the average is about 132 × 90 mm; the weight of an egg is about 600 g. Newly laid eggs of *Rhea americana* are golden yellow, but this quickly fades to an off-white colour. The eggs of *Pterocnemia pennata* are green.

After an incubation of 35–40 days by the male alone, the young hatch, one shortly after the other. They are grey with dark stripes. The young soon leave the nest, led by the male. They keep contact with each other by long-drawn plaintive whistles. Even so they get lost at times, especially when they lag too far behind after cowering low at the sign of danger. The strays will join another flock, if possible, and this results in considerable age variations within flocks. The development of the young is rapid; after 5 months they are already as big as the adult birds. Sexual maturity, however, is not reached for 2 years. H.S.

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RHEAE; RHEIDAE: suborder and family of STRUTHIONIFORMES; RHEA.

RHINOCRYPTIDAE: family of PASSERIFORMES, suborder Deutero-Oscines; TAPACULO.

RHINOTHECA: term sometimes applied to the part of the rhamphotheca covering the upper jaw (see BILL).

RHIPIDURIDAE: a family of PASSERIFORMES, suborder Oscines; FANTAIL.

RHOMBOID SINUS: a structure in the avian spinal cord (see NERVOUS SYSTEM).

RHYNCHOKINESIS: a form of upper jaw mobility seen in some birds with schizorhinal nostrils, in which the flexible region has shifted rostrally, and bending occurs instead at various points along the length of the upper jaw (zonae elasticae maxillares) (see SKULL (Cranial kinesis)).

RHYNOCHETI; RHYNOCHETIDAE: see under GRUIFORMES; KAGU.

RHYTHMS AND TIME MEASUREMENT: processes which recur at regular intervals in organisms or groups of organisms are commonly referred to as rhythms or periodicities. Four groups of biological periodicities constitute a special category in that their periods match natural environmental periodicities: tidal, daily, lunar and annual rhythms with periods of 12.4 h, 24.0 h, 29.5 days and 365 days, respectively. The 4 corresponding kinds of biological rhythms represent special adaptations which have evolved in many organisms to cope with the conspicuous temporal changes in the environment associated with the tides, the succession of day and night, the phases of the moon, and the cycle of the seasons. Since these environmental periodicities are highly stable and predictable, organisms have been able to evolve innate endogenous temporal programmes in physiology and behaviour, with the result that particular biological activities are performed at specific appropriate phases of the environmental cycles. In that respect biological rhythms often serve as clocks, i.e. time measuring systems that both couple temporal programmes of performance with environmental cycles and guarantee the appropriate sequence in the successive events of the programme.

In birds, as in most other organisms, all physiological and behavioural processes are organized on the basis of a daily periodicity. Similarly, annual rhythms are common, at least in birds inhabiting the temperate and higher latitudes with their pronounced seasons. Overt tidal and lunar rhythms, on the other hand, are less widespread in birds, but in some species they serve a significant function; for some seabirds and waders that feed in the intertidal zone, a tidal rhythm is superimposed on the daily pattern of foraging activity. Lunar rhythms related to the variations in nocturnal light-intensity are sometimes found in the time of onset and end of activity in crepuscular birds such as the foraging flight of Nightjars *Caprimulgus europaeus*, the LEKS of Black Grouse *Tetrao tetrix*, and in the duration of nocturnal restlessness in migratory passerines. The breeding cycles of the Sooty Tern *Sterna fuscata* on Ascension Island and of 2 passerines on Borneo closely approximate 10 lunar cycles, suggesting that reproduction in these birds is somehow controlled by the phase of the moon. But, whereas endogenous tidal and lunar rhythms have been investigated in other organisms, nothing is known about the properties of such rhythms in birds. The following account is therefore restricted to daily and annual rhythms.

Daily rhythms

General features. Although daily rhythms in biological activities closely match the daily environmental cycles to which they are adapted, they are not usually caused by them. This is indicated by the persistence of daily biological rhythms in experimental conditions devoid of daily variations. The daily rhythm of perch-hopping in the Chaffinch *Fringilla coelebs* continues for many cycles even when the bird is maintained in continuous light and at constant temperature. During the first 12 days of the experiment shown in Fig. 1, the bird was exposed to a 24-h light–dark cycle, but when the light was kept on continuously, the times of onset of successive bouts of activity shifted progressively forward relative to local time, indicating a 'free-running' rhythm of activity and rest with a period shorter than 24 h. Such a deviation of the period from 24 h—usually not exceeding about ±20% of 24 h—is characteristic of daily biological rhythms in constant conditions. This observation excludes the possibility that uncontrolled daily environmental cues might cause the rhythmicity in the animal and thus justifies the designation of these periodicities as 'circadian rhythms' (from *circa* = about and *dies* = day).

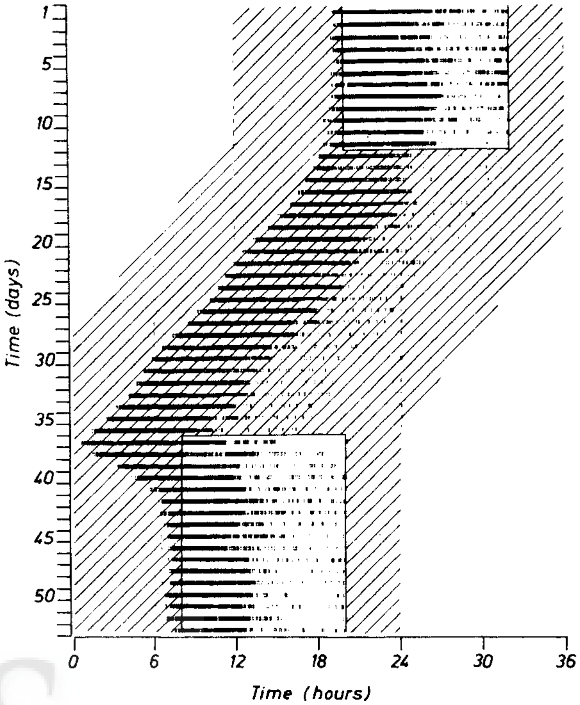

Fig. 1. Circadian rhythm in perch-hopping activity of a Chaffinch *Fringilla coelebs*. Each day's record is displayed below the record of the previous day. Black bars indicate intense activity. The bird was kept from day 1 through 12 (top box) in conditions of bright light from 2000 h to 0800 h (light area in the box) and dim light from 0800 h (shaded area outside the box) each day. From day 13 onwards it was kept in continuous dim light until day 37 (bottom box) when it was exposed once again to alternating bright and dim light on a 24 h light cycle. Note the persistence of the rhythm under constant conditions with a circadian period shorter than 24 h, and its entrainment by the light-dark cycle.

Whereas circadian rhythms have a period slightly different from 24 h under constant conditions, their period is exactly 24 h under natural conditions. There must, therefore, be daily rhythmic factors in the animal's normal environment which are capable of synchronizing circadian rhythms with the natural day. Such environmental cycles capable of synchronizing (entraining) biological rhythms are called Zeitgebers. For birds, as for essentially all other organisms, the most important Zeitgeber of circadian rhythms is the 24-h rhythm in light-intensity, i.e. the alternation between day and night. In Fig. 1 the free-running activity rhythm of the Chaffinch in constant darkness is 'caught' by the light–dark cycle; the bird's natural free-running period is altered to the period of the Zeitgeber. Other Zeitgebers of avian circadian rhythms are 24-h temperature cycles of an amplitude greater than 30°C, and acoustical signals consisting of regular daily alternations between noise and silence. However, the effectiveness of these supplementary Zeitgebers is small compared with that of light–dark cycles.

Since circadian rhythms persist without damping for many cycles in constant conditions they behave like self-sustaining oscillators in the technical sense. Therefore, the terminology of general oscillator theory is often used for describing them. They are innate: circadian locomotor activity rhythms develop even in chicks raised from the egg in constant darkness. Their period length τ is relatively unaffected by environmental influences. It is particularly significant for the use of these rhythms as clocks that τ shows little variation over a wide range of temperatures. This holds true for all sorts of organisms, including cold-blooded. A change in temperature of 10°C usually changes τ predictably, but by less than 5%. For birds, an increase in environmental temperature usually leads to a slight shortening of τ. Apart from temperature, light intensity has slight but consistent effects on τ. In diurnal birds τ usually shortens as light-intensity increases, whereas in nocturnal birds the reverse may be true, at least under high light intensities. In addition, physiological factors (e.g. reproductive state) may affect τ.

Within a single organism different biological functions are often controlled by different discrete circadian clocks. When, under constant environmental conditions, circadian rhythms are no longer synchronized, those of, e.g. body temperature and locomotor activity, may free-run with different τs. Even a single function may be under the control of more than one circadian oscillator. Thus, locomotor activity of birds kept in continuous dim light may, under certain conditions, 'split' into two components, the morning and evening peaks of activity, which separate and free-run with different periods. Under normal conditions of synchronization, however, the various circadian rhythms usually assume rather rigid phase-relationships to each other, ensuring that each circadian function occurs at the right phase of the environmental cycle and in the proper sequence relative to the other functions.

Whereas a Zeitgeber of circadian rhythms is by definition capable of changing τ so that it matches its own period T, the range of possible T-values to which circadian rhythms can entrain is limited: it extends from about 18 h to about 30 h. Between these limits, the range of T-values within which entrainment occurs depends on the nature of the Zeitgeber cycles, its amplitude, and the natural period τ_n of the animal's circadian rhythm. As the Zeitgeber period increases or the natural period of the circadian rhythm decreases, the phase of the biological rhythm shifts forward relative to the phase of the Zeitgeber rhythm. The phase relationship (ψ) between the two rhythms is given by $\psi \sim T/\tau_n$, as predicted if entrained circadian rhythms were to behave like self-sustaining oscillators under the influence of an external periodic driving force. Many aspects of circadian rhythms of animals under different Zeitgeber conditions are consistent with this relationship. For instance, it has been found that the circadian locomotor activity rhythm in many diurnal birds is relatively more phase-advanced in summer than in winter; the size of this seasonal difference increases with increasing latitude. Such changes are to be expected if the animal responds to the average light intensity it experiences in the course of a day, since this is higher in summer than in winter (and the extent of this seasonal difference is greater at higher latitudes). Since τ_n of a diurnal bird shortens with increasing light-intensity but T does not change, one should expect higher ψ values in the synchronized state in summer. Hence, some of the systematic seasonal and latitudinal changes in ψ can be interpreted as a consequence of the seasonal and latitudinal changes in day length. It must be emphasized, however, that other variables such as the duration of twilight affect the activity pattern as well.

Synchronization, in principle, is possible only if there is a periodically changing sensitivity of the circadian rhythm to stimuli from the Zeitgeber. This phenomenon has been explored in detail for the sensitivity of circadian rhythms to light. Light pulses and transitions from light to darkness or from darkness to light cause phase shifts of the circadian rhythm which are dependent in direction and amplitude on the phase of the rhythm hit by the light signal. This relationship is represented in so-called phase-response curves. On the assumption that light-pulses mimic the dark/light/dark transitions occurring during a natural day, phase-response curves can be used to predict the behaviour of circadian rhythms under various Zeitgeber conditions. This model of entrainment has proved successful in explaining the behaviour of avian circadian rhythms in, for instance, the Japanese Quail *Coturnix japonica* and the House Sparrow *Passer domesticus*. For these, the limits of the range of entrainment and the dependence of ψ on T or on photoperiod can be quantitatively derived from phase-response curves.

Localization of circadian pacemakers. Although it is clear that in higher vertebrates there is a multitude of circadian rhythms occurring at various levels from the organ down to the cell, there is now equally good evidence that this circadian system is integrated by central circadian pacemakers. In at least some passerine birds such a pacemaker seems to be localized in the pineal gland. If House Sparrows held in constant darkness are pinealectomized, their free-running rhythms of locomotor activity and body temperature are almost instantaneously abolished. Rhythmicity is restored, however, when the pineal of another sparrow is transplanted into the anterior chamber of an eye. The emerging rhythm has the phase of the rhythm of the donor bird. These results strongly suggest that the pineal is a circadian pacemaker, driving or integrating overt circadian rhythms, and that the information about circadian time is chemically transmitted to the subordinate system. Presumably melatonin, a hormone produced by the pineal, is the essential substance. In birds, as in other vertebrates, melatonin concentration shows a conspicuous daily rhythmicity with high values during the dark (inactive) and low values during the light (active) phase of each day. The synthesis of melatonin is controlled by the activity of the enzyme N-Acetyl-transferase which exhibits a strong daily (circadian) rhythm, persisting for at least two cycles in chickens kept in continuous darkness, and even in isolated chicken pineals cultured in vitro. Chronic melatonin treatment affects the free-running circadian activity rhythms in both sparrows and European Starlings *Sturnus vulgaris*. The highly disorganized circadian activity rhythms of pinealectomized Starlings kept in continuous dim light can be synchronized by daily injections of melatonin. All these facts, taken together, suggest that the pineal is the seat of a self-sustaining circadian oscillator, which controls overt circadian rhythms by its rhythmic output of melatonin.

Whereas pinealectomy results in arhythmic activity in the House Sparrow, the White-crowned Sparrow *Zonotrichia leucophrys* and the White-throated Sparrow *Z. albicollis*, pinealectomy of European Starlings leads to impairment and instability but not complete abolition of the circadian rhythm of locomotor activity. In Japanese Quail and the chicken *Gallus gallus*, in contrast, pinealectomy has no profound effect on circadian activity rhythms. These interspecific differences may reflect differences in the degree of self-sustainment, not of the circadian oscillator in the pineal itself, but of a subordinate oscillatory system which is affected by the pineal output. If this subordinate system is comprised of a population of circadian oscillators, the different effects of pinealectomy in the different species might be due to differences in the mutual coupling among these oscillators. In the gallinaceous birds, coupling may be strong, so that even in the absence of the pineal driver a normal circadian rhythm persists, whereas in sparrows coupling may be weak, so that the rhythm deteriorates in the absence of the pineal pacemaker, with the Starling intermediate. Even in pinealectomized sparrows a residual rhythmicity can be observed, as their locomotor activity rhythms can still be synchronized by light as for normal birds: it takes the rhythm about a week to disappear if such birds are subsequently transferred to constant darkness. This observation can be interpreted in terms of an internal uncoupling of circadian suboscillators controlling locomotor activity.

Another important part of the circadian system controlling locomotor activity is localized in the suprachiasmatic nuclei (SCN), in the anterior hypothalamus. In sparrows, their ablation has effects similar to pinealectomy. However, it is not clear yet how the pineal and the SCN interact, and how both of them eventually control the overt circadian functions.

Photoreceptors for the entrainment by light. In birds, the eyes are not the most important photoreceptors involved in the perception of the light-synchronizing circadian rhythms. Blinded House Sparrows can still entrain to 24-h light-dark cycles. However, the eyes are normally also involved, because after sparrows are blinded they require a greater minimum light intensity for synchronization to a 24-h light–dark cycle. The extraocular photoreceptors are located in the brain. This has been shown in experiments in which the entrainment response of normal sparrows to low-amplitude light–dark cycles was abolished by opaque material, placed on top of the bird's skull, which greatly reduces the light intensity reaching the brain. Conversely, the entrainment threshold can be lowered by plucking feathers from the head, thereby drastically increasing the light-intensity penetrating the skull. So far, the photoreceptors in the brain have not been identified.

Adaptive functions of circadian rhythms. The selective forces, which have led to the evolution of endogenous circadian rhythms in all eukaryotic organisms, are still obscure. It is possible that their primary function early in evolutionary time was the maintenance of internal temporal order among various metabolic functions. This, indeed, may still be a major function of some modern circadian systems. However, it is clear that many organisms now utilize circadian rhythms for a variety of other purposes as well. Many physiological and behavioural functions follow endogenous daily programmes that match periodically recurring and therefore predictable environmental demands. For instance, feeding activity of many diurnal birds shows a bimodal pattern, with morning and evening peaks. The evening peak may be adaptive in that it enables a bird to store a surplus of energy for the coming night, whereas the morning peak may be a mechanism to make up for the deficiencies built up during the previous night of starvation. However, this daily pattern does not depend on the availability of or demand for food, since it persists in constant conditions with a circadian period, even if food is available *ad libitum*. One of the possible advantages of such preprogramming is that the complex biochemical and behavioural events related to food uptake and digestion can be temporally organized relative to each other, early enough that the organism is ready for feeding at the appropriate times of day. Anticipation of future demands is also a major function of both physiological and behavioural circadian rhythms. For example, body temperature begins to increase long before the daily onset of activity, so that the animal's metabolic state is already elevated when it becomes active. In diurnal birds that migrate at night, both normal day-time activity and nocturnal migratory unrest are under circadian control. The alternation between these two types of activity is accompanied by circadian changes in preferred light intensities in a gradient. European Robins *Erithacus rubecula* select high intensities during their daytime activities (such as feeding) but low intensities during their nocturnal activities (such as migratory calling). Obviously the naturally occurring variations in light intensity have become incorporated as an 'expectation' in the endogenous circadian organization of these birds.

Circadian programmes are often highly flexible and subject to modification by individual experiences. In a sense, the circadian system provides a '24-h continuous loop tape recorder' on which the experiences of an individual animal at particular times of a day are stored. This ability is illustrated by the phenomenon of Zeitgedächtnis or time memory, first described for the honey bee but later also demonstrated for birds. Under experimental conditions bees can be trained to search for food at particular places at particular times of day; even if no longer rewarded, this temporal and spatial pattern persists for some days before it eventually becomes extinguished. Presumably, many of the daily habits that can be observed in free-living animals result from a similar circadian programming of learned behavioural functions based on some form of time memory.

Circadian rhythms also provide the basis for special adaptations. One of these is 'time-compensated sun-compass orientation', first discovered in birds and bees by G. Kramer and K. von Frisch respectively. Birds tending to fly in a particular direction during migratory unrest, or searching for food in a direction to which they had been trained, compensate for the sun's apparent movement by continuously changing their orientation angle relative to the sun in such a way that a constant compass direction is maintained. That a circadian clock is involved can be demonstrated by experiments in which birds are exposed to artificial light–dark-cycles shifted relative to the natural day; this procedure resets the animals' circadian rhythms within several days. If then tested under the sun again, they select the compass direction predicted by the hypothesis that the birds relate the sun's position to subjective circadian time. This can be shown even more convincingly in experiments in which the circadian clock of birds is allowed to free-run under constant conditions, and by testing birds under an artificial stationary sun: each bird behaves as though the sun was moving and changes its orientation angle relative to it in the expected counter-clockwise direction (see NAVIGATION).

Many seasonal events are controlled by the annual variations in photoperiod, the light fraction of the 24-h day. The stimulatory effect of long photoperiods on the development of avian reproductive systems has been extensively investigated. If temperate-zone birds are exposed in winter to a long photoperiod simulating spring or summer conditions, the pituitary begins to secrete gonadotrophins which in turn initiate gonadal recrudescence. Neither the duration of light time nor the duration of dark time is important; the release of this response depends only on the phase of the animal's circadian rhythm which is exposed to light. If birds are exposed to a short non-stimulatory light period, followed by an extended (more than 24 h) dark period, which is then interrupted by another short light period (given at different times in different experimental groups of birds), their responses are usually a function of the circadian phase hit by the second light period, as shown in Fig. 2. Light periods with maximal effects and those with minimal effects on release of luteinizing hormone from the pituitary of White-crowned Sparrows are spaced approximately 24 h apart; the pattern of response is a circadian rhythm itself. These results are consistent with the hypothesis proposed in 1936 by E. Bünning, according to which organisms are equipped with a circadian rhythm in photosensitivity which measures day-length by determining whether or not light falls on a particular photo-inductive phase of that rhythm. Details of this circadian time-measuring process are still unknown but there is now compelling evidence that a circadian rhythmicity is involved somehow, not only in mediating the gonadal growth response to long days, but also in other seasonal activities such as migratory behaviour, moult and gonadal recrudescence (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; MIGRATION; MOULT).

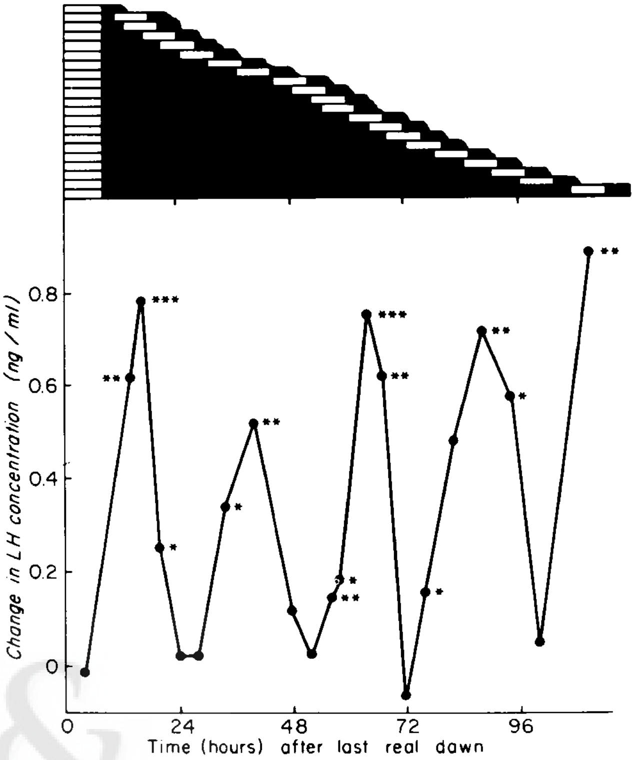

Fig. 2. The effect of an 8 h light period given at various intervals after beginning of darkness on plasma luteinizing hormone concentration in White-crowned Sparrows *Zonotrichia leucophrys*. The white and black bars at the top illustrate the various treatments. (White = period of light, black = period of darkness). Birds were previously maintained on 8 h of light per day and a pre-experimental blood sample was taken for all birds early in the last 8 h light period. The post-experimental sample was taken 7–16 h after the end of the test photoperiod. The ordinate shows the change in hormone concentration between these two samples that resulted from a particular treatment. (From Follett *et al* 1974).

Annual rhythms

General features. Like daily rhythms some annual biological periodicities are endogenously pre-programmed as circannual rhythms. Figure 3 demonstrates that annual variations in testicular width persisted in European Starlings maintained for 3½ years under constant photoperiodic conditions. Periods of increased testicular size alternated regularly with periods of moult. The interval between successive corresponding events deviated from one year, indicating that these rhythms are not driven by uncontrolled annual environmental cues.

Circannual rhythms persisting for at least two cycles, with periods deviating from 12 months, have been demonstrated for at least 15 avian species. Functions shown to be under circannual control are gonadal activity, migratory disposition, moult, feeding and body weight. In Garden Warblers *Sylvia borin* and Blackcaps *S. atricapilla* up to 9 successive circannual moult cycles have been measured under constant photoperiodic conditions, suggesting that in these species a circannual clock keeps running throughout the entire lifetime. In some species, however, circannual rhythms tend to damp out with time; and yet others show no annual rhythmicity at all if kept under seasonally constant conditions. This suggests that circannual rhythms are not as ubiquitous as circadian rhythms, and represent special mechanisms that have evolved in only a few species, for special purposes.

Circannual rhythms behave in many respects like circadian rhythms. There is evidence that they are innate. Their period in constant conditions seems to be relatively insensitive to environmental variables such as the actual duration of the constant photoperiod. And some results suggest that different functions may be controlled by different circannual clocks. Like circadian rhythms, they can be synchronized by cyclic variations in environmental conditions. In birds, the annual cycle in photoperiod constitutes such a circannual Zeitgeber; the period of the circannual rhythm can be altered by compressing the period of the normal annual change in photoperiod into less than 12 months. Using this technique in the European Starling, up to 8 cycles in testicular size and moult can be squeezed into one calendar year, indicating that the range of entrainment of these circannual rhythms is large compared to that of circadian rhythms.

Adaptive functions of circannual rhythms. Since circannual rhythms, in contrast to circadian rhythms, appear to be restricted to certain species, it appears likely that they have evolved independently several times to serve specific biological functions. In migratory birds, one such function may be the timing of seasonal events at those times of year when reliable seasonal timing cues are not available. Circannual rhythms appear to be most strongly involved in the control of migratory disposition and moult in equatorial migrants that live for about 6 months each year in a tropical environment where seasonal environmental changes are absent or highly variable. However, they also occur in some short-distance migrants and even in entirely resident species such as the Crested Tit *Parus cristatus*. In migrants, timing of seasonal activities is not the only function of circannual rhythms. Nocturnal migratory restlessness of caged first-year warblers shows a seasonal pattern similar to the changes in average migratory speed of free-living conspecifics during their actual migration. Moreover, when warblers of various species, which normally migrate over different distances, are maintained in cages, corresponding differences are found in the duration and amount of migratory restlessness. These differences are related to the distance normally covered by the birds on their actual migration: the longer the distance between breeding grounds and winter quarters, the greater the intensity of autumnal migratory restlessness observed in the caged birds. These results suggest that the time course and distance normally covered by these warblers during their first autumn migration may be controlled, at least in part, by a circannual programme determining the seasonal time course and total intensity of migratory unrest and, hence, that a circannual clock may be part of these birds' navigational system.

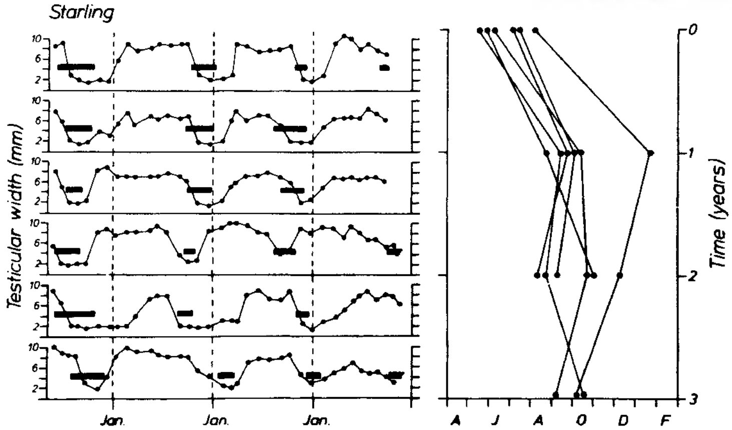

Fig. 3. *Left*: Variations in testicular width (curves) and occurrence of moult (black bars) of 6 European Starlings *Sturnus vulgaris* kept for 43 months under an 11:11 (upper three) or a 12:12 (lower three) hour light-dark cycle.

Right: Symbols connected by lines indicate dates at which the same birds began to moult in the successive years of the experiment. Note the persistence of the rhythms under these seasonally constant conditions and the deviation of the period of the rhythms from year to year. (After Gwinner 1981).

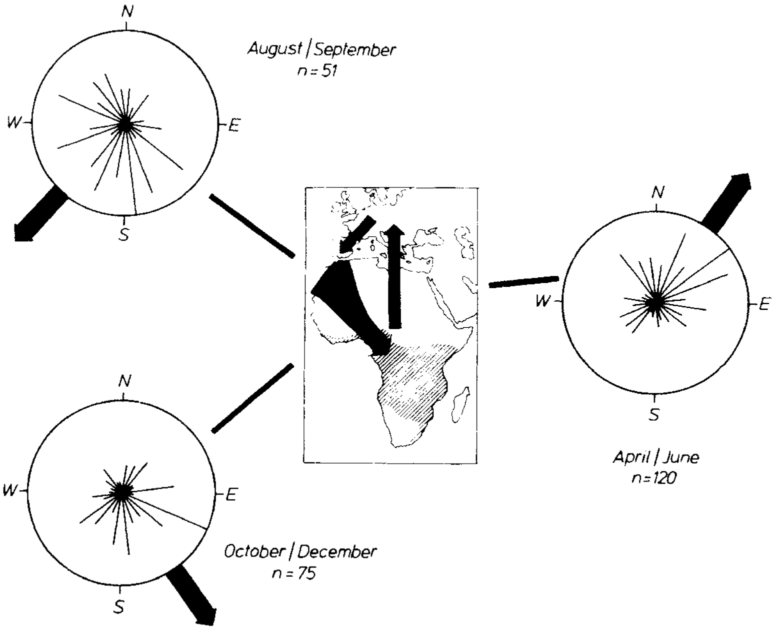

Fig. 4. Spontaneous seasonal changes of directional preferences in Garden Warblers *Sylvia borin* during nocturnal migratory restlessness. Garden Warblers were kept throughout the experiment under a constant 12:12 hour light-dark cycle and tested repeatedly in circular orientation cages. The birds had no view of the sky but were exposed to the natural earth's magnetic field. The three circular diagrams summarize the results obtained in August and September (*upper left*), in October through December (*lower left*) and in April through June (*right diagram*) of the following year. The data are plotted on a relative scale such that the radius equals the greatest amount of activity in any one 15° sector. The large arrows at the periphery of the diagrams show the direction of the mean vector calculated for each test series. Numbers in the diagrams refer to the number of tests. The map in the centre shows schematically the changes in migratory direction known to occur in Garden Warblers in the wild in the course of the year (After Gwinner & Wiltschko 1978, 1980).

Even the directional component of migration appears to be affected by a circannual rhythm. If Garden Warblers are maintained under a constant 12-h-photoperiod and tested repeatedly in orientation cages for directional tendencies of their nocturnal migratory unrest, they show changes in their directional preferences corresponding to the changes in migratory direction of free-living conspecifics (Fig. 4). This suggests that the shifts in migratory direction occurring in these birds along their way to and from their winter quarters may not be controlled primarily by exogenous cues but rather be the result of spontaneous circannual changes in the birds' internal physiological state. E.G.

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Menaker, M. (ed.). 1971. Biochronometry. Washington, D.C.
Pengelley, E.T. (ed.). 1974. Circannual Clocks. New York.
Saunders, D.S. 1977. An Introduction to Biological Rhythms. Glasgow.

RICE BIRD: alternative name for the Bobolink *Dolichonyx oryzivorus* (see ORIOLE (2)).

RICHMONDENINAE: see EMBERIZIDAE; CARDINAL-GROSBEAK.

RICTAL: pertaining to the gape; often applied to bristles in that area.

RIDING: young on parents' backs, see CARRYING.

RIFLE-BIRD: substantive name of species of *Ptiloris* (see BIRD-OF-PARADISE).

RIFLEMAN: *Acanthisitta chloris* (see under WREN (3)).

RINGDOVE (or RINGED DOVE): name (also 'Ring-dove', 'Ring Dove') applied to the so-called *Streptopelia 'risoria'*, a domesticated variety of one of the subspecies of *S. decaocto*; liable to confusion with 'Ring Dove' (etc.) used as an alternative name for the Wood-pigeon *Columba palumbus* (see PIGEON).

RINGING: see MARKING.

RINGNECK: substantive name sometimes used for the 2 Australian parrots of the genus *Barnardius*; not to be confused with Ringneck(ed) Parakeet, sometimes used for Rose-ringed Parakeet *Psittacula krameri* (see PARROT).

RING OUZEL: *Turdus torquatus*, a western Palearctic THRUSH of mainly montane distribution.

RING-SPECIES: term (for which R. Meinertzhagen has alternatively suggested 'rejungent species') expressing the concept that a species may differentiate into a graded series of geographical forms and that extreme members of the series may later come into direct contact, through range expansion, and then prove to be so different from each other as to behave as separate species; this occurs in that fraction of the total range in which both forms are found, whereas elsewhere (the long way round the ring, so to speak) they remain connected by intermediate forms. In such a case, when the extreme forms are recognized as separate species, the allocation of intermediates as subspecies of one or the other becomes somewhat arbitrary. Examples are to be found in *Parus major/minor*, *Lanius schach/tephronotus*, *Pycnonotus barbatus/tricolor/capensis*, *Acrocephalus arundinaceus/stentoreus*, *Apus apus/pallidus*, *Merops superciliosus/philippinus* and *Larus argentatus/fuscus*. See also ISOLATING MECHANISM; SPECIATION; SPECIES; SUBSPECIES.

RITUALIZATION: the evolutionary process responsible for the origin of displays and for the changes which occur in these to make them more effective in evoking the appropriate behaviour in the partner (see DISPLAY). For example, displacement preening movements have been incorporated into the male courtship display of ducks (see DISPLACEMENT ACTIVITY): in some species they have been reduced so that they can no longer make any contribution to feather care, and instead simply draw attention to features such as the 'sail' of the Mandarin drake *Aix galericulata*. The formal pointing movement, made more conspicuous by this enlarged feather ('morphological enhancement' of the display) serves purely to influence the behaviour of others. Ritualization also plays a role in the evolution of inter-specific signals, such as the 'broken wing' display of certain waders, which serves to draw predators away from the nest or chicks (see DISTRACTION BEHAVIOUR).

This article concentrates on the ritualization of visual displays; similar principles apply to the evolution of auditory signals. Explanation of this process requires description of the various types of change which are found to occur during the evolution of displays, and the analysis of the reasons for them and of the mechanisms involved. The functional analysis of the changes involves two distinct problems. Where a display modifies the behaviour of a member of a different species (as in anti-predator displays) so that the interests of the partners in the interaction are opposed, the evolutionary changes must make the display better able to tap a pre-existing responsiveness in the partner. For instance, the eyespot displays of certain moths tap an avoidance response in small birds which must be of benefit to these birds in interactions with predators. Here, selection must fit the display to a feature-detecting mechanism which is maintained by independent selective forces. In contrast, when displays operate within a species, or between species that compete for resources, it is not always obvious what selective forces determine the pattern of responsiveness of the reacting individuals. One possibility is illustrated by aggressive displays. These operate in some instances to allow opponents to assess their chances of success in combat with the rival, and in this case the reactor should respond to cues which provide reliable information about the rival's fighting ability. The selection acting on the display, enhancing the apparent potential of the displaying animal, will be opposed by selection on the reactor, making it unresponsive to bluff. An alternative possibility is illustrated by parent–offspring interactions where the interests of parent and offspring are in harmony. Here, the responsiveness of the reactor to signals may be constrained by general features of its perceptual system, and the fact that signals must be detected against a particular background. Within these general constraints, any appropriate changes in the responsiveness alone, or the signal alone, or changes in both together (providing they were compatible) might benefit the partners. In this situation we have no idea what factors determine which change, or combination of changes, will occur.

Black-headed Heron *Ardea melanocephala* greeting display at nest. (*Photo: J. Taylor*).

The types of change that have occurred in displays over the course of evolution are well known as a result of 'comparative ethology'. Comparison of the behaviour of many species from a family or smaller taxonomic group allows us to infer the origin of many of the components of their displays, and the way in which they have evolved. For example, in the Estrildid finches, males of many species carry a grass-stem in their bill during courtship. This originated as an element of nest-building behaviour, and in the Red-browed Finch *Aegintha temporalis* the stem is carried throughout courtship and copulation, and may subsequently be built into the nest. In other species, which drop it before copulation, it becomes symbolic rather than functional behaviour, and in the Crimson Finch *Neochmia phaeton* it is entirely symbolic in nature, since the type of stem chosen for the courtship dance is different from the material chosen for nest building. Among the other groups which have received particularly intensive comparative study are the gulls, gannets and boobies, weavers, ducks, finches and buntings.

Comparative work has shown that displays arise from a variety of sources: intention movements of locomotion, attack or escape and nest building; displacement activities such as preening or feeding; and autonomic responses such as feather raising. Ritualization has produced changes in the speed of performance of motor patterns, the omission or differential exaggeration of components or other changes in their detailed co-ordination, and the development of rhythmic repetition of elements. Displays may also evolve a 'typical intensity' rather than vary in intensity with the underlying motivation. Associated with these changes may be the development of morphological structures which emphasize the displays. Since the changes are all of the sort which make the display conspicuous to the human observer, it seems likely that they increase its conspicuousness to the reactor, but there is little direct information on this point. Hailman's (1977) demonstration, that the winter plumage colours of bay and sea ducks (Aythyinae) fit the particular requirements for signals visible against the background of the water surface, shows what can be done for the static colour-badges which enhance displays, but there is no equivalent work on the properties required for conspicuousness in the actions themselves.

Often, ritualization increases the appearance of formality in an action (leading ultimately to such elaborate behaviour as the courtship dance of the Great Crested Grebe *Podiceps cristatus*). In some cases (for example, the 'strut display' of the Sage Grouse *Centrocercus urophasianus*) the display has become highly stereotyped, but not all displays are as stereotyped as was once believed. Detailed film analysis of a few displays has revealed unsuspected variation in the presence or intensity of elements, so that earlier descriptions of these as unitary displays involved oversimplification: this fine variation was related to the stimulus situation and the motivation of the displaying animal. While the displays in question came from the lower vertebrates, analogous examples in birds may include the 'song spread' display of the Carib Grackle *Quiscalus lugubris* (in which independent variation of beak and wing elevation is related to the sex of the partner), and also the 'upright facing away' display of the Laughing Gull *Larus atricilla* (in which two forms of the display, differing in whether the brown hood is hidden from the partner, are used differentially in sexual and aggressive contexts). Use of film and videotape should make possible a more thorough analysis of ritualized displays than was possible with the eye alone, but the underlying problem is one of pattern-recognition, and cannot be solved by simple measurement. However, it is clear that the appearance of formality in many ritualized displays need not be synonymous with their stereotypy.

A more dramatic change which has sometimes occurred as a result of ritualization is the transfer of signal function from one structure to another. The Greater Bowerbird *Chlamydera nuchalis* presents a conspicuous patch on the back of its head to the female as it manipulates the objects in its bower, and the objects themselves play little part in its display. But in the Fawn-breasted Bowerbird *C. cerviniventris*, the head-patch has been lost (although the movements for its presentation remain) and presentation to the female of the objects in the bower plays a much more important role in the display. With the transfer of display function to the bower, this species has been able to respond to predation pressure by losing the conspicuous male plumage, so that male and female are alike.

This example illustrates the point that even when used for communication within a species, ritualization must involve response to several selection pressures: predation pressure will limit the evolution of conspicuous displays and unwieldy ornaments; selection for interspecific divergence may occur where closely-related species occupy the same habitat and, within the species, there may be selection for contrast between two displays (for example, aggressive and appeasement displays are often antitheses of one another). The habitat will influence the types of action available as a starting point for ritualization (for example, the importance of bathing and cleaning movements in duck displays can be understood in the context of their aquatic display), and constraints arising from existing displays will also influence the direction of future evolution. For example, the symbolic carriage of nest material in estrildid courtship displays is a modification of earlier displays in which the material was functional.

Blue-footed Booby *Sula nebouxii* greeting display. (*Photo: F. Pölking*).

It has been argued that the further evolution of a display is also constrained by its underlying motivation: for example, that selection will act by changing the strength of aggressive or fearful tendencies underlying a threat or courtship display rather than modify the display as a unit. (This interpretation is based on the 'conflict hypothesis' of display; see AMBIVALENCE.) But we know much less about the evolutionary changes in the motivation of displays than about changes in their form, and the possibility that phylogeny constrains displays in this way should not lead to the neglect of current selective forces which might be responsible for the constraints. The conflict hypothesis makes sense of the phylogeny of many displays, but it is not yet certain that, in its present form, it provides the best interpretation of their causation; and the possibility that during the course of evolution the elements of displays have become divorced from their original motivation (the process of 'emancipation') must also be considered. There is little direct evidence on these points, and statements about the motivational changes underlying ritualization must still be considered tentative. P.G.C.

Barlow, G.W. 1977. Modal action patterns. *In* Sebeok, T.A. (ed.). How Animals Communicate. Bloomington.

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Dawkins, R. & Krebs, J.R. 1978. Animal signals: information or manipulation? *In* Krebs, J.R. & Davies, N.B. (eds.). Behavioural Ecology. Oxford.

Hailman, J.P. 1977. Optical Signals. Bloomington.

Huxley, J.S. *et al.* 1966. A discussion on ritualisation of behaviour in animals and man. Phil. Trans. Roy. Soc. Lond., B, 251: 249–524.

ROA: former Maori name for a bird that may have been *Apteryx haasti*,

Black-headed Gulls *Larus ridibundus* greeting display. (*Photo: H. Schouten*).

as some authorities have concluded, or possibly a late surviving species of Dinornithiformes (see MOA).

ROADRUNNER: substantive name of *Geococcyx* spp. (see CUCKOO).

ROATELO: in the plural ('roatelos'), alternative general term for the Mesitornithidae (see MESITE).

ROBIN: commonest name in Britain today for *Erithacus rubecula*, the more formal alternative 'Red-breast' having become an almost pedantic usage. From this original source, the name has been transplanted to other parts of the English-speaking world and attached to local species actually or supposedly resembling the prototype, in being red-breasted or in other ways. Thus, in North America it is applied to the familiar *Turdus migratorius*, a larger but also red-breasted bird; and the Indian Robin *Saxicoloides fulicata* is a chat with chestnut underparts. It has also been used by ornithologists in fabricating English names for foreign species of Turdinae, either as a simple substantive name or in compounds such as 'magpie-robin', 'scrub-robin', 'bush-robin', and 'robin-chat' (see under THRUSH; also CHAT; SCRUB-ROBIN).

Outside the Turdinae, 'robin' is the substantive name used in the Australasian Region for various Muscicapinae, some of them with red breasts, e.g. *Petroica* spp. in Australia and New Zealand; and in Australia for certain Pachycephalinae, e.g. *Eopsaltria* spp. (see THICKHEAD). And it is an avicultural name ('Pekin Robin') for *Leiothrix lutea* (see BABBLER).

Further, 'robin' is misapplied in some quite unrelated groups, e.g. as a popular misnomer for the Jamaican Tody *Todus todus*, a small, dumpy, red-breasted bird (see TODY).

See photos BILL ABNORMALITIES; COMFORT BEHAVIOUR; VOCALIZATION.

ROC: see FABULOUS BIRDS.

ROCKET NET: see TRAPPING.

ROCKFOWL: substantive name of *Picathartes* spp. (see BABBLER).

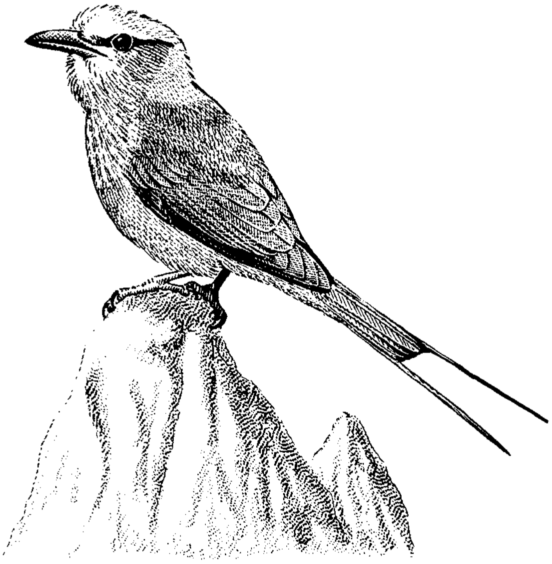
ROCKJUMPER: substantive name of *Sphenoeacus pycnopygius*, a warbler confined to arid rocky areas in south-western Africa (for family see WARBLER (1)).

RODENT RUN: see DISTRACTION BEHAVIOUR.

RODING: the territorial or patrolling flight of male birds (from the Anglo-Saxon 'rode', meaning to raid). The term is usually applied only to the characteristic twilight display flights performed by male Eurasian Woodcock *Scolopax rusticola* during the period February–July (in Britain). When roding, woodcock fly above the woodland canopy with a distinctive, deliberate wing action, uttering every few seconds a series of croaks followed immediately by a far-carrying squeak. Research with radio-tagged birds suggests that roding woodcock are not defending exclusive territories but are searching for females with which to mate. Males are successively polygynous and differ significantly in their success at locating and mating with females, but unlike other waders with polygynous mating behaviour, they do not defend either an exclusive or specific area to which females are attracted and in which mating and/or nesting takes place. Instead the male displays solitarily over an extensive area (sometimes more than 100 ha in extent) until called down by a receptive female. Then, probably to ensure that he alone copulates with her, he remains with the female constantly, close to the nest site, until the eggs are laid, before resuming display flights. G.J.M.H.

ROLLER: substantive name of the 11 species of the family Coraciidae (Coraciiformes, suborder Coracii); see also GROUND-ROLLER and CUCKOO-ROLLER. Rollers comprise 2 genera of Old World, essentially paleotropical, insectivores; species of *Coracias* are sit-and-wait predators searching from tree perches for large arthropods on the ground, and species of *Eurystomus* hawk insects in flight and are markedly crepuscular.

Characteristics. The head is large, the neck short, the legs rather short and syndactylous feet small but robust. In *Coracias* the beak is crow-like—strong, arched and hook-tipped, and in *Eurystomus* (the broad-billed rollers) it is short and wide. Flight is strong and the wings quite large. The tail is narrow and of medium length, and several species have elongated outer rectrices. Rollers are handsome birds with strong but muted colours, mainly dark blue and azure, with olive, chestnut and pink in *Coracias* and lilac and cinnamon in *Eurystomus*. The sexes are alike and juveniles resemble adults.


Lilac-breasted Roller *Coracias caudata*. (*N.A.*).

Rollers get their name from their impressive courtship flight, a fast, shallow dive from considerable elevation with a rolling or fast rocking motion, accompanied by loud raucous calls. Whether they actually somersault as has been claimed needs confirmation. Most are aggressive and readily fly at people and raptors, using the same rolling action. All are arboreal, and when *Coracias* species land on the ground in pursuit of their prey they may use a clumsy hop.

Systematics and distribution. Relationships among the coraciiform families remain controversial. There is good evidence that rollers have close affinity with the ground-roller (Brachypteraciidae) and less close affinity with the cuckoo-roller (Leptosomatidae) (both of Madagascar). Studies of anatomy, behaviour, ectoparasites, pterylosis and egg proteins suggest some affinity of rollers with bee-eaters and, decreasingly, with motmots, kingfishers and todies, hoopoes and hornbills.

Within the Coraciidae relationships are easier to discern (Fry 1978). *Coracias* comprises 8 species and systematically they fall into two groups and an isolated species. The first group are 3 large (length 33–38 cm, excluding long tail-streamers), olive-backed, full-tailed rollers: *C. benghalensis* of southern Asia, and *C. naevia* of African savannas and *C. temminckii* of Sulawesi, both of which seem to be derivatives of *C. benghalensis*. The second group are 4 lightly-built species (length range *c.* 28–30 cm) with brown backs and narrow tails: *C. garrulus* of the western Palearctic, its allospecies *C. abyssinica* of the northern tropical woodlands of Africa, the east and southern African *C. caudata* whose range borders with *C. abyssinica* along the Rift Valley, and *C. spatulata*, which is restricted to mopane and *Brachystegia* woodlands of south–central Africa and is broadly sympatric with *C. caudata*. All 3 African birds in this group have long outer tail feathers, racqueted in *C. spatulata*. The isolated roller is *C. cyanogaster*, a small azure and dark blue bird of the *Isoberlinia* woodlands north of the African equatorial rainforests, with whitish hood, black back, and short tail streamers. In the genus *Eurystomus* (length 27–30 cm) there are 3 species, and they resemble *Coracias* rollers in their raucous voices, rolling display flights, aggressiveness, and also somewhat in plumage. They hawk insects from elevated perches and have a strong, buoyant flight on rather long wings—feeding at dusk they resemble hawks or nightjars. Beaks are short, strong and very wide, and the tail is narrow and short, without streamers. *E. glaucurus* is widespread in sub-Saharan Africa and in Madagascar, a migratory woodland bird having rich brown plumage, violaceous below, with purple primaries and light blue in the tail. *E. gularis* of the African rainforest zone is very similar, and both have bright yellow beaks. *E. orientalis* is larger, dusky blue with scarlet beak and legs, and is distributed in 11 races from New South Wales to Nepal and through China north to 50°N on the lower Amur R.; a white patch showing conspicuously in flight gives it the name Dollar-bird.

Distribution, habitat and movements. The habitat is varied tropical woodlands and all types of open country from thornveld in South Africa to parks, cultivated fields and suburban gardens in the tropics, grassy hillsides with scattered trees, plains, scrubland and forests in Europe, Asia and Australia. Rollers breed from about 60°N in the west Palearctic and 50°N in the east, south to about 30°S in Africa and 35°S in Australia, being absent only from desert regions and from central and north-west Europe. Most species are migratory, and move by day. From Europe and south-west Asia *C. garrulus* migrates to winter, exclusively, in open country from tropical Africa to the Cape. Madagascan *E. glaucurus* winter in south-east Africa. High-latitude populations of *E. orientalis* migrate towards the Equator and the species winters in India, south-east Asia and Indonesia between the Tropic of Cancer and Java and New Guinea.

Food. *Coracias:* large arthropods taken on the ground—mainly beetles (93%) in Asia, and grasshoppers and crickets (27%) and ants and termites (40%) in Africa; also mantises, bugs, cockroaches, centipedes and scorpions. Rarely slugs, frogs, small lizards and birds; also grapes, figs and other small fruits. *Eurystomus:* insects taken in flight, mainly beetles in Asia and ants and termites (80–95%) in Africa. Occasionally they take prey from trees or the ground—molluscs, centipedes, spiders, small frogs and fruits (Thiollay 1971).

Behaviour and voice. In monogamous pairs for most of year and family parties after breeding; but *C. naevia* is reportedly more gregarious. Some rollers form small loose flocks during migration; *Eurystomus* also congregates to feed at a hatch of flying termites. Otherwise, rollers are strongly territorial when breeding, and probably also on their wintering grounds. The voice is a harsh, guttural *aaa–aaaaa*, repeated in a frenzied staccato during courtship flights. Birds call periodically several times an hour, perched or flying, often in response to each other. Intense calls are accompanied by a lively bowing.

Breeding. Rollers nest in holes in trees and bamboos, in hollow stumps, old walls, cliffs and mud-banks; feathers or a few chips of rotting wood may be added as nest-lining. Eggs are glossy white, subspherical; 4 is the commonest clutch at both low and high latitudes. Both sexes incubate and feed the young. The incubation period is 17–19 days (data for 3 species only); the nestling period is not known but is not less than 20 days.

C.H.F.

Cracraft, J. 1971. The relationships and evolution of the rollers: families Coraciidae, Brachypteraciidae, and Leptosomatidae. Auk 88: 723–752.

Fry, C.H. (In press). Rollers. *In* Fry, C.H., Keith, S.K. & Urban, E.K. (eds). The Birds of Africa, vol. III. London.

Thiollay, J.-M. 1971. Les guêpiers et rolliers d'une zone de contact savane–forêt en Côte d'Ivoire. L'Oiseau et R.F.O., 41: 148–162.

ROLLER CANARY: see CAGE BIRD.

ROOK: *Corvus frugilegus* (see CROW (1)).

ROOKERY: primarily a nesting colony of Rooks *Corvus frugilegus*; but applied to colonies of some other birds, including penguins (Spheniscidae).

ROOKOOING: the production of a bubbling sound by the male Black Grouse *Tetrao tetrix* at the LEK.

ROOSTING: derived from an old German word meaning 'a sleeping house for fowls', the term has often been used synonymously with SLEEPING, but while roosting birds usually sleep, at other times they simply rest. Roosting also includes the act of going to or taking up a roost, i.e. travelling, gathering and establishment of site.

Roosting has also been confused with 'loafing' (Amlaner and Ball 1983), a term stemming from a German word for tramp or vagabond, and meaning 'to spend time idly'. In contrast to loafing, the main purpose of roosting is for sleep. Loafing also includes activities involved in COMFORT BEHAVIOUR and digestion. Although loafing flocks almost inevitably include sleeping birds, they do not always form for sleeping, and hence are not always roosting flocks. Birds may loaf at any time of day or night, singly or communally, between periods of any sort of activity, notably feeding. As in roosting, birds may use habitual loafing sites, and resort to them from some distance. Some categories of birds, e.g. immatures, non-breeders and off-duty breeders, may loaf at times when other birds are occupied with parental duties (see CLUB). The off-duty bird may also loaf at the nest-site, while its mate may loaf whilst sitting on the nest itself. In general, the use of the term loafing should be encouraged wherever quiescent behaviour does not have a strictly roosting function (N.J. Ball).

Several recent papers discuss the functions of communal roosts, and observations on particular species are scattered throughout the literature; for reviews see Ydenberg and Priss (1981), Amlaner and Ball (1983). Roosting habits of Western Palearctic species are summarized in Cramp and Simmons (1977 *et seq.*). Most recent papers dealing especially with roosting refer to timing, thermal benefits and shelter, censusing, and pest control.

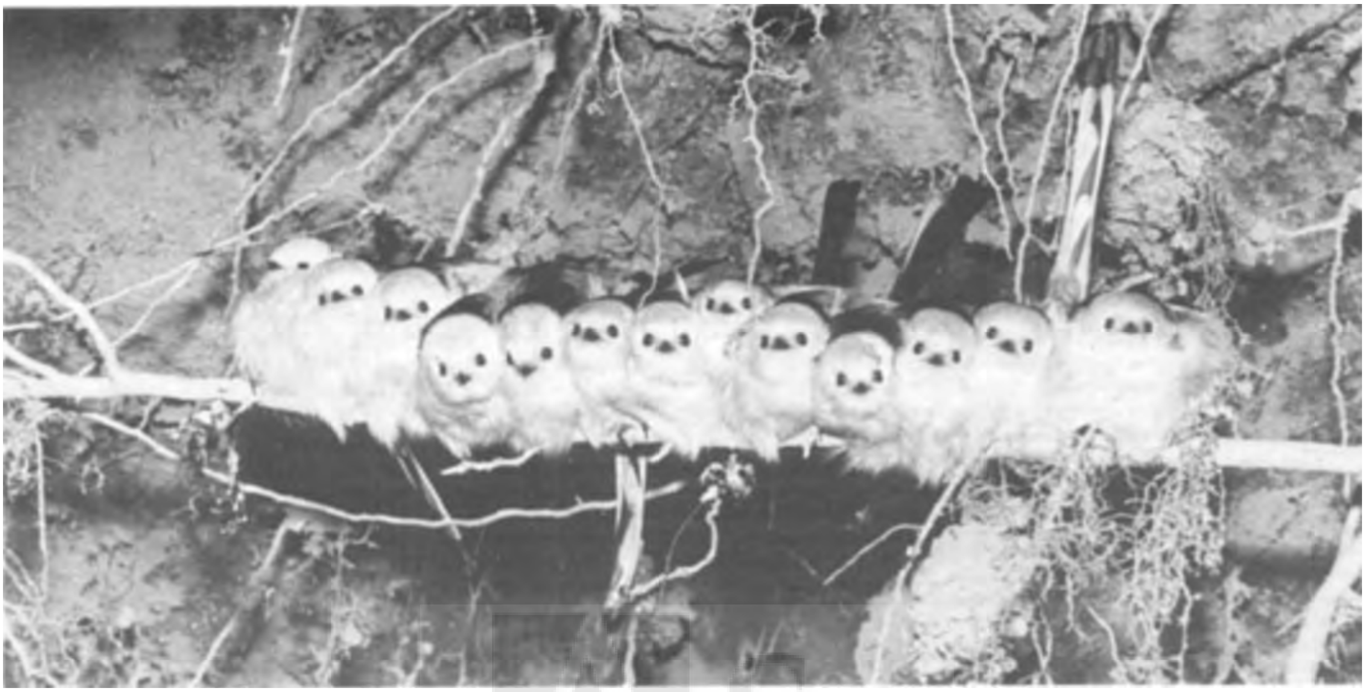
Times of roosting. The times of day when birds roost are adapted to their other activities, especially feeding. Unless sick, birds generally roost only when there is nothing more important to do, such as feeding or defending a territory, or when temporary (weather) conditions preclude their normal activity. Most species accordingly roost at night, although night feeding species roost during the day. Waders (Charadrii) and wildfowl feeding in the inter-tidal zones may, depending on the state of the tide, roost either during the day or at night, as they feed largely by touch and can find food in the dark. Other species are known to feed nocturnally, for example, swans (on submerged vegetation), some diving ducks (e.g. Pochard *Aythya ferina*) and Sooty Terns *Sterna fuscata*. Tits (*Parus* spp.), have been observed feeding by the light of street lamps.

Birds roost for a shorter time in summer than in winter, but even in the continuous daylight of high latitude summers they spend periods asleep, some species sleeping sporadically throughout the 24 hours, but others at a particular time, usually around midnight (see SLEEP).

Precise timing. As times of sunrise and sunset change throughout the year, so do the times at which birds roost. Some authors claim a characteristic light intensity for awakening ('Weckhelligkeit') for each species but this term does not seem very useful for, although there may be thresholds below which activity normally ceases, prolonged studies show that these threshold intensities change gradually with the season. Moreover, experiments in which birds were kept under constant conditions showed that they retain a sleeping rhythm similar to their natural one, at least for a few days. Seasonal changes in timing of roosting are most obvious at high latitudes, e.g. northern Scandinavia, where in the middle of winter passerines awaken and retire at far lower light intensities than in summer. This is presumably due to the amount of time they require to find sufficient food relative to day length, as food reserves of many passerines may only just exceed their requirements for a single night in extreme conditions (extreme conditions may also pertain during long tropical nights). For example, in temperate latitudes Murton *et al* (1963) have shown that Woodpigeons *Columba palumbus* need to spend 95% of available winter daylight feeding.

Superimposed on these general seasonal changes are day to day variations, due in part to weather, particularly if this affects light intensity. Several brief studies have referred to this aspect, but none of them adequately. The researchers have tended to concentrate on the effects of minor factors, such as temperature, even though the influence of major factors, such as light intensity, are as yet little understood. Moreover, they often overlook the fact that cloudy days are, on average, both darker and warmer than clear days. Unpublished evidence suggests that birds use both their knowledge of the time of day at which it generally 'gets dark' (from their 'internal clock', see RHYTHMS AND TIME MEASUREMENT) and the prevailing light intensity to predict when it will 'get dark' on a particular day, and therefore by what time they need to be at the roost. It is then reasonable to suppose that other factors would determine their response to this prediction, so that individuals which had, early on, found sufficient food would be likely to play safe, and arrive earlier at their roost than those that were still hungry. Similarly, it is known that birds flying long distances to a roost will leave their feeding ground earlier on darker days and on days when they must fly into the wind.

Dawn chorus. A number of papers refer to dawn awakening, particularly the relative times at which different species start to sing in the (spring) dawn chorus. The times, and light intensities, for these onsets of song also vary seasonally and daily. In a series of experiments Kacelnik (1979) has investigated the reasons for the dawn chorus and its timing in the Great Tit *Parus major*. He considers the dawn chorus to be a special case of a 'trade-off' between the competing demands of feeding and territorial defence. Thus the dawn chorus of Great Tits occurs at a time of



Long-tailed Tits *Aegithalos caudatus* in winter roost in December, southern Primorskiy, USSR. (*Photo: Y. Shibnev*).

day when low light intensity and low temperature (affecting prey mobility) reduce feeding efficiency, while territorial intrusions are at their peak and vocal defence of territory, by song, is more effective due to enhanced sound transmission (poor visibility militates against visual display). Kacelnik concludes that no single factor hypothesis can explain the timing of the dawn chorus.

Roost site. Birds have two basic requirements of a roost site, namely, protection from predators and shelter from the elements. Holes are presumably both safe and warm. City centres are warmer than surrounding land (1.4°C warmer, and drier, in London), while street lights may permit birds to find roosting perches later (if they can see adequately by street lighting), or even serve as warm roost sites themselves, while the better lighting should aid detection of predators. Wildfowl and many seabirds tend to roost on islands, on the water or in open sites where predators can approach them less readily. Many ground-feeding birds roost either in the open or perch on low branches, out of the reach of foxes *Vulpes* spp. and other predators. Many species roost as solitary individuals. The nest site may be an important roost both prior to, as well as during, nesting (incubating birds are often asleep). In communal roosts the alarm calls of the more alert individuals may often function to warn their companions of danger, as with quails *Coturnix* spp. which roost in grouped circles, each individual facing outwards. The fine structure of roosts, for group or communal roosting species, may be important, as birds at the centre of a line or group are presumably less vulnerable to predation. Swifts *Apus apus* may pass the night on the wing, although they also use more conventional sites, such as the nest.

Shelter is needed to help the bird maintain its body temperature, as it must burn food reserves during the night which it cannot replenish until morning. Small birds, with a large surface to volume ratio, lose heat more rapidly, and particularly in cold climates. Those that roost in holes have the advantage that the heat they lose warms the air around them, but even roosting under cover, such as in a conifer wood, can appreciably reduce heat loss by radiation. Several species of grouse tunnel out roosts under snow. More important, however, is shelter from rain and wind, which reduce the insulative benefits of fluffing up the feathers and thereby lead to more rapid chilling. Swingland (1977) has shown that communally roosting Rooks *Corvus frugilegus* apparently compete for sheltered sites: the more dominant older birds force younger individuals, which also have lower food reserves, from the higher, more sheltered sites to lower, more exposed ones; those lower sites may also incur greater risk from predators. Yom-Tov (1979) has shown that birds low down in a communal roost may have the water-repellent properties of their feathers seriously impaired by droppings from those roosting above them. Small waders may roost among larger species, using them as 'windbreaks'. In extreme cold weather some species may huddle closely together, e.g. Long-tailed Tits *Aegithalos caudatus*, treecreepers, wrens, swifts, Australian wood-swallows (Artamidae), Emperor Penguins *Aptenodytes forsteri*, Bobwhite Quails *Colinus virginianus* and many others. Hummingbirds may also roost in enclosed spaces, but have a remarkable ability, rare among birds, of becoming nocturnally torpid, their body temperature dropping to as low as 4°C. Reducing the temperature difference between their body and the environment also reduces their energy loss, thus helping them to survive long cool nights and live in areas they could not otherwise inhabit (see TORPIDITY).

Communal roosting. Many territorial species roost within their territory boundary during the summer, and some during winter too. Outside the breeding season birds that feed in flocks generally roost communally, e.g. Rooks, Starlings *Sturnus vulgaris*, finches, hirundines (Hirundinidae), pigeons and many waders. Some relatively unsociable feeders may also congregate to roost, e.g. the Pied or White Wagtail *Motacilla alba*. Terns form communal roosts just prior to the breeding season, where courtship and copulation may take place. Large mixed roosts of several species are not uncommon, e.g. Starlings, Common Grackles *Quiscalus quiscula*, Brown-headed Cowbirds *Molothrus ater* and Red-winged Blackbirds *Agelaius phoeniceus* in North America. Waders for example, roosting communally on a tide-island in an estuary, may simply resort to the safest site available from their dispersed feeding areas. In other instances, however, the reasons for communal roosting are much less obvious. Starlings, for example, often roost near their feeding sites in autumn, but desert these in winter in favour of larger roosts that may be 50 km or more away. These sites may be used year after year. It is difficult to assess the numbers of birds using them, but some Starling roosts contain several hundreds of thousands, while the Quelea *Quelea quelea*, a serious pest of grain crops in large parts of Africa, collects at night into roosts of millions (see QUELEA CONTROL). Many species that roost communally perform spectacular aerobatic displays around the roost, and often have conspicuous staging posts ('pre-roost gatherings') where groups congregate before a mass entry into the roost. Such displays may act as visual markers, locating the present roost site for birds unfamiliar with it; this could be particularly useful if unpredictable disturbance, e.g. predators, should alter the precise location of a roost from one day to the next. Similarly, there are typical sequences of behaviour for dawn emergence, and the mass dawn exits of Starlings, at 3- or 4-minute intervals, even produce spectacular patterns of radially dispersing 'rings' on RADAR screens. The larger communal roosts may contain so many birds that vegetation is damaged, even destroyed, either by physical damage or by the toxic effects of accumulated droppings; in exceptional circumstances this may cause serious local problems to man, e.g. in city centres, or to forestry and agriculture.

It seems unlikely that predator avoidance is responsible for the enormous total numbers in the larger roosts, and there has been much speculation as to their likely function. An attractive hypothesis, proposed by Ward and Zahavi (1973), suggests that these roosts serve as 'INFORMATION CENTRES' as to where to find food locally. They point out that communal roosts are normally composed of species whose food is patchily distributed, locally super-abundant and ephemeral, so there is accordingly no advantage to be gained from trying to 'defend' such a food source, nor in 'keeping its location quiet'. Conversely, birds not knowing of such food sources would gain from following others to feeding sites. In these circumstances (patches of super-abundant, ephemeral food) all individuals could benefit from the pooled information. Cheating (trying to keep a patch quiet, but still knowing about those of others) would be difficult and, if the patches are ephemeral, risky. Accordingly, a system of mutual benefit might persist due to advantages accruing to individuals. (For Posture see SLEEP.) P.J.B.

See photo COMFORT BEHAVIOUR.

Starlings *Sturnus vulgaris* above mass roost. (*Photo: F. Pölking*).

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ROSEFINCH: substantive name of most species of *Carpodacus*, a Holarctic and mainly montane genus of finches (for family see FINCH).

ROSELLA: substantive name of the Australian *Platycercus* spp. (Psittacinae, Platycercini) (see PARROT).

ROSTRATULIDAE: see CHARADRIIFORMES; PAINTED SNIPE.

ROSTRUM: the bill or beak (see BILL); adjective, 'rostral'.

ROSY-BILL: *Netta peposaca* (see DUCK).

ROULROUL: *Rollulus roulroul* (see under PHEASANT).

r-SELECTION: see K-SELECTION.

RUBY: *Clytolaema rubricauda* (for family see HUMMINGBIRD).

RUBY-CHEEK: name, alternatively 'Ruby-cheeked Sunbird', of *Anthreptes singalensis* (see SUNBIRD).

RUBYTHROAT: substantive name of some *Luscinia* spp. (for subfamily see THRUSH).

RUFF: name of *Philomachus pugnax* as a species; also a term particularly for the male, the female then being termed 'reeve' (see SANDPIPER). See photo LEK.

RUKH: see FABULOUS BIRDS.

RULES: statements formulating what appear to be regularities in natural phenomena, e.g. in the correlation of morphological variation with geographical, climatic, or other factors—e.g. ALLEN'S RULE; BERGMANN'S RULE; GLOGER'S RULE.

RUMP: see TOPOGRAPHY.

RUNNING: see LOCOMOTION, TERRESTRIAL; LEG.

RUSH: a fall of birds on migration (see FALL).

RUSHBIRD: substantive name of *Phleocryptes melanops*, a South American furnariid (see OVENBIRD (1)).

RYNCHOPIDAE: see under CHARADRIIFORMES; SKIMMER.

S

SABREWING: substantive name of *Campylopterus* (including '*Pampa*') spp. (for family see HUMMINGBIRD).

SACRUM (adj. **SACRAL**): the part of the vertebral column between the lumbar and caudal portions (see SKELETON, POST-CRANIAL).

SADDLE: term used where the colour of the upper surface of the wings continues across the mantle without a break. See TOPOGRAPHY.

SADDLEBACK: *Creadion* ('*Philesturnus*') *carunculatus* (see WATTLEBIRD (2)).

SADDLEBILL: sometimes used alone as the name of the Saddle-billed Stork *Ephippiorhynchus senegalensis* (see STORK).

SAGITTAL: in the median longitudinal plane of the body, e.g. a section from head to tail in the mid-line; the 'sagittal suture' is the junction of the parietal bones of the skull.

SAGITTARII; SAGITTARIIDAE: see under ACCIPITRIFORMES; SECRETARY-BIRD.

SAHEL ZONE: the belt of grassland with trees (savanna) and thorny scrub which lies immediately south of the Sahara, and which is subject to drought.

SAKABULA: *Euplectes progne* (see WEAVER).

SAKER: *Falco cherrug* (see FALCON).

SALIVARY GLANDS: see ALIMENTARY SYSTEM; TONGUE.

SALPORNITHIDAE: family of PASSERIFORMES, suborder Oscines; CREEPER, SPOTTED.

SALTATOR: generic name used as substantive name of *Saltator* spp. (see CARDINAL-GROSBEAK).

SALT GLAND: alternatively 'lateral nasal gland' (see EXCRETION, EXTRARENAL; NARIS).

SALTING or SALTMARSH: an area of intertidal mud which has been colonized by salt-adapted plants.

SAMPLING: see BIOSTATISTICS.

SANCTUARY: see CONSERVATION.

SANDERLING: *Calidris* (formerly *Crocethia*) *alba* (see SANDPIPER). See photo LOCOMOTION, TERRESTRIAL.

SANDGROUSE: substantive name of the species of Pteroclididae (Pteroclidiformes); in the plural (unchanged), general term for the family. This mainly Afro-Asian group has affinities with the waders (Charadriiformes, suborder Charadrii) and the pigeons (Columbidae), but is best regarded as having separate ordinal rank; resemblance to true grouse (Tetraoninae) is purely superficial.

Characteristics. Sandgrouse are terrestrial birds, much like pigeons in size and shape. They vary in length from 25–48 cm, including the elongated tail feathers in the larger species; weights range from 170 g to 650 g; most are between 230 and 300 g. They are coloured in soft shades of grey, red, yellow, brown and buff, often marked with white and black. The males of most species have breast bands and all show sexual differences in coloration. Species inhabiting semi-desert tend to be paler than those of savanna habitats. The plumage is close and thick with a dense underdown, even on the apteria (see APTERIUM; PLUMAGE), which insulates the birds against extremes of heat and cold. The central tail feathers of 6 species are elongated and pointed. The wing is aquintocubital (lacks the fifth secondary remex: see PLUMAGE; WING) and has 11 primaries which are long and adapted to strong sustained flights undertaken daily to water.

Despite their short legs, sandgrouse walk and run well. Their toes are also short, sometimes partially webbed. The family includes 2 genera, *Syrrhaptes* (tarsus and toes completely feathered, hind toe absent) and *Pterocles* (tarsus feathered in front only, toes naked, hind toe rudimentary and raised above ground level). Other generic divisions based on plumage characters or drinking times are generally considered unacceptable except perhaps as subgenera which from time to time have included *Eremialector*, *Namapterocles*, *Parapterocles*, *Macleanornis*, *Nyctiperdix*, *Dilophilus* and *Calopterocles*.

Habitat. Most sandgrouse inhabit arid to semi-arid regions, including the major deserts of Africa and Asia. They prefer areas covered with stones or low shrubby growth. A few species live in rather dry savanna. The Tibetan Sandgrouse *Syrrhaptes tibetanus* is montane.

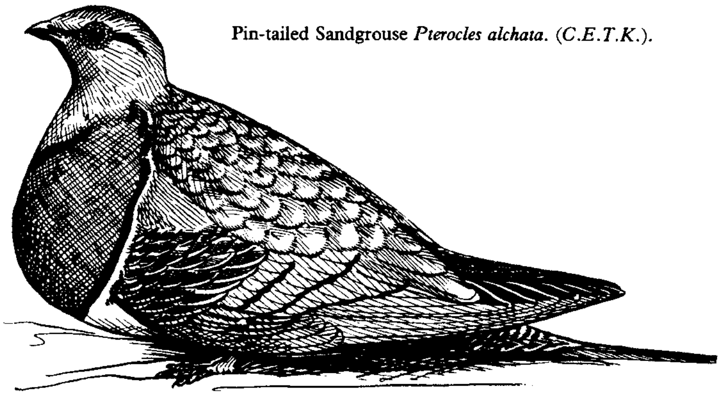
Distribution. The 14 species of the genus *Pterocles* occur in Africa, southern Europe and southern Asia, including the Indian subcontinent. *P. personatus* is confined to Madagascar. The 2 species of *Syrrhaptes* inhabit the steppes and mountains of central Asia. The main centres of sandgrouse distribution are the Sahara, the Kalahari and the deserts of the Middle East.

Movements. Most sandgrouse are resident or locally nomadic, but the most southerly populations of the Namaqua Sandgrouse *Pterocles namaqua*, the Zambian populations of the Yellow-throated Sandgrouse *P. gutturalis* and the Indian populations of the Black-bellied Sandgrouse *P. orientalis* are truly migratory. Pallas's Sandgrouse *Syrrhaptes paradoxus* of the central Asian steppes has undergone eruptive 'migrations' in certain years as far west as Britain and nearly as far east as Peking (see IRRUPTION). British immigrants remained and bred, although they are unlikely ever to have become established.

Food. All sandgrouse feed mainly on small hard seeds picked up from the ground. They may sometimes take small bulbs, green leaves, shoots, berries and even insects (termites and ants) especially during the breeding season. Grit is eaten for grinding food in the gizzard. The largely dry food necessitates daily drinking, particularly in hot weather. Drinking times are regular and species-specific (either in the morning or at dusk). Ten species are morning drinkers, 4 drink at dusk, and 2 are said to drink both morning and evening, but this needs confirmation. A few individuals of both kinds of sandgrouse may drink twice a day—probably mainly birds that have been incubating in the hot sun during the day, since most evening drinkers of morning-drinking species appear to be females.

Sandgrouse drink by taking a draught of water into the mouth by sucking once or twice and then raising the head to swallow (see DRINKING); this process is repeated up to 10 times but takes just a few seconds. When the crop is full the bird flies directly away from the water unless it is a member of a mated pair whose mate is still drinking: then it waits until the two can fly away together.

Behaviour. Although sandgrouse pair off monogamously when breeding, they are all highly gregarious, especially when gathering to drink.



Pin-tailed Sandgrouse *Pterocles alchata*. (*C.E.T.K.*).

The birds call in flight as they travel to the waterholes, thereby attracting others of the same species (and sometimes other species) along the way, until drinking flocks may number thousands of birds. Sandgrouse may fly up to 80 km to water each day (a round trip of 160 km) at a cruising speed of about 70 km/h. Depending on the species, the birds may land right at the water's edge (or even in the water), drink quickly and depart at once, or they may assemble some distance from the water and then fly or run down to it once the coast is clear. Both these methods reduce the possibility of attack by predators.

Voice. Sandgrouse calls are characteristic whistles or clucks, usually in phrases of two, three or more syllables. These calls are most often heard in flight, but other quieter calls are also heard from birds on the ground.

Breeding. Sandgrouse pair off during the breeding season which is largely determined by rainfall and the resulting adequate food supply. The nest is a shallow scrape on the ground, usually out in the open, but sometimes against a stone, shrub or grass tuft. The scrape is sparsely lined with small stones or bits of dry vegetable matter gathered by the parents during incubation. The clutch is almost invariably 3 eggs, rounded at both ends, coloured dull pinkish or greenish and more or less heavily marked with grey, brown and olive. The female incubates by day and the male by night; both sexes have a brood patch.

The eggs hatch after 21–31 days. The downy chicks leave the nest as soon as the last to hatch is dry, following the parents to forage for seeds. They are not fed at all by either parent, but are shown food by the parents pecking at suitable items. They are provided with water by a unique mechanism. The male soaks his belly feathers during his daily drink and the chicks take the water from his wet plumage on his return. He adopts an upright 'watering posture' which exposes the wet belly and attracts the chicks from their hiding places under shrubs.

Female sandgrouse seldom soak their belly feathers, probably doing so only if the male has been killed by a predator, or perhaps when the brood has reached the age at which the male's water-carrying capacity needs to be augmented by the female. The belly feathers of both sexes are specially adapted to taking up water in a bed of microscopic filaments on the inside surface of the feathers against the body, where evaporation is reduced to a minimum while the birds are in flight. Nevertheless the distance over which enough water can be carried in this way is limited to about 30 km. Young sandgrouse are watered thus until after their first moult when they fly to water like the adults. Only *Syrrhaptes tibetanus* appears not to water its young from its belly feathers, but lets them drink at open water which is freely available in streams resulting from snow-melt in their high mountain habitat; this species also lacks the specialized feather structure.

When the chicks are very young, the parents fly to water separately so that the chicks are not left unattended; from the age of about 3 weeks, they are left alone as the parents fly together to drink. The young can fly at the age of 4–5 weeks.

BELLY-SOAKING behaviour and a similar, though less well developed microscopic feather structure occurs in the closely related waders (Charadriiformes), but waders that transport water in their belly feathers do so only for cooling eggs and chicks, not for providing drinking water.

See photo BELLY-SOAKING. G.L.M.

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SANDPIPER: a term often restricted to the members of 2 genera (*Tringa* and *Calidris*) of long-billed wading birds (waders = shorebirds) in the family Scolopacidae (Charadriiformes, sub-order Charadrii); more broadly used to include the whole of the family of sandpipers and snipe, many of which are referred to normally by other substantive names which encompass only single species or small groups of species (as outlined below). (For reference to related families see under CHARADRIIFORMES.)

Characteristics. Members of the Scolopacidae vary in length from 12–60 cm but frequently a large proportion of this is the slender, long and often decurved bill (recurved in a few species). The bill is flexible and can be opened at the tip only (see RHYNCHOKINESIS). It is often assumed that long bills have evolved for probing but this delicate mechanism is also well suited for collecting seeds and berries. Usually sandpipers have long legs, the tibia is partially bare and the toes are long; the hallux is short, and absent in one species (Sanderling *Calidris alba*). The wings are normally long and pointed, the tail short and the neck long. In summer plumage the upper-parts of most species are a mixture of rich browns and greys and, in some species chestnut reds, the underparts being often well spotted and streaked. In winter these markings are usually lost and the upper parts are also more uniform. It is generally assumed that the plumage is cryptic and this is certainly the case in summer in the nesting habitat. However, at communal roosts flocks of Knot *Calidris canutus* can be seen for several km from the air, and clearly the plumage draws particular attention to them at this time (Ward and Zahavi 1973). Other species of flocking waders have similar plumage characteristics, though perhaps do not stand out as much as Knot.

Habitat. In the breeding season sandpipers are birds of open habitats, moorland and tundra. In the non-breeding season they are mainly gregarious and to be found in coastal areas, particularly in the intertidal regions of estuaries.

Distribution. Most sandpipers inhabit the Northern Hemisphere during the breeding season and occur into the high Arctic; the majority breed at high latitudes and several species have a circumpolar distribution. Most are highly migratory and in winter many species occur well into the Southern Hemisphere. Generally speaking, the more northerly breeding populations undertake the longest migrations and the temperate breeders the shortest migrations; these latter often winter within the breeding range whilst the former perform transequatorial migrations.

Due to their extensive distribution, it is not surprising that several species show variation in both size (often clinal) and colour (more than one morph). These have probably evolved in some cases through isolation and it is possible that some previously recognized sub-species, e.g. Southern Dunlin *Calidris alpina schinzii*, British Redshank *Tringa totanus britannica*, are hybrids derived from previously separated breeding populations. Usually there is a large degree of overlap of populations in winter quarters but some, e.g. Knot, seem to be almost totally separated, Greenland/N. Canada and Siberian populations wintering in western Europe and N. Africa respectively.

Food. During winter, invertebrates form the major part of the diet, most food being collected from, or not far below, the surface of the intertidal zone, or from shallow water. Occasionally insects are taken on the wing, and form a high percentage of the diet during the breeding season; at this time berries are also important to some species at higher latitudes. In winter a large part of the food is taken at night.

Behaviour. During feeding and roosting sandpipers mainly form single species parties or flocks, but species often intermingle, particularly when leaving the estuary roosts. All species are strong flyers and those which flock often perform complex aerial movements, which, like their winter plumage, are clearly evolved to attract attention. These flights are very spectacular and the precision with which they are performed is remarkable, particularly in tightly packed flocks of Knot.

Many species are territorial during the breeding season but others, e.g. Redshank, lack specific territorial boundaries and are semi-colonial. The pair bond is usually monogamous and, at least in some species, for life. It is established in smaller sandpipers in the first or second year of life, and perhaps as late as the third year in some species. Female Redshanks have been recorded incubating a full clutch within 10 months of hatching. Polygamy has been suggested as occasional in some species, e.g. Greenshank *Tringa nebularia*, but it is difficult to be certain of this. There is often an elaborate courtship display, beginning with a song flight (often later used in distraction display) associated with pair formation; in some species at least there are ground chases and complex pre-copulatory ceremonies. Distraction displays vary from repetition of display flight (e.g. Oystercatcher *Haematopus ostralegus*, Redshank) to 'rodent-runs' (Purple Sandpiper *Calidris maritima*) and injury feigning (Reeve *Philomachus pugnax*).

There is a great variety of call notes, from raucous squeaks to extended songs. Some species, especially snipe, also produce non-vocal sounds (see MECHANICAL SOUNDS).

Breeding. The nest is usually on the ground, often concealed in herbage, though a few species use disused nests of arboreal birds e.g. Fieldfares *Turdus pilaris*. The scrape, often made during a 'scraping ceremony' by the male in the presence of the female, is lined usually after laying the first egg and more lining is added during incubation. Eggs usually number 4, but in some cases 2 or 3. Most species have pyriform eggs, with dark brown and black markings, on a paler ground; all are cryptically coloured. Incubation normally begins with the last egg and chicks hatch almost simultaneously. Both sexes usually share incubation, though one bird often takes the greater share. Downy young leave the nest within a day of hatching and may make extensive journeys (often 1–2 km) to suitable feeding areas. The chicks crouch when alarmed and may be carried over obstacles by parent birds. The parental role varies with species. In some populations of Sanderling (Arctic Canada but not Greenland) and in Temminck's Stint *Calidris temminckii*, the female lays 2 clutches and each bird of a pair incubates a clutch; in other species e.g. Pectoral Sandpiper *C. melanotus*, only the female incubates, while only male phalaropes incubate (see PHALAROPE). Normally both parents tend chicks for at least part of the fledging period but in Pectoral and Curlew Sandpipers *C. ferruginea* only the female remains; in these cases the bird leaving the brood migrates south first, which may relieve pressure on the food supply.

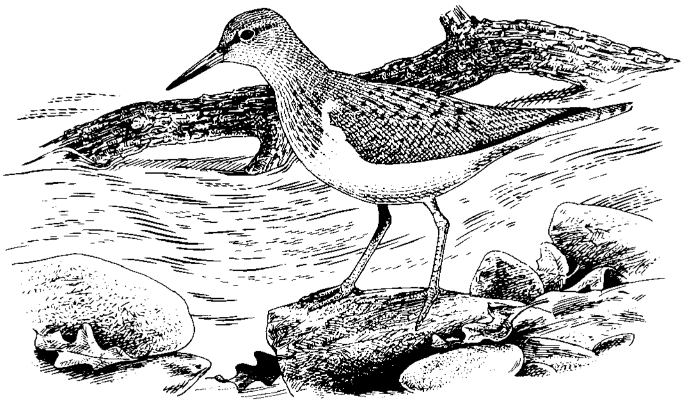
Taxonomic sub-divisions. The taxonomic sub-division of the group is based largely on skeletal structure and external morphology but has been improved by recent work on the colour pattern of downy young and studies of electrophoretic protein patterns. The sub-families recognized are: Tringinae (curlews, godwits and tringine sandpipers); Arenariinae (turnstones); Scolopacinae (woodcock); Capellinae (dowitchers and snipe); Calidriinae ('calidritine' sandpipers, the Eroliinae of some authors); Aphrizinae (Surfbird). Within the Scolopacidae there are 85 species in 27 genera.

Curlews, Godwits and Tringine Sandpipers. The curlews are the largest members of the family and are characterized by their long decurved bills. The Eskimo Curlew *Numenius borealis* is now extremely rare; however, its close relative the Little Curlew *N. minutus* is not in immediate danger in eastern Siberia where it nests in an interesting association with the Golden Eagle *Aquila chrysaetos* from which it apparently derives a degree of protection through other predators being excluded from the eagles' territories. The Eurasian Curlew *N. arquata* is the largest Palearctic species and is replaced in the Nearctic by the Long-billed Curlew *N. americanus*. The Whimbrel *N. phaeopus*, which has a circumpolar distribution, occupies a more northerly range and in North America is referred to as the 'Hudsonian Curlew'. The Slender-billed Curlew *N. tenuirostris* is now quite rare and restricted to a small area of Western Siberia. Curlews make extensive migrations, the Little Curlew, which nests in Siberia, reaching Australia.

Like the curlews, the godwits are large waders but they have long, slightly recurved bills. There are 4 species in a single genus *Limosa*, the Marbled and Hudsonian Godwits (*L. fedoa* and *L. haemastica*) being Nearctic forms whilst the Bar-tailed and Black-tailed Godwits (*L. lapponica* and *L. limosa*) are Palearctic breeders.

The Upland Sandpiper (Bartram's Sandpiper or Upland Plover) *Bartramia longicauda* is a North American species in a monotypic genus and is possibly more closely related to the curlews and godwits than to the tringine sandpipers. There are 9 species in the genus *Tringa*, the largest of which are the Greater Yellowlegs *T. melanoleuca* of North America and the Greenshank *T. nebularia* of Eurasia, both a little smaller than godwits. The Greenshank occupies a range in Eurasia intermediate between that of the more northerly Spotted Redshank *T. erythropus* and the more southerly Common Redshank *T. totanus*, though there is overlap of ranges in western Europe. In North America the Lesser Yellowlegs *T. flavipes* replaces the Redshank ecologically. Two species, the Solitary Sandpiper *T. solitaria* and the Green Sandpiper *T. ochropus*, nest in trees, in the abandoned nests of other birds, as may the Wood Sandpiper *T. glareola*.

Two species closely related to the genus *Tringa* are placed in the genus *Actitis*. These are the Common Sandpiper *A. hypoleucos* and its North American replacement the Spotted Sandpiper *A. macularia*; both occur in temperate latitudes. The Terek Sandpiper *Xenus cinereus* breeds from Finland to eastern Asia; the latter is the only area from which the Spotted Greenshank (Armstrong's Sandpiper) *Pseudototanus guttifer* has been recorded breeding. The Grey-rumped Sandpiper *Heteroscelus brevipes* and the Wandering Tattler *H. incanus* are thought by some authorities to be conspecific but their ranges overlap in Anadyrland (N.E. Siberia), and there are morphological differences of an order justifying their being regarded as specifically distinct.



Common Sandpiper *Actitis hypoleucos*. (*A.H.*).

The Willet *Catoptrophorus semipalmatus* is a large (for tringine sandpipers) species with no obvious relatives; it is an inhabitant of middle North American latitudes.

The rare Tuatamu Sandpiper (Peale's Sandpiper) *Aechmorhynchus parvirostris* is another species with no obvious present day close relatives, though 2 closely related species (one of them possibly conspecific) are now extinct, the White-winged Sandpiper *Prosobonia leucoptera* of Tahiti and the Sharpbilled Sandpiper *Aechmorhynchus cancellatus* known only from a single specimen. Like the Tuatamu Sandpiper both these latter species had a limited distribution in Polynesia.

Turnstones. From both electrophoretic studies and downy chick patterns it appears that turnstones *Arenaria* are a tringine off-shoot, rather than relatives of the plovers. There are 2 species, the Ruddy Turnstone *A. interpres*, which has a circumpolar breeding distribution mainly within the Arctic but south to the Baltic Sea, and the Black Turnstone *A. melanocephala* which is restricted to Alaska. Turnstones usually occur in small flocks on rocky shores where they often feed in the company of Purple Sandpipers. Flocks seldom exceed 100 birds and they feed mainly on invertebrates found under stones which they push over with their short, blunt bills. The bill is also used for excavation but never for true probing. Turnstones will also feed on carrion and eggs of their own and other species.

Turnstones are the most littoral of all waders and only rarely are they found far from the coast. On such occasions they remain on moss and lichen tundra in short vegetation and do not close their toes in walking as do some waders which are adapted to deeper vegetation.

Turnstones make extensive migrations and the Ruddy Turnstone can be found wintering in South America, South Africa, Australia and New Zealand.

Woodcock. Five species of woodcock are generally recognized, the European Woodcock *Scolopax rusticola*, 3 oriental species of the same genus, and the American Woodcock *Scolopax minor*, which is smaller than the European species. All have a relatively long, straight bill and the eyes are set well back on the head. The legs are relatively shorter than in most other waders, the neck is short, the body compact and the head relatively large, the external opening of the ear being below, instead of behind the orbit.

Woodcock are the only group of waders to frequent woodland; woods with damp floors on fertile mull soils with a high earthworm content are preferred. The spring display flight of the European Woodcock is known as RODING. It occurs at dusk and is an owl-like flight, much more frequently seen than the ground display of courtship which leads to coition. This display involves the male strutting round the female with drooping wings and fanned tail, but very little is known of the courtship of woodcock.

As in the snipe, normally only the female incubates, in contrast to most waders where the sexes share incubation. The eggs of woodcock tend to be more rounded than other wader species and paler in colour than most sandpipers'. The European Woodcock has been recorded on several occasions carrying the young between the legs, against the belly.

Snipe. Like woodcock, snipe have long, straight bills and relatively short legs. They often remain undisturbed until almost trodden on, even when feeding, and then flush in a characteristic zig-zag flight. They are birds of open marsh land throughout the year and seldom occur on the shore. Some species are solitary though others occur in small groups ('wisps'), but seldom in large flocks. Several species produce loud non-vocal sounds ('drumming' or 'bleating') with the outer tail feathers in flight and a similar habit has been recorded in the Little Curlew.

Snipe are birds of lower latitudes and generally do not perform extensive migrations. They are found in most temperate regions of the world; members of the genus *Gallinago* (*Capella*) of which there are 13 species occur also as visitors to southern Asia and Australia. The Common Snipe *G. gallinago* is a cosmopolitan species and is known as the Fantail Snipe in India. Like the Jack Snipe *Lymnocryptes minimus*, the Great Snipe *G. media* has a more restricted range in the Palearctic and is unique in being, apart from the Ruff *Philomachus pugnax*, the only wader with a lekking system (LEK) of courtship. Perhaps of particular interest in this group is the sub-antarctic Snipe *Coenocorypha aucklandica*, races of which occur in subsidiary islands around New Zealand; uniquely in the group, this species nests in burrows excavated by other birds; it appears to fly little and to be largely nocturnal.

Recent work has shown that dowitchers are probably more closely related to snipe than to godwits. The Asian Dowitcher *Limnodromus semipalmatus* is the only Old World species, nesting in Siberia. Most authorities now treat the American dowitchers as 2 species, the Long-billed Dowitcher *L. scolopaceus* and the Short-billed Dowitcher *L. griseus*. These nest in the Arctic and sub-arctic and perform long migrations, unlike most snipe.

Calidritine sandpipers. These are, perhaps, the true sandpipers and most are placed in the genus *Calidris*, which contains the smallest waders, the stints. The 23 species are birds of high latitudes with a circumpolar breeding distribution and because of this many perform extensive migrations; out of the breeding season they are birds of the shore and generally highly gregarious. They are known as 'peeps' in North America. Their twittering calls are not as loud as those of tringine sandpipers. The Knot *C. canutus* is the largest species, 25 cm in length, whereas the Least Sandpiper *C. minutilla* is only half this size. The most southerly breeder is the Dunlin which nests as far south as south-western England and the southern Baltic.

Most calidritine sandpipers have medium sized pointed bills, used for picking and probing. The Spoon-billed Sandpiper *C. pygmeus* of North-east Asia is exceptional in having flattened and broadened tips to both mandibles. This species feeds differently from most sandpipers, not running from place to place, but running forward often up to its belly in water, moving its bill in semi-circles in front of it. Its feeding mechanism is not clearly understood. A second exception is the Sanderling, often placed in the monotypic genus *Crocethia*; it is the only sandpiper lacking a hind toe. Whilst most calidritine sandpipers feed outside the breeding season on sandy and muddy shores, the Purple Sandpiper and Rock Sandpiper *C. ptilocnemis* feed on rocky shores often in the company of turnstones.

The most aberrant member of this group is the Ruff, so named because the male sports an erectile collar of feathers and ear tufts during the breeding season; the female (reeve) lacks these adornments and is much smaller. The male's breeding plumage is associated with communal displays on a 'hill' or LEK, to which females are attracted. The female incubates and tends the young alone and there is no permanent pair bond. In this it is unique in the Scolopacidae. The Ruff breeds right across northern Eurasia and migrates south as far as Ceylon or Cape Province.

Surfbird. Some authorities have included the Surfbird *Aphriza virgata* with the turnstones but recent work has shown that, whereas turnstones have affinities with the tringine sandpipers, the Surfbird has calidritine origins. Like turnstones, the Surfbird lives on rocky shores and its short bill suggests a convergence with the plovers. It breeds in Alaska, in mountainous regions above the tree line.

See photos COMFORT BEHAVIOUR; COPULATION; DISTRACTION BEHAVIOUR; EGG-TOOTH; FACILITATION, SOCIAL; FEEDING HABITS; HATCHING; LEK; LOCOMOTION, TERRESTRIAL; PELLET; VOCALIZATION.

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SAND-PLOVER: substantive name of some species of *Charadrius* (for family see PLOVER (1)). See photo ENERGETICS.

SANITATION, NEST: see PARENTAL CARE.

SAPPHIRE: substantive name of *Chlorestes notatus* and many *Hylocharis* spp. (for family see HUMMINGBIRD).

SAPPHIREWING: *Pterophanes cyanopterus* (for family see HUMMINGBIRD).

SAPPHIRONIA: substantive name (some authors) of *Lepidopyga* spp. (for family see HUMMINGBIRD).

SAPSUCKER: substantive name of *Sphyrapicus* spp. (see WOODPECKER).

SARMATIC: derived from the coastal fauna of the brackish or salt inland 'Sarmatic Sea' of late Tertiary and Pleistocene times, an extension of the eastern Mediterranean.

SAUROGNATHOUS: see PALATE.

SAUROPSIDA: term embracing reptiles and birds.

SAURORNITHES: name formerly used for a sub-class equivalent to the Archaeornithes (see under CLASS).

SAVANNA: also written 'savannah', a type of open country found in semi-arid regions or in those with a long dry season; term originally applied in South America but now used widely as a habitat description. For example, in Africa immediately south of the Saharan desert there is a belt of 'thorn-scrub savanna', characterized by a sparse vegetation of spiny bushes and tufted grass; south of that, where there is a substantial rainfall during part of the year, is a belt of 'grass-woodland savanna', park-like country characterized by patches of woodland and isolated trees in a general area of abundant long grass withering in the dry season.

SAWBILL: general term for the mergansers *Mergus* spp. (see DUCK).

SAW-WHET: *Aegolius acadica*, a very small North American OWL.

SAW-WING: substantive name used in East Africa for rough-winged swallows of the genus *Psalidoprocne* (see SWALLOW).

SCALY-WEAVER: name of 2 species of weavers of uncertain systematic position. For family see SPARROW-WEAVER AND SCALY-WEAVER.

SCANSORIAL: pertaining to the act of climbing, especially on tree-trunks (see LEG; LOCOMOTION, TERRESTRIAL).

SCAPULA: a paired bone ('shoulder blade') of the pectoral girdle (see SKELETON, POST-CRANIAL).

SCAPULARS: (plural) the feathers above the shoulder (see TOPOGRAPHY).

SCAPUS: term sometimes applied to the whole stem of a feather, i.e. calamus and rachis combined (see FEATHER).

SCARING: a scaring stimulus is one that produces stress within birds so that they will try to avoid it. In this article bird scaring refers to the use of such stimuli to deter birds from areas where they cause damage. There is a great diversity in the sorts of bird damage that can occur, whether to agricultural or horticultural crops, fisheries or property. Traditionally the term bird-scarer has been applied to devices that deter birds without physical contact; such scarers therefore involve visual and/or auditory stimuli. Deterrents using tactile or gustatory stimuli, which clearly require physical contact, have been called 'bird repellents' (see REPELLENTS, CHEMICAL).

Traditional scaring techniques have involved the use of sudden loud sounds and/or bright novel objects which startle birds and cause them to flee (see Frings and Frings 1967). Purely visual devices range from the classic scarecrow to brightly coloured material suspended from poles, tethered balloons and various 'windmill-like' devices with vanes of different colours. A folklore has grown up that some colours, in particular red and orange, are 'naturally' repugnant to birds; there is however, no scientific evidence to support this belief.

By far the most common acoustic scarer is the propane gas gun. Gas from a cylinder is periodically released into a firing chamber where it is ignited, the interval between explosions being adjustable. The sound level of these explosions can measure as much as 130 decibels at a distance of 1 m from the mouth of the gun. In order to minimize noise nuisance it has been suggested that ultrasonic scarers, emitting sound frequencies above the normal human hearing range, should be used. Unfortunately the upper frequency limits of the bird species so far investigated are very similar to man's. Even in those species that can detect frequencies as high as 25,000 cycles/sec in laboratory tests (e.g. the Bullfinch *Pyrrhula pyrrhula*), the frequency range over which the birds' hearing is most sensitive is much lower, between 2,000 and 4,000 cycles/sec.

Just as people living next to a main road may slowly adapt to the traffic noise, so birds gradually lose their fear of loud and/or novel scarers. This process is called habituation. To slow the rate of habituation, one should, where possible, use periodic rather than continuous presentation, frequently vary the site and type of scarer, and occasionally reinforce the response by providing a real source of danger, such as shooting at birds around the scarers (for a recent review see Slater 1980).

More recently, scarers have been developed that employ natural frightening stimuli encountered by birds. Most avian pests are prey to mammals and other birds at some stage of their life cycle and thus scarers that seek to mimic aspects of encounters with predators will to some degree be reinforced naturally outside the scaring context. The birds' fear response to devices of this kind should therefore persist longer than to scarers that rely upon the startle response produced by novelty, for a bird that does not quickly and repeatedly respond to predators is unlikely to survive. Indeed many species have a genetically inbuilt tendency to respond to various cues associated with the presence of predators.

Trained raptors have been used with some success on airfields where birds pose serious dangers to aircraft (Blokpoel 1976). Models of birds of prey suspended from balloons or mounted on poles are generally ineffective, probably because raptor recognition can involve quite complex visual cues, such as plumage details, as well as features based upon flight characteristics. Much more successful have been attempts to deter birds using the calls they emit when they sight a predator (alarm calls) or are actually caught by one (distress calls). Broadcasts of these calls are now commonly used on airfields to clear the runways of birds before aeroplanes land or take off (Busnel and Giban 1965, Blokpoel 1976). Such calls are at present less widely employed in agriculture; perhaps their most common use is in the dispersal of Starling *Sturnus vulgaris* roosts. Responses to broadcast calls vary between species, some (e.g. Starlings) disperse immediately whilst others (e.g. Rooks *Corvus frugilegus*) approach and mob the loudspeaker before dispersing.

Several species (e.g. Woodpigeon *Columba palumbus*) seem not to have alarm or distress calls, but apparently use visual means to communicate fear. For example, geese, when disturbed, frequently adopt a pre-flight posture which involves the vertical straightening of the neck and a rapid side-to-side shaking of the head. By using models that mimic this posture, Inglis and Isaacson (1978) successfully deterred skeins of Dark-bellied Brent Geese *Branta bernicla bernicla* from landing in fields containing the models. Similarly work by Murton and his colleagues (Murton *et al* 1974) suggested that the white wing bars of Woodpigeons were used as a visual alarm signal eliciting flight, and prototype devices that mimic these characteristics can deter Woodpigeons from landing in their vicinity (see Inglis 1980).

The development of devices that employ the pest species' own acoustic and/or visual alarm signals seem to offer the best prospect for the production of an efficient scarer, although this is something that it is very difficult to quantify; firstly because within any given area there will be variation over time in the numbers of birds attempting to feed, and secondly because at any given time, areas will differ in their attractiveness to birds. An obvious general 'rule-of-thumb' is that scarers are most effective at those times of the year when alternative food sources are available nearby. The provision of cheap decoy crops together with the erection of scarers on the more valuable areas is likely, therefore, to be the most satisfactory method of protection. A problem could arise, however, if the decoy crops were provided throughout those periods of the year when starvation has a powerful influence on the population size of the pest, in that more birds may survive to return the following year.

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SCAUP: substantive name of some *Aythya* spp.; used without qualification in Britain for *A. marila* (see DUCK).

SCHIZOGNATHOUS: see PALATE (Neognathous).

SCHIZORHINAL: see NARIS.

SCIMITAR-BABBLER: see BABBLER.

SCIMITAR-BILL: substantive name of *Rhinopomastus* spp. (see WOOD-HOOPOE).

SCISSOR-BILL: alternative substantive name of species of Rynchopidae (see SKIMMER).

SCLEROPHYLL FOREST: evergreen forest in which the dominant tree species have hard leathery leaves normally less than *c.* 10 cm long, resistant to water loss. Very variable in species composition, occurring throughout the world in areas with periodic (usually seasonal) water shortage.

SCLEROTIC: see SKULL; VISION.

SCLERURINAE: see OVENBIRD (1).

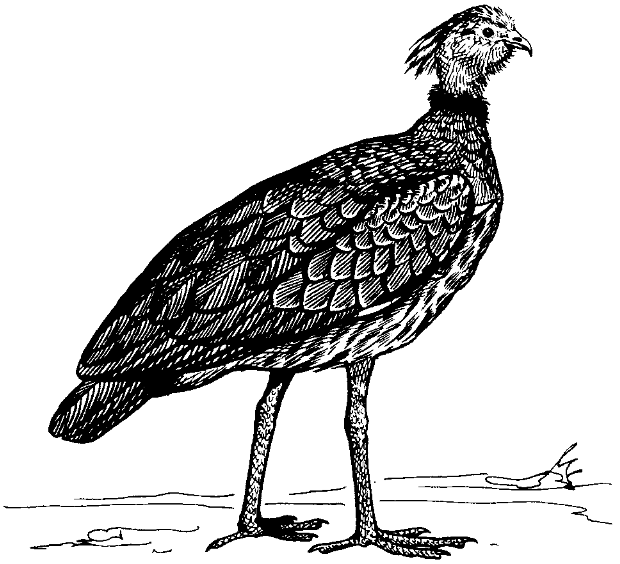
SCOLOPACIDAE: see under CHARADRIIFORMES. The family includes species known as 'woodcock', 'snipe', 'sandpipers', 'curlews', and 'godwits', and by various special names (see under SANDPIPER).

SCOPI; SCOPIDAE: suborder and family of CICONIIFORMES; HAMERKOP.

SCOTER: substantive name of *Melanitta* spp. (see DUCK).

SCRAPE: a shallow water-filled hollow excavated to attract water birds. See also NEST SCRAPE.

SCRATCHING: for head scratching see COMFORT BEHAVIOUR; for scratching the ground see FEEDING HABITS. See photo COMFORT BEHAVIOUR.



Crested Screamer *Chauna torquata*. (*C.E.T.K.*).

SCREAMER: substantive name of the 3 species of Anhimidae (Anseriformes, suborder Anhimae).

Characteristics. Screamers are goose-like birds (length 69–90 cm) with heavy bodies and small heads, but longer, fleshy legs, and semi-palmate feet with the hind toe long and not elevated. The bill is more like that of gallinaceous birds. On the leading edge of wing are 2 spurs 2–5 cm long which shed their outer layers periodically. Such shells found imbedded in breasts of other screamers suggest that the spurs are used in aggressive encounters. One species has a long (up to 15 cm) cartilaginous horn attached to the crown, but its delicate structure suggests decoration rather than armament. Screamers are unique in lacking uncinate processes on the ribs that provide support for the delicate body cage of other living birds. Unlike other waterfowl, they lack well-defined feather tracts, simultaneous wing moult and copulatory organ. Small air cells between the skin and muscle are more widespread than even in Pelecaniformes and create rumbling or crackling noises on take-off. The sexes differ little in size. They swim well but high on the water and somewhat belaboured; diving has not been recorded. They are strong flyers and at least one species soars regularly.

Habitat and distribution. The Crested Screamer *Chauna torquata* is grey with white and black rings on the neck. It is well known because of its extensive distribution in the pampas of Argentina, Uruguay and southern Brazil and in the subtropics in Bolivia and Paraguay. Crested Screamers are most numerous near marshes where they may graze with livestock. Pairs and flocks roost in shallow water at night. The Black-necked Screamer *Chauna chavaria* occurs in a small area in Colombia and Venezuela, and differs from the Crested Screamer in its more extensive black neck, chin and face. The largest of the 3 is the Horned Screamer *Anhima cornuta* of the tropical savannas of the Guianas, northern Venezuela, Colombia, western Ecuador, Peru, Brazil and Bolivia. Whereas the other 2 screamers are predominantly grey, this species is a glossy greenish-black. Horned Screamers perch in trees regularly, where they probably roost overnight, and like other screamers, feed on grasses and sedges near water.

Food. Screamers are herbivores that graze near lakes and marshes or feed on aquatic plants. Insects are thought to be taken by or for young.

Behaviour. Information is based mostly on studies of Crested Screamers. Pairs are obvious year-round, but they seek isolation in marshy areas in late winter or early spring where they trumpet (duet) and mutual-preen. Mating occurs on land. Large flocks of non-breeding birds suggest that maturation is delayed for several years.

Voice. They are highly vocal birds with piercing trumpet-like alarm calls, also uttered while soaring.

Breeding. The nest is constructed of aquatic plants or sticks, usually over water. Both sexes build the nest and probably incubate. Down is rare or lacking in nests. Four to 7 eggs are laid at intervals of 35–40 h, and incubation requires 43–45 days. The young remain in or near the nest for several days and stay in wet areas until they are old enough to run to safety. Black-necked Screamer adults feed chicks in captivity.

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SCRUB-BIRD: substantive name of the 2 species of the Atrichornithidae (Passeriformes, suborder Oscines); in the plural the general term for the family.

Characteristics. The Noisy Scrub-bird *Atrichornis clamosus* (21 cm) and the Rufous Scrub-bird *A. rufescens* (16 cm) are small terrestrial birds with strong pointed bills; long powerful legs; short rounded wings and long graduated tails. The dorsal plumage is brown (more rufous in *A. rufescens*) with fine black cross bars; the ventral plumage grades from white on the chin to rufous at the vent. Males are larger and also have a black bar across the upper chest which in *A. rufescens* extends down the flanks.

Systematics. Traditionally, this small endemic Australian family has been grouped with the lyrebirds in the suboscine suborder Menurae. This arrangement is based mainly on the facts that both families have only 3 pairs of intrinsic syringeal muscles compared to 4 in other Passeres, and that the lower tracheal rings are not fused into a 'drum'. In addition, certain skeletal features such as the rudimentary clavicles in the scrub-birds and the number of flight and tail feathers in the lyrebirds were used to support this arrangement. Both families are ancient and relict members of the Australian avifauna.

Habitat. Both species are primarily birds of wet forest, and occupy the ecotone between forest and swamp or where the canopy is broken. Such areas have a dense zone of shrubs and rushes, which provides essential nest sites, nest material and cover. The feeding habitat is on the forest side of this zone where the decreased density of shrubs and rushes allows the development of a litter layer which is the main food source. The only known population of the Noisy Scrub-bird is confined to the narrow gullies and soakage lines on an elevated headland of about 2,000 ha. The Rufous Scrub-bird is found in scattered areas of suitable habitat.

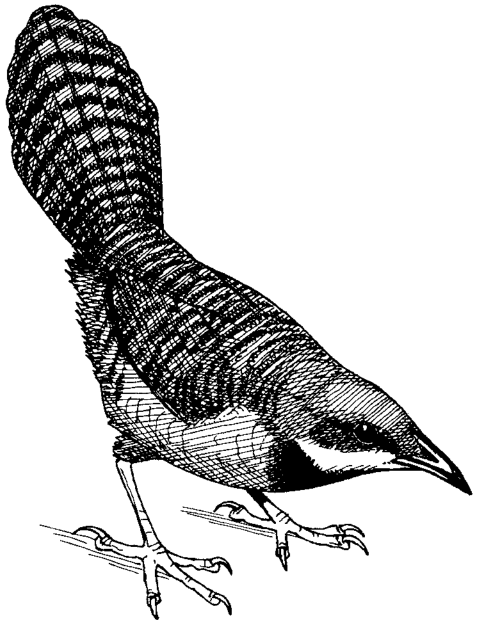
Distribution. The scrub-birds have an interrupted distribution. *A. clamosus* is only known from an isolated headland on the south coast of Western Australia, while *A. rufescens* is found in a small number of isolated montane locations from southern Queensland to northern New South Wales.

Though formerly more widespread, the reduced distribution and population of scrub-birds since the mid 1800s has been caused by the destruction of habitat for agricultural pursuits and forestry and by the increased frequency with which their habitat has been burnt. Drought and introduced predators may also have played a minor role.

Populations. Because of the dense habitat and their secretive habits no census of scrub-birds is possible, but counts of singing males provide an index of the number of breeding pairs. During the 1960s the number of *A. clamosus* breeding pairs was of the order of 40–50; since 1970 the number has increased from 45 to 138 in 1983. It is unlikely that there are more than a few hundred breeding pairs of *A. rufescens*.

Food. Both species are generalized insectivores, who may also prey occasionally on small lizards or frogs. Most of their prey is obtained from the litter layer which they poke into or turn over with a sideways flick of the bill. Occasionally they flush insects by a rapid drumming on one foot on the litter, or more rarely by vibrating the erected breast feathers on the litter. Less frequently, they hunt insects at the base of lower levels of the rushes and shrubs that form the understorey of their habitat.

Behaviour. Scrub-birds are fast, alert ground-dwelling birds, who



Noisy Scrub-bird *Atrichornis clamosus*. (*N.W.C.*).

rarely fly and then only a few metres. They are seldom seen, and usually only the song of the male indicates their presence. *A. clamosus* male territories are well dispersed and adjacent males rarely make contact except by song. Their territories range from 5–10 ha, within which the males may spend up to 80% of their time in an area of 1–2 ha centred on the best feeding places. Males have a number of roosting sites in trees or taller shrubs away from their feeding area to which they move after sunset and leave before sunrise. Males are generally monogamous, although they may mate with females on adjacent territories who have lost their mates. Polygamy was observed in the captive colony. Females occupy areas with suitable breeding habitat and good feeding on the periphery or away from the males' preferred station. They nest in the same area year after year and only move their site after losing the egg or chick. The little contact between males and females is probably confined to the breeding season. At its beginning, young males may occupy territories in sub-optimal habitat for 1–15 weeks. They do not develop their territorial song until the second, and may not be sexually mature until their third year. Females may breed in their first year and, if they cannot acquire a territory, may nest adjacent to an established pair. What little is known of *A. rufescens* suggests that it is similar to *A. clamosus* except that the males only defend their territories during the breeding season.

Voice. The male *A. clamosus* has a loud and far reaching territorial song of 10–20 notes. Individual males may have 4 or 5 song patterns, all of which may be given in the same bout of singing. Males within hearing distance of each other have similar patterns of song. These continually change and the songs of any group may be quite different from year to year. The plasticity of the song pattern is in marked contrast to that of *A. rufescens* which has a very stereotyped and simple song not varying significantly throughout its range. *A. clamosus* males have another song, briefer than territorial song, more variable and of lower intensity, and which incorporates modified segments of the song of other species; it is used in interactions with other scrub-birds. In similar situations *A. rufescens* uses pure mimicry. *A. clamosus* also has a three-note call and two alarm notes. These alarm notes are the only vocalizations of the females of both species.

Breeding. Both species breed during the wet season, winter for *A. clamosus* and spring/summer for *A. rufescens*. The male *A. clamosus* plays no role in nest building, incubation, feeding the chick or nest sanitation. The female builds a domed nest with a side entrance, lining the bottom with decayed rushes or wood which dries hard. Nests are built close to the ground, usually near a stream, and take about 3 weeks to build; the single egg is laid 1–2 weeks after the nest is completed. Incubation takes 36–38 days in the wild, but only 30–33 days in captivity. The difference may be attributed to the increased time needed to feed in the wild. For about 7 days after hatching the female broods after each feed, but subsequently only at night. The chick fledges at about 25 days, after which it stays with the female, probably until the start of the next breeding season. Chicks are fed a wide variety of invertebrates and occasionally a small lizard or frog. The female removes the faecal sacs which she deposits in a stream or under a bush. If the egg is lost, the female will build another nest and relay. Little is known of the breeding of *A. rufescens*, but it is probably similar to *A. clamosus* except that 2 eggs are laid and the nest is completely lined.

Conservation. Following the rediscovery of *A. clamosus* in 1961, a reserve was established with a resident ranger. Constant policing and the development of a fire-break system have prevented any fires in this area since 1970. The consequent regeneration of habitat has contributed to the increase in population since 1970. In the short term the population appears reasonably secure. In 1975/76 a captive colony of 1 male and 3 females was established and in 1979 the first chick was successfully reared. Knowledge of how to breed the species in captivity should assist in the long term survival of the species. *A. rufescens*, although rare, is not endangered because all the known localities are within National Parks and are of sufficient number that its long term survival seems as assured.

G.T.S.

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SCRUB-FOWL: name sometimes applied to *Megapodius* spp. (see MEGAPODE).

SCRUB-ROBIN: substantive name of *Drymodes* spp. (see RAIL-BABBLER; THRUSH); also used for *Erythropygia* (or '*Cercotrichas*') spp., alternatively 'bush-robins' or (in one case) 'Rufous Warbler' (for families see WARBLER (1); THRUSH).

SCRUB-WREN: substantive name of *Sericornis* spp. (see WARBLER, AUSTRALIAN).

SCUTELLATE: term applied to a podotheca consisting of rather large and often overlapping scales (see LEG).

SCYTHEBILL: substantive name (formerly 'sicklebill') of *Campylorhynchus* spp. (see WOODCREEPER).

SEA EAGLE: see HAWK (True kites and fish eagles).

SEARCH IMAGE: a predator can be said to 'adopt a Search Image' when it can be shown that it has learnt to see prey which it at first overlooked. Many of the insects and other animals which are preyed upon by birds are highly camouflaged in that their colour and patterning blend in very closely with their background. Birds have, nevertheless, been shown to be able to 'break' the camouflage when they have had experience of finding a particular type of prey.

As an example of this, de Ruiter (1952) found that, when Jays *Garrulus glandarius* and Chaffinches *Fringilla coelebs* were first shown the stick-like caterpillars of geometrid moths resting among twigs, they apparently failed to see them. But although the birds took a long time to find their first caterpillar, some birds which had eventually found an insect were then able to pick out the other insects without difficulty. They were thus 'taken in' by the camouflage at first, but were able to detect the difference between sticks and caterpillars after they had sampled the first insects. The birds could then be described as having adopted a Search Image for stick insects. Similar phenomena have been observed in crows, domestic chicks and other birds.

It should be pointed out, however, that not everyone uses the term Search Image in the same way. Some people use the term to cover cases where a predator simply develops a taste for a type of food even when it is not camouflaged, and there is no suggestion of a change in how easily the predator can see it. (The predator might just be learning, for example, which of several conspicuous foods are best to eat.) These different uses have led to confusion and, in some quarters, a feeling that the term should be dropped altogether. But without it, we would have no name to give the process of a predator learning to see through its prey's camouflage. So, used in this restricted sense, the term Search Image does serve a useful function. It is a graphic way of describing an important behavioural phenomenon. M.D.

de Ruiter, L. 1952. Some experiments on the camouflage of stick caterpillars. Behaviour 4: 222–232.

SEASONAL CHANGE: occurring in birds in respect of physiological condition and behaviour, and very often also of external appearance and location (either or both). The cycle of a bird's life is usually an annual one, linked with the recurring seasons—whether these be summer or winter, or wet season and dry (see RHYTHMS AND TIME MEASUREMENT; WEATHER AND BIRDS). The alternation in physiology and habits is, in adults, between reproductive and non-reproductive periods (see BREEDING SEASON). It may involve a greater or lesser degree of geographical displacement (see MIGRATION; and IRRUPTION). The physiological changes include the seasonal replacement of feathers and other integumentary structures (see MOULT). This may or may not involve marked change in external appearance, as when there is a distinctive breeding plumage in one or both sexes (see PLUMAGE).

SEA-SWALLOW: popular name for TERN.

SEA-WATCHING: a form of BIRDWATCHING from a single observation point, usually a prominent headland, whence passing birds are counted and identified over a period of hours or days. Sometimes sea-watches are co-ordinated over a number of stations to yield comparative data. The term is not usually applied to watches from on board ship, which have been carried out all over the world, notably by the Royal Naval Birdwatching Society.

SECONDARY: or 'secondary feather', any one of the flight feathers borne on the forearm (ulna), as contrasted with the 'primaries' borne on the manus (see PRIMARY; also PLUMAGE; WING); they are sometimes called 'cubitals'. The secondaries are customarily numbered inwards from the carpal joint.

SECONDARY COVERTS: see TOPOGRAPHY.

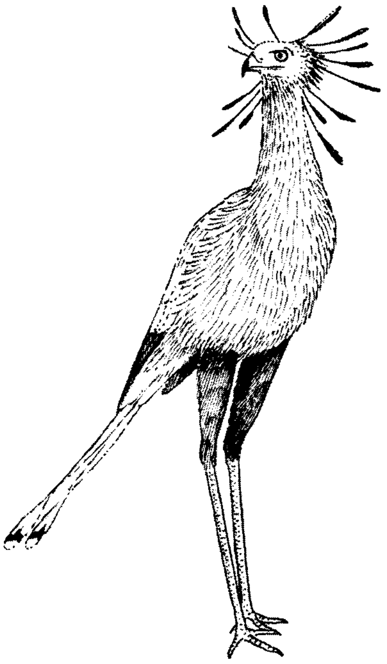
SECONDARY SEXUAL CHARACTERS: see SEXUAL DIMORPHISM.

SECRETARY-BIRD: *Sagittarius serpentarius*, sole extant species in the Sagittariidae, a family currently placed in the Accipitriformes, suborder Sagittarii.

Characteristics. A large bird with a wing span of just over 2 m, weighing about 4 kg, and standing over 1 m tall, characterized by long legs that are feathered to the inter-tarsal joints, a well-developed basal web which joins the 3 front toes, elongate central tail feathers and a loose crest of spatulate feathers on the nape. The hooked bill, display flights and carnivorous diet suggest affinities with large eagles. The long legs and nesting habits are stork-like, but there are also many similarities with the seriemas (Gruiformes) of South America. Bustards and cranes have also been suggested as relatives, but until the species is properly studied and homologous and convergent characters are separated, the true relationships will remain obscure.

Habitat and distribution. The Secretary-bird is found in open savanna, grassland and steppe, shunning areas that are heavily wooded or densely vegetated or of broken terrain. It is found in Africa south of the Sahara desert, although fossils are known from France.

Populations and movements. No regular movements are known, but in many areas and at certain seasons it is locally nomadic as food supplies fluctuate. Densities of a breeding pair per 45 km^2 (grassland in South Africa) to one per 20 km^2 (tropical savanna in South Africa) are known, but higher densities in richer environments or lower in more arid areas are likely.



Secretary-bird *Sagittarius serpentarius*. (*K.J.W.*).

Food. Largely rodents, reptiles, large beetles and grasshoppers, but any small animal up to the size of a hare may be eaten if caught. Eggs and nestlings of ground-nesting birds (e.g. plovers) are also taken. All hunting is done while walking with long, measured strides over the ground, prey being immobilized by kicking with the short, stout toes and their nail-like claws. The reach attained with the long legs and agility obtained by using wing movements allow active prey to be killed, such as birds and mice, or dangerous prey avoided such as venomous snakes. If snakes cannot be subdued on the ground, they are taken aloft and dropped from a height. Small animals burnt in fires may be scavenged.

Behaviour. Adults are usually in pairs, holding and residing in a territory as long as conditions permit. Numbers may congregate at water-holes to drink or bathe, or at temporarily abundant food sources such as grassland fires, but often these appear to be non-breeding birds. Territorial advertisement consists of soaring flights made almost daily and during the heat of the day, sometimes with calling, and defence may involve aerial chasing or running and kicking fights on the ground.

Voice. The Secretary-bird is mostly silent, but has a variety of deep croaking calls. Loud croaking precedes breeding and is uttered perched or during display flights. A single high pitched croak signifies alarm, a deep croak indicates threat. Small chicks make a loud chucking noise, later croaking and sometimes they throw back their heads as they call. Mewing calls are made at roosts.

Breeding. Displays consist of undulating diving flights by either sex, with croaking calls. The nest, which is used year after year, is built of sticks, weeds and grass and forms an extensive platform on top of a tree or bush, often rather low (3–7.5 m above ground) and usually in a thorny species. The basin is lined with dry material, mainly grass tufts. Up to 3 white eggs, rather pointed, and small for the size of the bird, are laid at intervals of several days. Incubation proceeds for 45 days, almost entirely by the female, the male delivering food carried in the crop and regurgitated on the nest rim. The chicks hatch in white or grey down, the second down being darker, and the feathers appear on the crest when they are 3 weeks old. The female gives most attention to them at first, although either parent may brood and feed them. Within a month of hatching the female leaves the nestlings for much of the time to help the male search for food. At first a liquid diet, probably of partly digested food, is fed to the chicks, but later whole items are given and latterly the food is left on the nest for the chicks to feed themselves. They leave the nest 65–80 days after hatching, being barely able to fly, and spend about a month in the nest area learning to hunt before moving off to join the parents on their foraging expeditions. Breeding may occur at any time of the year, usually in spring or summer, and is probably linked to food availability. The immature bird resembles the adult but has a pale grey eye (which is hazel in the adult) with black barring on the underwing and undertail coverts (both white in the adult). A.C.K.

Brown, L.H. & Amadon, D. 1968. Eagles, Hawks and Falcons of the World. Feltham.
Kemp, A.C. & M.I. 1978. *Bucorvus* and *Sagittarius*: two modes of terrestrial predation. Proc. Symp. Afr. Predatory Birds. pp. 13–16.
van Someren, V.G.L. 1956. Days with birds. Fieldiana: Zoology 38.

SECRETION, INTERNAL: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

SEDENTARY: commonly used in the special sense of 'non-migratory' (compare RESIDENT).

SEED-CRACKER: substantive name of *Pyrenestes* spp. (see ESTRILDID FINCH).

SEED DISPERSAL: in this context, the dispersal of seeds, and hence of the plants producing them, by birds.

Many seed-eating birds act as distributors; they do so, however, more or less accidentally, by failing to digest a proportion of the seeds or by dying with a full crop or stomach. Nevertheless, by such means plants are on occasion dispersed over great distances (Ridley 1930). A primary distinction should be made between such birds, which are essentially seed-predators (although some, such as the parrots and many pigeons, are commonly referred to as frugivores), and the true or 'legitimate' frugivores, which digest the fleshy parts of fruits and void the seeds intact. Avian frugivores of the latter sort are the main distributors of many trees, shrubs and epiphytic plants, and of a smaller number of herbaceous plants. They are especially numerous in tropical forest, and the interaction between them and their food plants has led to mutual adaptations (see COEVOLUTION). There is reason to think that fleshy fruits of the kind eaten by birds evolved early in the history of the flowering plants in equable, tropical conditions; and that other kinds of fruits, such as those dispersed by wind, evolved later, perhaps in association with the climatic deterioration that took place during the Pliocene.

The interaction between a frugivorous bird and its food plant is in the nature of a bargain: the bird obtains nourishment from the fleshy part of the fruit, and in exchange disperses the seed or seeds. To understand the details of the bargain, in particular the benefits obtained by each party, it is necessary to know the relative mass of flesh and seed, the number of seeds per fruit, the nutritive content of the flesh, the proportion of the crop harvested by the frugivore, the distances and sites at which the seeds are dropped, and many other things. In spite of much recent research on frugivory in birds, few studies have been thorough enough to give quantitative data on all of the important factors, and generalizations remain tentative. A broad distinction can be drawn between unspecialized and specialized frugivores, and between the kinds of fruit on which they feed. An unspecialized frugivore is one that regularly takes other foods besides fruit, and cannot subsist indefinitely on fruit alone. It is typically an opportunist, taking fruits as and when they become available. In order to attract unspecialized frugivores, it will be advantageous for a plant to have conspicuous fruits and a well-synchronized fruit crop. The fruits are usually borne in profusion, and linked with this, the nutritive content of individual fruits is not very high; they tend to be watery (succulent) and to contain mainly sugars and little fat or protein. Typically they are small, and contain small seeds. Many small trees and shrubs that colonize clearings, edge habitats and other transient areas of secondary vegetation have fruits of this unspecialized sort. As colonizers of temporary open ground, they tend to be in competition with one another, not only for ground space but also for dispersal agents.

Thrushes, tanagers in tropical America, and bulbuls in the Old World tropics are typical unspecialized frugivores. It is characteristic especially of the tropics that temporarily superabundant supplies of unspecialized fruit are exploited by birds of many families that are not usually thought of as frugivorous, e.g. woodpeckers and tyrant-flycatchers. Many plant families produce unspecialized fruits, among the most important in the tropics being the Rubiaceae and Melastomataceae, and in North Temperate regions the Rosaceae and Caprifoliaceae.

Specialized frugivores are typically larger birds than unspecialized frugivores, and the fruits that they eat are correspondingly large. Plants producing such fruits are mainly trees of primary tropical and subtropical forest. A common type of fruit consists of a single seed surrounded by a dense and nutritious, and often surprisingly thin, layer of flesh. Specialized frugivores process such fruits remarkably quickly, stripping off the flesh and regurgitating the large seed, which represents so much useless ballast, intact. In another common type of nutritious fruit the seed is partly or entirely covered by an aril, which is an edible outgrowth of the seed itself. A number of fruits of both these types have been analysed and have been found to contain high percentages of fat and protein. Fruits of these kinds are often not very conspicuous, probably because they need to attract only a small number of regular frugivores which are likely to be resident and to know intimately the fruit resources available in their area. They also tend to be available over a longer period than the fruits that are produced in a mass to attract opportunist unspecialized frugivores.

Specialized fruit-eating birds belong to fewer families than the unspecialized fruit-eaters, and are mainly tropical. The most important families are the toucans and cotingas in the American tropics, the turacos in Africa, the hornbills in Africa and south-east Asia, the birds-of-paradise in Australasia, and the true fruit-pigeons (Columbidae, genera *Ducula*, *Alectroenas* and *Ptilinopus* only, other pigeons being seed-predators) in south-east Asia and Australasia. Trees producing fruits adapted for specialized frugivores belong to a variety of families, the Palmae, Lauraceae and Burseraceae being of outstanding importance.

A limited number of birds in all the main tropical and subtropical areas are specialized feeders on the fruits of mistletoes (Loranthaceae) and the chief dispersers of these plants. Some epiphytic plants may also be dispersed by these birds (bromeliads, aroids, and the epiphytic cactus *Rhipsalis*). The coevolutionary relationship between bird and plant is close, and there are some special features that set it apart from the typical bird-fruit relationship discussed above. The birds are mostly small (as are the fruits), with short and rather stout bills, and may have highly modified digestive systems. Effective dispersal depends on the seeds being lodged in a crack on a tree branch, and the fruits are adapted for this by having the seed embedded in a sticky coating which resists digestion in a bird's gut. The bird either swallows the fruits whole and passes them very rapidly through the alimentary canal, voiding them with their sticky coating intact so that they adhere to the branch on which they land, or squeezes the fruit in the bill, swallows the skin and pulp, and wipes the seeds off onto the branch on which it is perched. The most important mistletoe-berry eaters are the mistletoe-birds (Dicaeidae) of south-east Asia and Australasia, the small neotropical tanagers of the genera *Euphonia* and *Chlorophonia*, and the small African barbets of the genus *Pogoniulus*. A few species of other families are also more or less specialized eaters of mistletoe berries, for instance the Phainopepla *Phainopepla nitens* and the small neotropical flycatcher *Tyranniscus vilissimus*.

Among the seed-predators there is one group of birds that have apparently co-evolved with the plants that they exploit and act as their main dispersal agents. They are seed-hoarders or 'scatter-hoarders', birds of temperate or boreal regions that bury large numbers of seeds in late summer and autumn and dig them up and eat them, or feed them to their young, in the following winter and spring. All those that are known are nutcrackers and jays (Corvidae). Storing food for later consumption is a widespread habit in the Corvidae and some other families, especially the tits and nuthatches, and all these birds must occasionally act as dispersal agents for the plants whose seeds they store, but in most cases there is no evidence that they are the main dispersal agents or that any coevolutionary adaptations are involved. One species at least of pine, however, in the mountains of western North America, *Pinus edulis*, has co-evolved with Clark's Nutcracker *Nucifraga columbiana* and perhaps other corvids, producing seeds that are especially suitable for being harvested by the nutcracker. Similarly, the European Jay *Garrulus glandarius* is the main disperser of oak trees (*Quercus* spp.), and jays have probably been the main selective agent determining acorn size (Bossema 1979). (See also FOOD STORING.)

Seeds, and other parts of plants, furnished with hooks or barbs are occasionally distributed by birds, but probably are adapted primarily for dispersal by other kinds of animals. Birds may, however, be significant agents of dispersal of plants that they use for nest material. The melastomataceous herb *Nepsera aquatica*, whose fruiting panicles are used as nest lining by many small neotropical birds, may be mainly distributed in this way. Ridley (1930) gives other examples. No thorough study has, however, been made of the importance of birds as distributors of plants other than by ingesting or storing their seeds.

See photo FEEDING HABITS. D.W.S. (1)

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Ridley, H.N. 1930. The Dispersal of Plants throughout the World. Ashford.
Snow, D.W. 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113: 194–202.
Vander Wall, S.B. & Balda, R. 1977. Coadaptations of Clark's Nutcracker and the piñon pine for efficient seed harvest and dispersal. Ecol. Monogr. 47: 89–111.
Walsberg, G.E. 1975. Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. Condor 77: 169–174.

SEEDEATER: substantive name of species of *Sporophila* and allied genera in the New World, and of *Serinus* spp. in southern Africa (for family see FINCH).

SEED-FINCH: substantive name of certain small seed-eating species, particularly in the Neotropical genus *Oryzoborus*, also called 'rice grosbeaks' (for family see FINCH).

SEEDSNIPE: substantive name of the 4 species of Thinocoridae (Charadriiformes, suborder Charadrii, superfamily Thinocoroidea); in the plural (usually unchanged), general term for the family. The name derives from the birds' diet of seeds and other vegetable matter, and their snipe-like flight, including the *bzeep* take-off call, although they have no near relationship to snipe (*Gallinago* species, family Scolopacidae) on present evidence. Seedsnipe are undoubtedly charadriiform, but it has not yet been possible to establish which are their closest relatives.

Characteristics. Seedsnipe are entirely South American and range in size from that of a quail *Coturnix* to that of a small partridge *Perdix*. The genus *Thinocorus* contains the 2 smaller species, the Least Seedsnipe *T. rumicivorus* (measuring about 18 cm and weighing 50–60 g) and the Grey-breasted Seedsnipe *T. orbignyianus* (measuring about 20 cm and weighing 110–140 g). The genus *Attagis* comprises the 2 larger species, the Rufous-bellied Seedsnipe *A. gayi* (about 30 cm long and weighing 300–400 g) and the similar-sized White-bellied Seedsnipe *A. malouinus*. They resemble doves (Columbidae) or sandgrouse (Pteroclididae) with plump bodies, small heads and short legs, but they have relatively long toes; the middle toe is as long as or longer than the tarsometatarsus. The bill is shaped rather like that of a partridge and the nostrils are protected by shield-like coverings. The plumage is cryptically coloured in grey, black, brown, white and rufous. The belly is white in the 2 *Thinocorus* species and in the White-bellied Seedsnipe, but rufous in the Rufous-bellied Seedsnipe.

Males of the 2 *Thinocorus* species have dove-grey breasts bordered ventrally by a black collar. The Least Seedsnipe also has a vertical black line joining a black-bordered white throat to the chest band to give an anchor-shaped effect. The 2 *Attagis* species have the breast finely marked with black. Sexual dimorphism is well developed in *Thinocorus*, but almost absent in *Attagis*. Seedsnipe all have long wings and are excellent fliers.

Habitat and distribution. The White-bellied Seedsnipe lives on windswept hilltops above the treeline on Tierra del Fuego and the islands south to Cape Horn; it also extends northward into the southernmost parts of the Andes in Chile and Argentina. The Rufous-bellied Seedsnipe, the largest and most strictly montane member of the family, lives just below the snowline in the puna or páramo zone of the Andes of Ecuador, Perú, Bolivia, Argentina and Chile up to about 5,500 m. The Grey-breasted Seedsnipe is also an Andean bird, but of rather lower elevations, especially in the southern parts of its range in Patagonia and Tierra del Fuego where it inhabits open grasslands. The Least Seedsnipe is not montane, occurring in arid country down to sea level, from Ecuador in the north to northern Tierra del Fuego in the south. It is common in Argentine Patagonia.

Movements. Southern populations of the Least Seedsnipe migrate northward in winter as far as the province of Buenos Aires; more northerly populations are sedentary or nomadic, especially in the more arid areas. The other species of seedsnipe may merely move to lower elevations in winter, but do not appear to undergo long migrations.

Food. Seedsnipe spend most of their time on the ground feeding on seeds and green leaves. The arid-zone Least Seedsnipe feeds on succulent leaves as a source of water. None of the 4 species of seedsnipe appears to drink under natural conditions, although they will do so in captivity.

Behaviour. During the breeding season seedsnipe are monogamous and move about in pairs or family groups. In winter when they are not breeding, the birds gather in large flocks which are migratory or nomadic. They roost at night on the ground, often in groups, making shallow scrapes in which to lie. The males have characteristic territorial flight displays in the breeding season, accompanied by a mellow song which may also be given from a perch on top of a rock or, in the case of the Least Seedsnipe, a bush or tall weed. Territorial males frequently fight vigorously at their territory boundaries.

Voice. The songs of seedsnipe are mostly mellow-toned, incorporating hooting notes like *puku puku puku* and may be uttered for many minutes at a time without a break. When taking off they give a short *bzeep* call like that of a snipe.

Breeding. Seedsnipe nest on the ground, either in the open or next to a grass tuft or low shrub. They lay 4 eggs in a scrape filled with dry plant material. The eggs are usually creamy to pinkish in ground colour, spotted with shades of brown, grey and mauve. The White-bellied Seedsnipe and some females of southern populations of the Least Seedsnipe lay eggs of a greenish ground colour; this seems to be an adaptation to the greener habitats in the higher-rainfall regions inhabited by these birds. Incubation is by the female only in the *Thinocorus* species and possibly in the others too. Both *Thinocorus* species invariably cover their eggs completely with nest material when they leave the nest (whether to feed or when disturbed). The White-bellied Seedsnipe may also do so (although only one nest has ever been recorded), but the Rufous-bellied seems not to line its nest scrape thickly enough to allow of egg-covering. Where it occurs, egg-covering is done rapidly with sideways movements of the feet. An incubating female leaves the nest to feed for about an hour in the morning and again in the late afternoon.

During the incubation period the male seedsnipe spends much time on a perch near the nest, where he acts as a lookout, giving a warning call and running away with the female as soon as danger is sighted. If disturbed suddenly at the nest, especially if she has not had time to cover the eggs, the female performs an elaborate injury-feigning distraction display as she flutters away low over the ground.

The incubation period of the Least Seedsnipe is about 26 days. The young are led away from the nest by both parents as soon as they are dry, but only the female broods them. From the start they feed by themselves on seeds and green leaves and do not need to be shown food by their parents. Like the adults they do not normally drink water. The young fly at about 7 weeks of age. If disturbed with young, both parents will perform distraction displays, but those of the male are less elaborate, usually consisting only of the 'rodent-run' typical of waders (see DISTRACTION BEHAVIOUR). See photo COLORATION, ADAPTIVE. G.L.M.

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Maclean, G.L. 1969. A study of seedsnipe in southern South America. Living Bird 8: 33–80.
Sibley, C.G., Corbin, K.W. & Ahlquist, J.E. 1968. The relationships of the seed-snipe (Thinocoridae) as indicated by their egg white proteins and hemoglobins. Bonn. zool. Beitr. 19: 235–248.

SELECTION: see NATURAL SELECTION; and under SPECIATION.

SEMATIC: serving as a signal, e.g. of warning or attraction. This adjective is the base of such terms—applied particularly to coloration—as 'aposematic' (protective) and 'episematic' (aiding recognition), and of compounds thereof (see under APOSEMATIC; EPISEMATIC); also GAMOSEMATIC. 'Allosematic' (adventitiously derived from association with other organisms—see NESTING ASSOCIATION), and 'parasematic' (deflecting attention from one part of the body to another, e.g. from more to less vulnerable parts). Not all such terms as these have application in ornithology. See, in general, COLORATION, ADAPTIVE.

SEMICIRCULAR CANALS: in the ear (see HEARING AND BALANCE).

SEMIPALMATE: half webbed.

SEMIPLUME: a feather type intermediate between contour feather and down (see FEATHER; PLUMAGE).

SEMI-PRECOCIAL: newly hatched young which have eyes open, are down covered, stay at the nest until able to walk and are fed by parents (see YOUNG BIRD).

SEMI-SPECIES: a term of convenience for geographically isolated forms, with obviously near relatives elsewhere, that may be either species (members of a superspecies) or subspecies, there being no way of applying the objective test.

SENESCENCE: see under AGE.

SENMURV: see FABULOUS BIRDS.

SEQUENCE: see ARRANGEMENT.

SERAL COMMUNITY: a community of plants and animals associated with a stage of a SERE. For example, in Britain bare ground will develop through the seral stages of grassland, scrub and low woodland to deciduous forest. Each stage will have its characteristic seral community of birds. Grassland will support a bird community of Skylarks *Alauda arvensis* and Meadow Pipits *Anthus pratensis*, the low scrub stage species such as Dunnock *Prunella modularis* and Whitethroat *Sylvia communis*. A more advanced scrub seral stage will contain several warblers and Nightingales *Luscinia megarhynchos*, and the climax forest, with its components of mature and dead trees, a more varied community including tits *Parus*, Nuthatches *Sitta europaea*, treecreepers *Certhia* and woodpeckers.

SERE: a series of plant communities leading to climax vegetation.

SERICORNIS: substantive name of some Australasian warblers of the genus *Sericornis* (for family see WARBLER, AUSTRALIAN).

SERIEMA: substantive name of the 2 species of Cariamidae (Gruiformes, suborder Cariamae); in the plural, general term for the family. The birds are to be found in the drier areas in south-central South America. The common name is derived from the Tupi word 'çariama', rendered in Latin as *Cariama* by Marcgrave in his account published in 1648, copied by Willughby in his *Ornithologia* of 1676, and so given in many subsequent accounts. Seriema, a modification of the original American Indian word used in Brazil, is preferred and is now replacing the other form in current ornithological writings.

Numerous fossil species related to the modern Cariamidae have been described from middle Tertiary beds of Argentina, and a closely related fossil family, the Bathornithidae, with 4 species described in the genus *Bathornis*, was common during Oligocene time in the Great Plains area of North America.

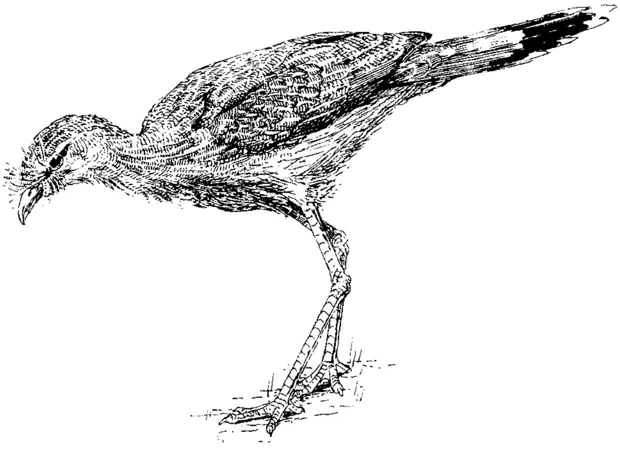
Characteristics, habitat and distribution. Seriemas are allied to cranes (Gruidae) and rails (Rallidae), and are placed in the same order. They show resemblance in form to small cranes (lengths 66–86 cm) as they have long necks, long slender legs, and elongated muscular bodies. The head is heavily feathered, with a frontal crest, the tail is long, and the wings are rounded.

The Crested Seriema *Cariama cristata*, which ranges from central and eastern Brazil south through Paraguay to northern Argentina and Uruguay, is the best known, from its wide distribution and from the fact that the young are readily domesticated and are often taken and reared among fowls, where they serve efficiently as guardians to give warning of predators. The Crested Seriema, which stands about 76 cm tall, is greyish-brown in colour with fine darker vermiculations throughout; the wings and tail are broadly banded with black and white, and the feathers of the underparts have pale longitudinal streaks. The frontal crest is conspicuous, and the bill and legs are red. It lives in areas of open scrub mixed with grasslands, where it moves about on foot and runs rapidly to escape any enemy.

Burmeister's Seriema *Chunga burmeisteri*, found only in Argentina and the western Chaco of Paraguay, is somewhat smaller, with a much less conspicuous frontal crest. It is greyer in plumage, unstreaked below and with a creamy white belly, and the bill and legs are black. It lives in areas of rather open, thorny woodland, where it ranges the ground like the other species. As they are hunted for game, they are wary, so that except for occasional distant glimpses of birds running swiftly through cover their presence is known mainly through their high-pitched yelping calls.

Food. Both species of the family are omnivorous in feeding, and are among those birds that regularly eat smaller snakes of any kind. The common supposition that seriemas have an immunity to the venom of the poisonous species is not true, since it has been found experimentally that birds of both species were killed by injections of attenuated amounts of a crotaline snake poison.

Voice. The loud calls of both seriemas often indicate their presence when the birds themselves are not seen.



Crested Seriema *Cariama cristata*. (*C.J.F.C.*).

Breeding. The nest of the Crested Seriema, rather compactly made of sticks, is recorded up to 3 m above the ground. The eggs, which regularly number 2, are faintly pink when fresh but fade to dull white, sparingly marked with lines or small blotches of brown that appear dark grey or dull purple where overlaid by deposits of shell. The young, covered with dark down when hatched, remain in the nest under the care of the parents until well grown.

The nest of Burmeister's Seriema is located low in trees, and the 2 eggs are similar to those of the other species but with heavier markings.

A.W. (D.W.S. (1)).

SERIN: substantive name of most *Serinus* spp.; used without qualification, in Britain, for *S. serinus* (see FINCH).

SEROLOGICAL CHARACTERS: those expressing differences between species in respect of the chemical nature of the proteins in, particularly, the blood serum—as shown by precipitation reactions and other tests. These proteins (also referred to as 'antigens' or 'serum globulins') represent an important part of the animal constitution and are conservative hereditary traits; they are thus of potential value as supplementary taxonomic criteria; and the same applies to the albumens of egg-white (see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA; TAXONOMY).

SERPENT EAGLE: same as HARRIER EAGLE (and see HAWK (Snake eagles)).

SERTOLI CELLS: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM (Reproduction).

SERUM: see BLOOD; SEROLOGICAL CHARACTERS.

SESAMOID: term applied to small, isolated pieces of bone or cartilage formed in tendons or ligaments.

SET: in respect of eggs, has the same meaning as CLUTCH (see also EGG).

SETOSE: carrying bristle-like feathers.

SEVEN SISTERS: name applied collectively to parties of the Jungle Babbler *Turdoides striatus* in India, from the habit of associating in small bands, often of about 7 birds, at all times of year (see BABBLER). Whistler points out that there is a vernacular (but masculine) equivalent, 'sath-bhai', in which the numeral is used in an approximate sense. Related species have similar habits and may sometimes have the term applied to them.

SEX, CHANGE OF: see OVOTESTIS.

SEX, DETERMINATION OF: see GENETICS.

SEXUAL CHARACTERS: those differentiating male and female. Primary sexual characters are the testis and ovary; accessory sexual characters are other parts of the reproductive system (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM); secondary sexual characters are those, apart from the foregoing, in which the sexes differ—in birds, notably in plumage and voice, sometimes also in size (see below).

SEXUAL DIMORPHISM: the existence of differences in appearance between male and female members of a species. (For dimorphism not related to sex, see POLYMORPHISM.) There are differences of size, structure, shape, plumage and coloration. Although sexual differences in behaviour (for example, singing by males but not by females) should not strictly be referred to as sexual 'dimorphism', because morphology means the study of physical form, in fact most of the theories of sexual dimorphism apply both to sexual differences in form and in behaviour.

Kinds of sexual dimorphism. Most sexual dimorphism in birds is of size and shape, and of coloration. There are a few examples of structural dimorphism. The bill of the extinct Huia *Heteralocha acutirostris* is one (see WATTLEBIRD (2)). The male's bill was relatively short, straight, and stout; the female's was longer, more slender, and more curved. Sexual differences in size are found in many species. The Capercaillie *Tetrao urogallus* is an extreme example, in which the male is more than twice the weight of the female. In the American Jacana *Jacana spinosa*, by contrast, the female is 75% heavier than the male. In most species there is smaller (less than about 10% of body weight) sexual dimorphism in weight, and males tend to be the heavier sex.

Plumage dimorphism is the main source of sexual differences of colour, although in some species the bills or the legs are of different colours. The sexual dimorphism of the Peafowl *Pavo cristatus* is largely due to the greater development in the male of the upper tail-coverts, to form the beautiful metallic green train with its array of eye-spots. Similarly bizarre plumage differences are found in the birds-of-paradise (Paradisaeidae). For instance, in the King of Saxony Bird-of-Paradise *Pteridophora alberti*, the male has two plumes, one growing out of each side of his head. The plumes are about 45 cm long, which is twice the length of the rest of the bird.

In most sexually dimorphic species the sexes show the same constant sex difference throughout the year. But this rule is not universal. In the phalaropes, for example, the males and female both moult into a very similar winter plumage, but in the summer they moult into differing plumages, the female being more brightly coloured.

Theories of sexual dimorphism. The general reason for the evolution of sexual dimorphism is that natural selection can favour different characters in males and in females. There are three particular theories, variously invoking sex differences in reproduction ('sexual selection'), in feeding, and in risk of predation.

Sexual selection. The theory of SEXUAL SELECTION was invented by Charles Darwin, who used it in his book *The Descent of Man, and Selection in relation to Sex* (1871) to explain sexual dimorphism in birds. Sexual dimorphism, he argued, evolves when males (substitute 'females' in role-reversed species) with certain characteristics mate more than do males with other characteristics. The mating advantage might be due either to success in competition with other males, or because females preferentially mate with males that possess some particular characteristic. Preferential mating by females with the most extravagantly adorned males is the most likely explanation of the extreme sexual dimorphism such as that found in the Peafowl. Sexual selection is the only known theory which can explain the evolution of deleterious sexually-dimorphic characters, characters that reduce survival. The Peacock would probably survive better without his long train, but the train might still be a net benefit if it conferred a sufficient advantage in mating. Males, then, in these sexually dimorphic species may have a higher mortality rate than females. There are few observations testing this supposition. In one study of the Great-tailed Grackle *Quiscalus mexicanus* the sex ratio among nestlings was found to be 1:1. Two samples of adults revealed female biased sex ratios (43% and 29% males in the two samples of 939 and 1,349 individuals). The male Great-tailed Grackle is more brightly coloured and has a longer tail than the female. The bright colour might attract predators, and the long tail was observed to inhibit flight, especially in strong wind.

Feeding. Some differences between the sexes may have evolved to reduce competition for food between the male and female of a pair. If the male and female have a different bill size, they may eat different food. Thus when the pair forage they will not compete for the same food. For example, Selander (1972) studied the feeding habits of male and female melanerpine woodpeckers *Melanerpes* spp., which live on Caribbean Islands, and in central America. The species inhabiting the islands of Hispaniola and Puerto Rico have bills which are strongly sexually dimorphic. When Selander watched the feeding habits of the two sexes he found differences. The male and the female therefore probably take different food.


Stonechat *Saxicola torquata* male (above) and female (below) showing sexual dimorphism. (*Photo: J.B. & S. Bottomley*).

To prove that sexual dimorphism serves to reduce competition for food between males and females it is not enough to show that males and females take different food. It must also be shown that food is in so short a supply that the pair catch more food than if they were not dimorphic. That food is in sufficiently short supply in the melanerpine woodpeckers has not been proved, but it is a reasonable assumption.

Predation. The colours of birds may act as signals of various kinds to predators. The most important kind in the evolution of sexual dimorphism is probably the signal to the predator that the signalling bird is an 'unprofitable prey'. Some kinds of prey are easy to catch, and so 'profitable' to the predator. Others ('unprofitable') are less easy to catch. The predator would, if it could distinguish the easy from the difficult prey, concentrate on the easy catches. Thus if a bird is a difficult catch it may evolve bright coloration so that the predator, after a few failed attempts, will learn not to try to catch that kind of prey. The theory is very similar to the evolution of warning coloration in which predators learn to avoid sickening or distasteful prey by virtue of its bright coloration. That predators learn not to eat sickening prey has been proved in experiments.

The two sexes may differ in how easy they are for a predator to catch. If one sex is bigger, it may be better able to fight back. If one sex has to sit on the eggs, it will not be able to run away from predators so easily as the other sex which is not tied to the eggs. The sex which sits on the eggs will then evolve camouflage—it will become cryptically coloured. The other sex will evolve to be conspicuous.

The 'predation' theory predicts that the brightly coloured sex will be eaten less than the cryptic sex. This is the exact opposite of the prediction of the 'sexual selection' theory. As was noted above, few facts have been collected on sexual differences in mortality due to predation.

Explaining trends in sexual dimorphism. The three theories are not completely exclusive of one another. Sexual dimorphism could be favoured at the same time both by sexual selection and by the reduction of competition for food. In other cases the theories are exclusive: the theories of sexual selection and of predation lead to exactly opposite predictions of the relative mortality of the two sexes. The different theories also explain different kinds of dimorphism. The feeding theory explains sexual dimorphism of the feeding organ such as the bill; the predation theory explains sexual dimorphism of coloration; the sexual selection theory is more versatile: it can in principle explain sexual dimorphism of coloration, or of the size of any parts of the bird.

The main force in the evolution of sexual dimorphism would ideally be discovered by testing the three theories on many individual species. In the absence of such detailed studies, some idea of the main forces can be obtained by deriving different predictions from the three theories about which kinds of species should show sexual dimorphism and which should not. In all three theories there is a connection between the mating system and sexual dimorphism; but the connection is not the same in each case.

If sexual dimorphism evolves to reduce competition for food between the sexes, sexual dimorphism should be commoner in monogamous than in polygamous species. If, for example, the breeding group is of one male and three females, all the females would compete for the same food, and sexual dimorphism would be ineffective in reducing competition. However, the general trend is the opposite. Sexual dimorphism tends to be greater in polygamous than in monogamous species. If sexual dimorphism does reduce competition for food, therefore, it is probably a secondary consequence. The theory of sexual selection predicts a greater degree of dimorphism in polygamous than in monogamous species because there is greater competition for mates in polygamous species. Species with the most extreme differences between the males in the number of matings should evolve the most extreme dimorphism. This prediction is borne out: the extremely polygamous LEK species tend to be the most dimorphic. Sexual selection also predicts 'reversed' sex dimorphism in role-reversed species such as jacanas and phalaropes. In these species only the males care for the young, so sexual selection is reversed and females compete for males.

The predation theory makes similar predictions to the theory of sexual selection. If one sex cares for the young while the other is active, the more active sex will be more brightly coloured. So both theories predict the same patterns of sexual dimorphism in polygynous and polyandrous species.

Sexual selection, feeding, and predation are the main (but not the only) factors affecting sexual dimorphism. We do not yet know their relative importance. See photos HEAT REGULATION; LEK. M.R.

Baker, R.R. & Parker, G.A. 1979. The evolution of bird coloration. Philosophical Transactions of the Royal Society of London B287: 63–130.
Selander, R.K. 1972. Sexual selection and dimorphism in birds. *In* Campbell, B. (ed.). Sexual Selection and the Descent of Man. London.

SEXUAL SELECTION: a form of natural selection resulting from competition between members of one sex for opportunities to mate with members of the opposite sex. Darwin pointed out that sexual selection could arise either by direct competition for access to members of the opposite sex, e.g. by fighting ('intrasexual selection') or by differences in ability to court members of the opposite sex ('epigamic' or 'intersexual selection'). The distinction is not absolute: males may compete with each other for high quality territories and females may choose to mate with males that possess such territories. Sexual selection often results in the production of characteristics, such as the bizarre plumage and exhausting courtship behaviour of the Ruff *Philomachus pugnax*, that benefits the individual but is wasteful in terms of the species as a whole. The realization that this is also true of other forms of natural selection has led evolutionists to consider sexual selection as part of natural selection, rather than as a distinct phenomenon (see NATURAL SELECTION).

In general, the number of offspring a female produces does not depend on the number of males she mates with but on her capacity to produce eggs. Selection will generally favour females that only allow themselves to be inseminated by males that are likely to have genetically fit offspring, since those offspring will bear the genetic output of the females. Males, however, can inseminate many females with little physiological effort, so selection generally favours males that inseminate any willing females, even females that are unlikely to produce many offspring. This is why females generally require to be courted whereas males are less discriminating. It is also why sexual selection is most intensive in males.

In birds, parental care is important in determining the survival of offspring and a male may increase his reproductive output more by caring for the offspring of one mate than by striving to obtain many mates but not helping to raise his offspring. This is why birds are typically monogamous, in contrast to the majority of animals. In those species where paternal care is less important, polygyny prevails and there is more intensive sexual selection. Many polygynous species show marked SEXUAL DIMORPHISM, with elaborate male plumages and much effort put into competition between males. In species where males, not females, are mainly responsible for parental care, the males are a resource for which females compete, so that sexual selection is more intensive on the females than on the males, leading to 'sex-role reversal' (e.g. PHALAROPE).

Though of reduced intensity, sexual selection still occurs in monogamous species. The members of each sex compete to mate with those members of the opposite sex that are likely to produce most surviving offspring, because they are ready to breed at the optimum season, are in possession of high quality territories, and are likely to be good parents.

While the processes of intrasexual selection are easy to understand, those involved in epigamic selection are less clear. Such selection arises because females (usually) choose males with certain characters. If some females show a preference for a particular type of male, and the rest of the females show no preference, then the preferred type of male will be selectively favoured, other things being equal. Furthermore, as first noted by R.A. Fisher, the preference itself is selectively advantageous. Males of the preferred type, and thus the females that prefer them, will tend to produce sons of the preferred type; these will be selectively favoured because they are of the preferred type; thus their mothers, females showing the preference, will tend to produce more grandchildren than females that do not show the preference. Thus there is a runaway process in the joint establishment of the preference and the preferred characteristics. The female choice may originate in various ways. Its origin may be 'accidental', a by-product of other selective forces operating on the behavioural repertoire of the female. Alternatively females may choose mates that are likely to be good fathers, either because they are able to care for their offspring well or because they are likely to pass on to their offspring genes that will result in the offspring being genetically fit. Courtship feeding by terns, for example, may be a way in which a male demonstrates his fish-catching abilities, on which his success as a father partly depends, to a potential mate.

Sexual selection may be important in the development of breeding barriers between species. Suppose that the hybrids between two populations are less fit than individuals of pure parentage, as may happen when the genetic constitutions of two populations originally of the same species come to diverge markedly. In each population, selection will favour those individuals that choose to mate only with members of their own population. The result will be the evolution of discriminatory behaviour and of species-specific recognition characters (see SPECIATION). J.J.D.G.

Halliday, T. 1980. Sexual Strategy. Oxford.
O'Donald, P. 1980. Genetic Models of Sexual Selection. Cambridge.

SHAFT: see FEATHER.

SHAG: substantive name almost interchangeable with 'cormorant' for *Phalacrocorax* spp.; but in the British Isles, each name standing alone, Shag means *P. aristotelis* and Cormorant means *P. carbo* (see CORMORANT).

SHAKESPEARE'S BIRDS: see POETRY, BIRDS IN (References).

SHAKETAIL: substantive name sometimes used for *Cinclodes* spp. (see OVENBIRD (1)).

SHAMA: substantive name of some *Copsychus* spp. (for subfamily see THRUSH).

SHANK: a popular term for the whole or some part of the leg, lacking definition (see LEG). In such bird names as 'redshank' it clearly refers to the visible part of the leg, and especially to the so-called tarsus (which is in fact the foot, and thus not equivalent to any part of the human leg that would be thus termed).

SHAPE AND POSTURE: see SIZE.

SHARMING: grunts and squeals of a Water Rail *Rallus aquaticus*.

SHARPBILL: substantive name of *Oxyruncus cristatus*, sole member of the family Oxyruncidae (Passeriformes, infraorder Tyranni). A Neotropical species with a rather discontinuous distribution in upper tropical and lower subtropical humid forests in Costa Rica, Panama, south-eastern Venezuela, Guyana, Surinam, south-eastern Brazil and Paraguay. It is about 16 cm long with a stout, short-legged, small-headed appearance. The bill tapers from a broad base to a sharply pointed tip. The plumage is olive green above and pale yellow below, profusely spotted with black. A flattened crest with elongated scarlet feathers is present but usually concealed. The sexes are similar in appearance but males have a serrated outermost (10th) primary of unknown function.

Sharpbills are occasionally encountered among canopy-feeding flocks of barbets, honeycreepers and tanagers. Birds watched in the Serra dos Orgãos, Brazil, in December were feeding largely on invertebrates, 'caught with great agility from among the leaves in the very outermost twigs of the canopy. A common technique involved hanging upside down and feeding tit-like with rapid pecks into the bases of leaf-clusters' (Brooke *et al* 1983), to which the bird's sharp bill is well adapted. Stomach contents and other field observations suggest a diet mainly of berries.

Males apparently call from expanded leks of 4 to 6 individuals. The advertisement call varies geographically but is basically a buzzy, high-pitched, long-drawn-out whistle, which gradually descends in pitch.

The first Sharpbill's nest was found in October 1980 in montane forest some 50 km north of Rio de Janeiro. It was situated just below the higher leaves in the canopy of a 30 m tall tree. Only one bird, assumed from its drab plumage to be the female, was ever seen. The nest was a shallow cup made of leguminous petioles and a few dry leaves, coated with mosses, liverworts and spiders' webs, and was saddled, like a hummingbird's nest, on a slender horizontal branch. There were probably 2 eggs, which hatched after between 14 and 24 days' incubation; the fledging period was probably 25–30 days. N.G.S.

Brooke, M. de L., Scott, D.A. & Teixeira, D.M. 1983. Some observations made at the first recorded nest of the Sharpbill *Oxyruncus cristatus*. Ibis 125: 259–261. (Contains useful list of references.)

Mees, G. 1974. Additions to the avifauna of Suriname. Zool. Mededelingen 48: 55–67.

Ridgely, R.S. 1976. A Guide to the Birds of Panama. Princeton.

Wetmore, A. 1972. The Birds of the Republic of Panama, Part 3. Smithsonian Institution.

SHARPTAIL: abbreviated name of the Sharp-tailed Grouse *Tympanuchus phasianellus* (see GROUSE).

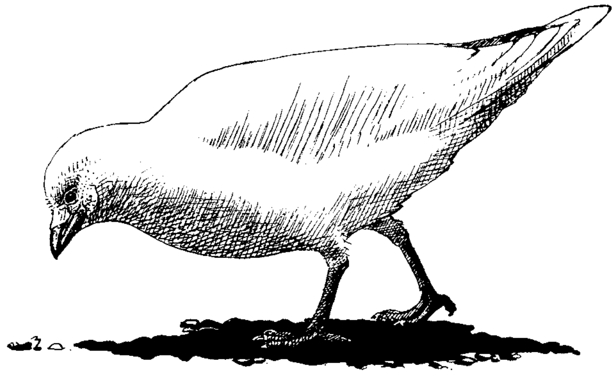
SHEARTAIL: substantive name of *Doricha* spp. and *Thaumastura cora* (for family see HUMMINGBIRD).

SHEARWATER: substantive name of certain species of Procellariidae, in the genera *Puffinus*, *Procellaria*, etc.; in the plural, a general term for these (see PETREL). The name is sometimes locally misapplied to other sea birds, e.g. *Rynchops* spp. (see SKIMMER). See photo NOCTURNAL HABITS.

SHEATHBILL: substantive name of the 2 species of Chionidae (Charadriiformes, usually placed in the suborder Charadrii); in the plural, general term for the family.

Characteristics. Sheathbills are small white pigeon-like shorebirds 36–42 cm long; biochemical indicators suggest slightly closer affinities with Lari than with Charadrii.

'Sheathbill' derives from the horny yellow-green sheath that covers the base of the short, stout bill. In American Sheathbills *Chionis alba* the bill is yellow and black, in the Lesser Sheathbill *Chionis minor* (which is slightly smaller) it is almost entirely black. The eyes are pink-rimmed and the cheeks bear wattles and patches which are small in juveniles, bigger in mature birds. The plumage is entirely white with grey underdown. The legs, blue-grey or pink, are short and stout, and the toes have only vestigial webs. Although sheathbills have been seen in flight several hundred km from land and are capable of long migratory flights, they spend much of their time on the ground, trotting busily about the shore in search of food and showing reluctance to fly even when pursued. The wings are small, with sharp carpal spurs that the birds use in fighting. Males are slightly larger and heavier than females.


Sheathbill *Chionis alba*. (*B.P.*).

Habitat and distribution. Sheathbills live on or close to the shore of islands in the sub-antarctic sectors of the Atlantic and Indian Oceans, often but not exclusively in association with penguin colonies. Sheathbills (or American Sheathbills) breed on South Georgia, the South Orkney and South Shetland Islands, possibly the South Sandwich Islands, and the Antarctic Peninsula to about 65°S; some winter in Patagonia, the Falkland Islands and Tierra del Fuego, others are resident through the year. Lesser sheathbills breed on Marion, Prince Edward and Heard Islands and Iles Crozet and Kerguelen; island races are postulated.

Food. Sheathbills feed on shore animals of the intertidal zone; they eat large quantities of *Ulva* and other algae, perhaps for the animals that live among them, and dig with their bills in crevices between rocks. Stranded plankton, faeces of seals and penguins, carcasses and offal of every kind are taken. On penguin colonies they scavenge for eggs and fallen chicks, darting between the brooding parents to pick up scraps of spilled food; some learn to flutter or peck at parents engaged in feeding their chicks, causing both to spill food. Though constantly in danger from darting beaks, they are usually quick enough to escape without harm.

Behaviour. Between breeding seasons they live in small flocks, quarrelling frequently among themselves and feeding communally. They are inquisitive and enterprising in searching for food, quickly learning to associate with men at expedition bases and campsites.

Voice. Sheathbills are usually silent; chicks have cheeping alarm and food calls, adults croaking or growling threat calls.

Breeding. The nests are built in crevices and under boulders, often on a rocky headland overlooking a penguin colony. Sheathbills continue to feed gregariously but nest in isolation; nests are well hidden and approached indirectly. Two to 4 brown eggs, flecked with grey or black, are laid in December/January; incubation (both parents) takes 29 days. Chicks hatch asynchronously in brown down, changing to grey mesoptile down at 7 days and fledging in 7 to 9 weeks. Most pairs rear one or 2 chicks only. B.S.

Burger, A.E. 1979. Breeding biology, moult and survival of Lesser sheathbills *Chionis minor* at Marion Island. Ardea 67: 1–14.

Jones, N.V. 1963. The Sheathbill, *Chionis alba* (Gmelin), at Signy Island, South Orkney Islands. Bull. British Antarctic Survey 2: 53–71.

SHELDGEESE: general term for some larger species of Tadornini (Anatidae) (see under DUCK).

SHELDUCK: substantive name of *Tadorna* spp.; used without qualification in Britain for *T. tadorna*, and sometimes written 'sheld-duck' or 'sheldrake' (see DUCK).

SHELL-GLAND: or 'uterus', part of the oviduct (see LAYING; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

SHIELD, FRONTAL: a hard, featherless plate extending from the base of the upper mandible backwards over the forehead, as in coots *Fulica* spp. and others (compare CASQUE).

SHIKRA: *Accipiter badius* (see HAWK).

SHOEBILL: name, alternatively 'Shoe-billed Stork' or 'Whale-headed Stork', of *Balaeniceps rex*, sole member of the Balaenicipitidae, a family of disputed affinities. It has usually been placed in the order Ciconiiformes, sometimes in the suborder Ardeae, sometimes, as here in the suborder Ciconiae—even in the Ciconiidae (see STORK) instead of in a separate family—and sometimes in a suborder of its own. Wetmore (1960) holds that it has affinities both with Ciconiae and Ardeae, and that the resemblance of the skull to that of Pelecaniformes is due to convergence. More recent behavioural and morphological studies have not altered this assessment (Guillet 1979).

Characteristics, habitat and behaviour. The Shoebill is a large bird, standing 120 cm high or more, with slaty plumage, long dark grey legs with very long toes. The most obvious character is the large head on a not very long neck, with a slight untidy crest on the nape and an enormous bulging bill, particoloured and carrying a hook on the upper mandible. It is a bird of swamps and water margins, often standing on 'islands' of floating vegetation. In such situations it remains motionless, bill on breast, waiting for fish or other aquatic prey to come within reach. The highly modified bill is adapted for catching and extracting prey among dense aquatic vegetation; and it is not used, as has been claimed, for digging lung-fish out of the mud. It is partly nocturnal in its habits and it is considered to be of a rather sluggish disposition; but it can fly strongly—and soar—on its broad wings, with neck drawn in and bill resting on the breast (as in the Pelecanidae). It is not a gregarious bird; and it is rather silent, apart from a laughing note and a stork-like clattering of the bill which is mainly performed during territorial and courtship displays.

Distribution. The species has a limited range in eastern tropical Africa, mainly in the southern Sudan, northern Uganda, and some eastern parts of Zaire. The semipermanently flooded White Nile valley and the swampy borders of Uganda lakes are typical habitats.

Breeding. The nest is a truncated cone of grass placed on floating vegetation, occasionally on an islet; in this, 2, sometimes only 1 or 3 bluish white chalky eggs are laid. The young are downy and nidicolous.

(A.L.T.) A.G.

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SHOEMAKER: name applied to the White-chinned Petrel *Procellaria aequinoctialis*, also called 'Cape Hen' in South Africa (see PETREL).

SHOOTING: see under UTILIZATION BY MAN.

SHORE-BIRD: term used in North America in the same sense as 'wader' is in the British Isles (see WADER).

SHORELARK: *Eremophila alpestris*, the 'Horned Lark' in American usage (see LARK).

SHORTWING: substantive name of *Brachypteryx* spp. (see THRUSH).

SHOULDER: see under MUSCULATURE; SKELETON, POST-CRANIAL; WING.

SHOVELER: substantive name of some *Anas* spp.; used without qualification in Britain for *A. clypeata* (see DUCK).

SHRIKE: substantive name (or part of compound name) of most species of Laniidae (Passeriformes, suborder Oscines); in the plural, general term for the family. Formerly considered by Rand (1960) to include 4 subfamilies: Prionopinae, the helmet-shrikes; Malaconotinae, the bush-shrikes; Laniinae, the true shrikes; and the monotypic Pityriasinae containing the Bornean Bristlehead *Pityriasis gymnocephala*. In this volume Voous, following others, places the helmet-shrikes in their own family Prionopidae and, in addition, places the Bristlehead in its own family Pityriasididae. Recently the bush-shrikes have been placed in their own family Malaconotidae (see Benson and Benson (1977) for reasons and references) but Voous retains them as a subfamily of Laniidae. Sibley (1970) has emphasized, however, that relationships between shrikes are complicated by the frequency of convergence of the shrikelike bill, and similarities of egg white protein patterns of some bush-shrikes and true shrikes are not sufficient proof of a relationship between them.

Of the 68 species of true shrikes and bush-shrikes recognized by Hall and Moreau (1970), the only ones not endemic to the Afrotropical Region are an isolated population of the Black-headed Tchagra *Tchagra senegala* in North Africa, and 13 species of *Lanius* which inhabit the Holarctic region, apart from a race of the Black-headed Shrike *L. schach* found in New Guinea. Six of the 8 *Lanius* species endemic to Africa are closely related to Eurasian species and a number of superspecies have been proposed (Hall and Moreau 1970, Mayr and Short 1970). Similarly Hall and Moreau have grouped 37 of the other 47 African shrikes into 9 superspecies. Their approach emphasizes the high degree of specialization and subsequent speciation that has occurred in African shrikes, and their groupings and nomenclature are followed here. They retain the genus *Rhodophoneus*, which Rand (1960) absorbs into *Tchagra*, and place the members of the genus *Telophorus* in *Malaconotus*. In the past these have been separated on the grounds of size but this ignores the remarkable evolutionary parallelism that exist in the 2 genera (White 1962).

Systematic characteristics. All shrikes have a sharply hooked bill with a tooth in the upper bill and a corresponding notch in the lower mandible. Their legs and feet are strong and the claws sharp for catching prey. The wing has 10 primaries and the tail 12 rectrices.

Malaconotinae. These are a mixed group. In some (*Malaconotus*) the bill is large and strong, in others (e.g. *Tchagra*) moderately so, and in others (*Dryoscopus*) relatively weak. The feathers on the rump are soft and elongated, particularly so in *Laniarius* and *Dryoscopus*. Seven genera are recognized: *Lanioturdus*, *Nilaus*, and *Rhodophoneus* (all monotypic), *Dryoscopus* (6 species), *Tchagra* (5 species), *Laniarius* (15 species) and *Malaconotus* (16 species). In many species, but not all, the sexes are dimorphic. Their lengths range from medium (14.5–19.5 cm) in *Dryoscopus* to large (18.5–27.0 cm) in *Malaconotus*.

Laniinae. These are the most typical of the shrike family. The bill is particularly strong and heavily notched, the external nostrils are oval and partly covered with small hairs, the rictal bristles are well developed, the tarsus scutellated only in front and lamellated behind. Two genera are recognized: *Lanius* (21 species) and *Corvinella* (2 species) which is occasionally split into a third genus *Urolestes*. The majority are sexually dimorphic. In *Lanius* lengths are in the range 15–31 cm and in *Corvinella* 30–35 cm.

Field characteristics, habitat and distribution

Malaconotinae. Of the 3 species in monotypic genera, the most widely distributed is the Brubru *Nilaus afer*. It inhabits moist and dry savanna woodlands north and south of the Equator and several races are recognized. Males are black above, females brown, and both are mottled with white and buff; the underparts are white with some chestnut.

Four of the 6 puff-backs *Dryoscopus* spp. are placed in a superspecies. They are similarly patterned black, white and grey above and white below. Differences between males mainly lie in bill size; the females have distinctive colours. Usually they are allopatric but when sympatry occurs the species are always ecologically separated. The Black-backed Puff-back *Dryoscopus cubla* occupies the mainly deciduous woodland in southern Africa and the Puff-back *D. gambensis* similar habitat in West Africa. The Black-shouldered Puff-back *D. senegalensis* occurs in secondary forest in Zaire and Nigeria, and Pringle's Puff-back *D. pringlii* in dry acacia steppe in north-east Africa. In contrast, the other puff-backs are forest birds.

The tchagras have rufous wings, brown backs, paler underparts, black and white graduated tails and patterned heads. Three of them have mainly brown heads and each may be distinguished from the others by the size of the bill and amount of black on the head; in addition, all 3 are allopatric. The Brown-headed Tchagra *Tchagra australis* is widespread in savanna woodland throughout Africa; it is replaced by the Three-streaked Bush-shrike *T. jamesi* in acacia steppe in Somalia and Kenya and by Levaillant's Bush-shrike *T. tchagra* in the coastal strip from Natal to Cape Town. In contrast, the Black-headed Tchagra *T. senegala* has a black crown and, although it has a similar distribution to *australis*, it, in general, prefers a drier habitat. The Blackcap Tchagra *T. minuta* is restricted to wetter areas than are the other tchagras and is the only one which is sexually dimorphic.

The *Laniarius* species divide into 3 colour groups in each of which the species are largely allopatric. In the crimson group, 3 out of the 4 species with crimson underparts inhabit acacia steppe and sometimes are considered conspecific; the Gonolek *L. barbarus* in West Africa, the Black-headed Gonolek *L. erythrogaster* in central Africa and Burchell's Gonolek *L. atrococcineus* in southern Africa. The fourth, *L. mufumbiri*, is smaller, has a distinctive orange tinge to the crimson, and is confined to papyrus swamps in central Africa. In other parts of Africa they are replaced by other members of the group which are coloured differently. The most divergent of the group is the Red-naped Bush-shrike *L. ruficeps* found in the arid acacia steppe of north-east Africa. The black of the back is mixed with grey and white and it has a prominent white eye-stripe not present in the others. The female is more olive grey on the mantle. In the other species of this group the sexes are alike.

The black and white group has 4 species often considered conspecific. The best known is the Bell Shrike or Tropical Boubou *L. aethiopicus*, which is glossy blue black above and pinkish white below. It inhabits thickets in savanna woodland throughout Africa, both lowland and montane. In southern Africa, coastal Gabon and Angola, and in the forests of Sierra Leone and Guinea, it is replaced by 3 other species of the group.

The black group, some of which show sexual dimorphism, range in colour from deep black to dark slate grey. The Sooty Boubou *L. leucorhynchus* occurs in West African and Zaire lowland forest blocks and, in contrast, the Slate-coloured Boubou *L. funebris* in acacia steppe in north-east Africa. The distribution of the other 2 species is restricted to separate montane forest blocks some 2,200 km apart.

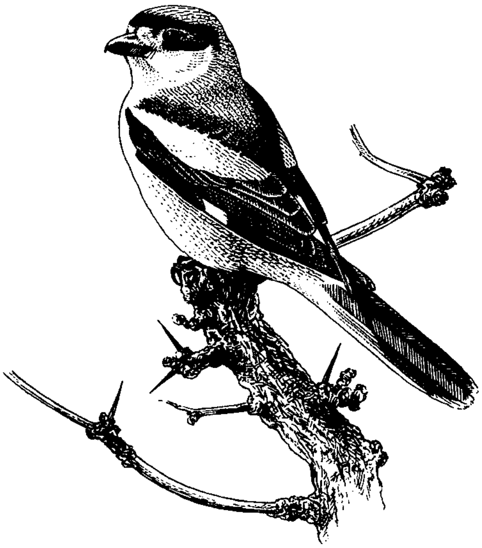
Of the *Malaconotus* species 10 are grouped into 2 superspecies. Both contain savanna and forest species, those in the lowland forest being polymorphic. The remarkable feature about them is that wherever a savanna or forest form of one superspecies meets a corresponding form of the second superspecies there is almost perfect colour match between them. Thus the savanna dwelling Sulphur-breasted Bush-shrike *M. sulfureopectus*, with green back, grey head and mainly yellow underparts, is simply a small replica of the much larger savanna species, the Grey-headed Shrike *M. blanchoti*. Similarly the small Many-coloured Bush-shrike *M. multicolor*, found in the forests of West Africa and Zaire, is matched in colour by the Fiery-breasted Bush-shrike *M. cruentus*, a larger forest species in the other superspecies (further details are given in Hall, Moreau and Galbraith 1966).

Of the remaining 6 species, 3 are grouped to form a third superspecies. They are all bright green above, their tails are black and breasts red with a black pectoral band. Two are birds of thicket and forest edge, Perrin's Bush-shrike *M. viridis* in Angola, and the Four-coloured Bush-shrike *M. quadricolor* in Kenya, Mozambique and South Africa. The other, Doherty's Bush-shrike *M. dohertyi*, is confined to mountains of eastern Zaire.

Laniinae. The true shrikes are birds of open woodland, rarely forest edge. They have the habit of dropping off a perch when alarmed and flying off close to the ground before swooping up to the next perch. When perched they frequently swing their tails from side to side, and up and down.

Two of the red-backed group occur in Africa. Emin's Shrike *Lanius gubernator* inhabits the savannas north of the Equator, and Souza's Shrike *L. souzae* the brachystegia woodlands south of the Equator. Both are similar but not identical to the Red-backed Shrike *L. cristatus* (*collurio* considered a race of *L. cristatus*) the male of which has a grey head, a black eye streak, and a grey rump. The races of *cristatus* in Asia are a uniform mouse brown on the upperparts and these have sometimes been treated as a separate species. Other red-backed shrikes replace it in south-east Asia and India and overlap its distribution in eastern Asia.

Five black and white shrikes, all with long graduated tails, are found in Africa. All are essentially allopatric, but when sympatry occurs there is ecological segregation between species. The most widely distributed is the Fiscal Shrike *L. collaris* which occurs throughout Africa in savanna woodland, forest clearings and cultivations. The Great Grey Shrike *L. excubitor*, a paler bird than *collaris*, is only found along the southern edge of the Sahara but is widespread in the Palearctic and is the only shrike found in North America (the Loggerhead Shrike being considered a race); numerous races have been described. Two other African black and white shrikes with very long tails, the Grey-backed Fiscal *L. excubitorius* and the Long-tailed Fiscal *L. cabanisi*, are noted for their sociability. They are allopatric and occur in wooded savannas of central and east Africa. Two other sociable shrikes in Africa have unusual coloration; the Yellow-billed Shrike *Corvinella corvina* of west and central Africa is a heavily streaked brown shrike with yellow bill, the Magpie Shrike *C. melanoleuca*, confined to the southern half of Africa, is black with some white on the flanks and in the tail.


Woodchat Shrike *Lanius senator*. (*A.H.*).

The Strong-billed Shrike *L. validirostris* is of interest as it is confined to the Philippines and found in oak and pine forest between about 1,300 m and 2,600 m. Its upperparts are grey, wings and tail brown-black, and underparts grey-white with rufous flanks; a black streak extends from the lores to the ear coverts.

Movements. Although there are no ringing data to show that shrikes endemic to Africa migrate within it, there are visual records which suggest that local movements occur in some populations of the Sulphur-breasted Bush-Shrike, and are likely in the Brubru and Magpie Shrike.

Africa is the wintering area for all populations of the Lesser Grey Shrike *L. minor*, Woodchat *L. senator* and Nubian Shrike *L. nubicus*, and for some populations of the Red-backed Shrike and the Red-tailed Shrike *L. isabellinus* (Moreau 1972); their other populations winter in south-east Asia. Of the other Laniinae found outside Africa only 4 migrate southwards after breeding further north; the Chinese Great Grey Shrike *L. sphenocercus* winters from Korea southwards; the Tiger Shrike *L. tigrinus* winters in the Malay peninsula, some stragglers reaching the Philippines and Sulawesi; some populations of the Bull-headed Shrike *L. bucephalus* winter in central Korea and south China; and some populations of the Black-headed Shrike migrate into northern India. Only the most northern populations of the Great Grey Shrike migrate southwards after breeding.

Food

Malaconotinae. These are predominantly insectivorous. All tchagras, *Rhodophoneus* and most, if not all, *Laniarius* species feed near or on the ground in or under thicket, but in more open areas *Rhodophoneus* is more arboreal. The Flycatcher-shrike *Lanioturdus torquatus* feeds both on the ground and in trees. All other members of the subfamily are arboreal feeders, the puff-backs feeding much like warblers. Occasionally the Grey-headed Shrike takes other food items (various vertebrates and bird's eggs), and so do the Southern Boubou *L. ferrugineus*, the Brown-headed Tchagra and the Black-headed Tchagra (van Someren 1956).

Laniinae. These characteristically search the ground for prey from a vantage point, from which they drop to the ground to catch it. Although a great variety of insects are taken, many depend on small vertebrates for an important part of their diet. They may catch insects on the wing, search for prey on the wing, hovering before pouncing on it, and some search leaf litter. Most Palearctic species use larders but only 2 shrikes in Africa are known to do so, Mackinnon's Shrike *L. mackinnoni* and some races of the Fiscal Shrike. None of the shrikes that winter in Africa are known to use larders while there.

Behaviour

Malaconotinae. In general, bush-shrikes are found singly or in pairs but small groups (5 or 6 birds), apparently not family groups, of Brown-headed Tchagras, Grey-headed Shrikes and Fiery-breasted Shrikes have been reported. They breed in pairs and some remain paired throughout the year (observed in *Laniarius*, *Dryoscopus*, *Tchagra* and *Malaconotus* species) (Kunkel 1974). What little data we have on this group suggest that both sexes build nests, incubate and feed young, and that territories are maintained outside the breeding season by some savanna species. The puff-backs and the Brubru form mixed feeding parties with other species in the non-breeding season.

Courtship display in *Dryoscopus* involves the raising of the rump feathers by the male to produce the puff from which the genus obtains its name; this also occurs in some *Laniarius* species (details in van Someren 1956). In the tchagras it involves a display flight with duetting, and some wing flapping, although less developed in the Blackcap Tchagra.

Little is known of the monotypic genera *Lanioturdus* and *Rhodophoneus*. Both are found in parties, particularly the latter which forms noisy display groups on the ground at dusk, the significance of which is not known.

Laniinae. The majority of true shrikes breed in pairs, are highly territorial even when on migration, and some are known to hold territories in their winter quarters (Red-backed Shrike, Lesser Grey Shrike and probably the Great Grey Shrike). The migratory species are usually solitary in winter quarters and usually migrate singly, but the Woodchat and some races of the Red-backed Shrike are paired on arrival at their breeding grounds. The Fiscal Shrike may remain paired for several years and Souza's Shrike remains paired outside the breeding season. In several species both sexes help in nest building, incubation and feeding young; in others the male has only been reported feeding young.

In contrast, the 2 *Corvinella* species, the Grey-backed Fiscal and the Long-tailed Fiscal, are all highly social. Although the first 3 breed in groups of 5 or more birds (Grimes 1980), some populations, at least, of the Long-tailed Fiscal breed in pairs with individual territories (van Someren 1956). Nothing is known about the permanency of the pair bond; in the Yellow-billed Shrike a female may remain the breeding female of a group for more than one breeding season and then become the breeding female of a subsequent group.

Voice

Malaconotinae. The bush-shrikes have a diverse range of calls rather than a recognized song, although the Olive Bush-shrike *M. olivaceus* is noted for its warbling song. The Brubru, an onomatopoeic name, utters a drawn out *brruuu*, reminiscent of a pea whistle, which often is answered by the female with a similar note of lower pitch. The calls of *Dryoscopus* species are variously described as loud, oft repeated or prolonged whistles; the Puff-back has a melodious song and the Black-backed Puff-back is known to duet. The tchagras are noted for their melodious, almost human whistles, given during a display flight, occasionally from a perch, while the female responds antiphonally with a call characteristic of the species. Duet song, usually antiphonal, is characteristic of all the *Laniarius* species. Each *Malaconotus* species has loud, distinctive and repetitive calls, that of the Bokmakierie *M. zeylonus* is onomatopoeic, and duetting is frequent.

Laniinae. Although the true shrikes have harsh and discordant contact and alarm calls, the majority of them have notable songs and many are good mimics.

Breeding. The nests of the Brubru, puff-backs, tchagras, gonoleks and boubous are inconspicuous but neatly formed shallow cups, either secured to a horizontal branch as in the Brubru, or placed in a fork of a tree from 2–7 m above ground. Occasionally nests of puff-backs are found as high as 18 m. Materials used include tendrils, spider webs, lichen, rootlets, grass and bark fibre.

In *Malaconotus* the nests of the majority of species are usually shallow cups of twigs, tendrils and root fibres, lined with finer materials, and placed 3–8 m above ground; some species build as high as 18 m. The nest of Lagden's Bush-shrike *M. lagdeni* is described as a bulky bowl of dry leaves and bracken.

The nests of the Laniinae also vary a great deal. Those constructed at high latitudes have wool, hair and feathers as lining, whereas those at lower latitudes are usually lined only with tendrils and fibres or grass. Nests are built from twigs, tendrils and other materials and usually placed 3–9 m high in a tree, although the Red-backed Shrike prefers thickets and brambles.

Shrike eggs have a range of ground colours, variously listed as white, greyish-white, pale-blue grey, blue, greenish blue, and pale pinkish. The eggs are either streaked, speckled or blotched with various shades of brown, purple-brown and chestnut-brown, the markings being concentrated usually at the large end. The clutch size of bush-shrikes is either 2 or 3, not 4 or more. By contrast, a clutch of 4 or more has been recorded in the following African *Lanius* species: Fiscal Shrike, Somali Shrike *L. somalicus*, Taita Fiscal *L. dorsalis*, Grey-backed Fiscal, Long-tailed Fiscal and the 2 *Corvinella* species; in others for which data are known the clutch is 2 or 3 (Mackinnon's Shrike, Souza's Shrike, Great Grey Shrike). The resident shrikes in India and south-east Asia have clutches between 3 and 6, although it is 2 for the New Guinea race of the Black-headed Shrike. The clutch size of shrikes breeding in higher latitudes is in the range 5–7, but larger clutches are not uncommon.

Incubation periods are most frequently in the range 12–14 days, occasionally 15–18 days for some *Lanius* species. The most frequently reported range for the nestling period is 16–20 days, but 12–15 days are recorded for the Red-backed Shrike and the Lesser Grey Shrike. The breeding seasons of shrikes in Africa, India, and south-east Asia are prolonged and overlap both dry and wet seasons. The migratory shrikes breed during the northern summer, some as early as April but mainly in late May, June and early July. L.G.G.

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SHRIKE, ANT-: see ANTSHRIKE; ANTBIRD.

SHRIKE-BABBLER: substantive name of *Pteruthius* spp. (see BABBLER).

SHRIKE, BUSH-: see BUSH-SHRIKE; SHRIKE. Also used as substantive name in some genera of Formicariidae (see ANTBIRD).

SHRIKE, CATERPILLAR-: see CUCKOO-SHRIKE.

SHRIKE, CROW-: name sometimes applied to *Strepera* spp. See CURRAWONG.

SHRIKE, CUCKOO-: see CUCKOO-SHRIKE.

SHRIKE, FLYCATCHER-: see CUCKOO-SHRIKE.

SHRIKE, HELMET-: see HELMET-SHRIKE.

SHRIKE, PEPPER-: see PEPPER-SHRIKE.

SHRIKE, SONG-: name sometimes used for CRACTICIDAE.

SHRIKE, SWALLOW-: see WOOD-SWALLOW.

SHRIKE-THRUSH: substantive name of *Colluricincla* spp. (see THICKHEAD).

SHRIKE-TIT: substantive name, in Australia, of *Falcunculus* spp. (see THICKHEAD).

SHRIKE-TYRANT: substantive name of the species of *Agriornis*, a genus of South American tyrant-flycatchers (see FLYCATCHER (2)).

SHRIKE, VANGA: see VANGA.

SHRIKE-VIREO: substantive name of species of the subfamily Vireolaniinae (Passeriformes, suborder Oscines); in the plural, general term for the subfamily. The shrike-vireos are a small group of arboreal song-birds confined to the forested regions of continental tropical America. The 2 genera and 3 species are sometimes placed in a separate family, the Vireolaniidae, but are now often included, as here, in the Vireonidae. The shrike-vireos differ from typical vireos in having a heavier bill, which is hooked at the tip (see VIREO; also PEPPER-SHRIKE). They feed mainly upon caterpillars and mature insects which they glean from the foliage of trees but vary their diet with berries. Like typical vireos and pepper-shrikes, they hold large objects beneath a foot while they tear them apart with the bill.

Characteristics, habitat, distribution and behaviour. The Chestnut-sided Shrike-Vireo *Vireolanius melitophrys*—the only member of its genus—is a stout, long-tailed bird about 17 cm long. The largest member of the subfamily, it is also the northernmost and the only one of which the sexes, although similar in plumage, are readily distinguished in the field. Its upper plumage in plain olive-green, with the top and back of the head slate-grey, bordered on each side by a yellow superciliary stripe, below which a black band stretches from the lores to the ear coverts. The ventral plumage is white, with black malar streaks and a chestnut band that crosses the breast and continues along the sides and flanks. This little-known bird is found, chiefly in forests of pine, oak, and other broad-leaved trees, from central Mexico to the volcanic highlands of Guatemala and from 1,200 to 3,000 m. It forages, often in pairs, amid the foliage of trees and shrubs at all heights, where it moves slowly and deliberately, peering from side to side, sometimes hanging inverted to pluck an insect from a leaf. Among its notes are a low, nasal rattle and a peculiar, long-drawn, high-pitched, far-carrying, whistled screech. The two known nests, built by both sexes, were hemispheric cups, attached by their rims to the arms of horizontal forks, in the usual manner of vireos. Situated amid foliage at heights of 7–8 m, they were composed largely of filamentous lichens and vegetable fibres. Eggs, incubation and care of young remain undescribed.

The 2 species of *Smaragdolanius* inhabit heavier, more humid forests at low and middle altitudes. The Green Shrike-Vireo *S. pulchellus* is about 14 cm long. Its upper plumage is bright parrot-green with more or less blue on the crown. The throat is yellow, and the remaining under parts light greenish yellow. From south-eastern Mexico to Colombia and north-western Venezuela, this bird lives in the upper levels of the forest, from which it sometimes ventures into neighbouring clearings with scattered trees. Although its loud, clear, tirelessly repeated whistles, grouped in trios or more rarely quadruplets, are often heard, its nest has apparently never been found. Equally unknown are the breeding habits of the Slaty-capped Shrike-Vireo *S. leucotis*, widespread in tropical South America. Both sexes are olive-green above, mostly bright yellow below, with the head boldly marked with a yellow superciliary band, a black streak through the eye to the hindhead, and below this a white streak.

A.F.S.

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SIBIA: substantive name of the species of BABBLERS of the genera *Heterophasia* and *Crocias*.

SIBLING SPECIES: 2 or more closely related species that are morphologically very similar but are reproductively isolated (i.e. able to inhabit the same area without interbreeding); sometimes called 'cryptic species'.

SICK BIRDS, CARE OF: see CARE OF INJURED, SICK AND ORPHANED BIRDS.

SICKLEBILL: sole or substantive name used for various species possessing the form of bill suggesting it; these belong to several widely separated families. Thus, it is the name of *Falculea palliata* (see VANGA) and of *Hemignathus procerus* (see HAWAIIAN HONEYCREEPER), the latter alternatively called 'Akialoa'. Again, it is the substantive name of *Drepanornis* spp. and *Epimachus* spp. (see BIRD-OF-PARADISE), and also of *Eutoxeres* spp. (see HUMMINGBIRD). Further, it has been used (but 'scythebill' is now preferred) as the substantive name of *Campylorhynchus* spp. (see WOODCREEPER); and it is sometimes applied, in Australia, to the White Ibis *Threskiornis molucca* (see IBIS).

SICKLES: term (plural) sometimes applied to elongated central tail feathers, found in certain species.

SIEGE: see ASSEMBLY, NOUN OF.

SIERRA-FINCH: substantive name of the species of *Phrygilus*, a genus of finches found in the Andes and the temperate southern extremity of South America (for family see FINCH).

SIGHT: see VISION.

SIGNAL: see DISPLAY; RELEASER.

SIGNIFICANCE: see BIOSTATISTICS; STATISTICAL SIGNIFICANCE.

SIGN STIMULUS: term coined by E.S. Russell to indicate those parts of the available environmental information to which an animal responds at any given moment, particularly when these are strikingly limited. One sees the first indications of this restriction to a few stimuli in observations of astonishing errors such as a Herring Gull *Larus argentatus* chick pecking at a cherry in the way in which it does at its parent's red bill-tip; or waders panicking when another wader descends in a wildly swooping flight, thus showing roughly the same type of movement as a striking Peregrine *Falco peregrinus*; or aggressive or sexual responses to animals only remotely similar to the adequate objects. Such 'errors' are in curious contrast to other evidence demonstrating the wonderful acuteness of a bird's perceptive abilities, and this apparent paradox has led to experiments in which the potentialities of the sense organs were compared with the actual stimulus situations releasing particular responses. In birds, the majority of papers on this subject deal with visible stimuli. The potentialities of the eyes are studied with as great a variety of methods as possible: by studying conditioned responses of the intact animal, by observing pupillary reactions, by electrophysiological recordings in or behind the retina, and so on. There is now much evidence to show that the visual acuity of birds is high, that they can recognize forms well, and that their discrimination of intensity and colour is of the highest order (see VISION). Observations on geese (*Anser* spp.), gulls, crows and other birds have shown that they can distinguish between individuals of their own species much better than even a highly trained human observer.

Actual stimulus situations releasing a particular response have been studied by means of tests with dummies. In these, precise imitation of the natural object normally releasing the response (the standard dummy) is offered in alternation with dummies lacking one or more characteristics, and the intensity or frequency of the response to these various dummies is compared. If there is no or little difference of effect between the standard dummy and one of the incomplete dummies, the character lacking in the latter can be of no or little importance as a stimulus; if the difference is striking, this is indicative of a sign stimulus. There are indications that the difference between a sign stimulus and a non-effective aspect of the environment is often one of degree only. In this way it was found, for instance, that the red patch on an adult Herring Gull's lower mandible is effective in releasing the chick's begging response, whereas the yellow of the rest of the bill is no more effective than any other colour, and this is expressed by saying that the red patch provides a sign stimulus. Further tests showed that it acts by its colour as well as by its contrast with the rest of the bill. Similarly, dummy tests with Song Thrush *Turdus philomelos* nestlings revealed that one of the sign stimuli is provided by the parent's head, which acts through being a protuberance of the outline of the body—above the body and with a certain size in relation to that of the body.

Precise investigations of this type, in which the potentialities of the sense organs involved and the actual stimulus situations are systematically explored and compared, are still very much needed, but there seems to be little doubt that many responses are released (and others inhibited) by very simple stimulus situations.

The fact that not all available information is 'used' or admitted for eliciting the response is posing an interesting physiological problem: where and how is the information refused passage? Lorenz (1935) pointed out that the restriction of a response to very few aspects of the total situation seems to be typical of 'innate' (i.e. non-conditioned) behaviour, and that conditioning usually leads to a fuller use of all details of the situation (unless special manipulations of the experimenter subsequently reduce the numbers of details used). Thus the conditioned responses to individual birds, or fear responses to (often amazingly slight) changes in the usual environment, are strikingly different from responses that occur prior to conditioning. This suggestion has not been followed up experimentally to any extent.

Sign stimuli often have to be described in 'configurational' terms, which means that they evoke complicated processes of reception that cannot, at the present stage of analysis, be measured on one linear scale. Thus, many responses can be elicited only by a special type of movement, or by a special shape, or by a certain degree of contrast between two colours. In such cases it has been possible to design 'supernormal' stimuli, exaggerating the quality of the natural object to which the animal responds. For instance, the speckling of eggs can be exaggerated in models until they are preferred to normal eggs. N.T.

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Tinbergen, N. 1951. The Study of Instinct. Oxford.

SILKTAIL: substantive name for the taxonomically perplexing, monotypic and sexually monomorphic *Lamprolia victoriae* (Passeriformes, suborder Oscines) of Vanua Levu (= *L. v. kleinschmidti*) and Taveuni (= *L. v. victoriae*) Islands, Fiji; locally called Satin Flycatcher (Watling 1982).

In general appearance it is extremely suggestive of a diminutive bird-of-paradise, to which family it has often been tentatively allied; but it has also been considered possibly part of the thrush-flycatcher-warbler complex Muscicapidae and of the Australasian Malurinae (Harrison and Parker 1965), within the babblers Timaliidae (Cottrell 1967). Olson (1980) reviews the evidence against a paradisaeid relationship, and on the basis of plumage, external morphology and zoogeography suggests a placement in the MONARCH FLYCATCHERS (Monarchidae) closest to the genera *Clytorhynchus*, *Metabolus* and *Monarcha*. Certainly the nest of *Lamprolia* is unlike those of Paradisaeidae but like those of Monarchidae. The present view of K.H. Voous is to place it close to the genera *Eremiornis* and *Cinclorhamphus* of the Sylviidae.

Characteristics. A small (13 cm long) fine-billed insectivorous passerine of velvet black plumage with a silky-white rump, upper tail coverts and upper tail, and with iridescent tipped scale-like feathers about the head, neck, throat and breast which may appear blue, green or violet. Juveniles are like adults but duller, less glossy and spangled; the white tail develops clearly in the first juvenile plumage, whereas other decorative plumage appears only gradually with age. An adult just completing moult, and others in fresh post-moult plumage, have been recorded in mid-July.

Habitat and food. The Silktail is a bird of mature forests, found from over 1,000 m to the coast where forest remains, but mostly above 400 m where it actively forages for insects in the lower understorey and on the leaf litter.

Behaviour. It is most frequently encountered singly, in pairs, or a pair with fledged young, but groups of up to 6 join mixed feeding flocks.

Voice. Adult song is an unimpressive series of slurred trilled whistles, three initial notes slightly descending in pitch, followed by two or three elaborations of the same note; the entire song lasting 5 seconds.

Breeding. Breeding takes place throughout the year, with a possible peak in June–September. Two aggressive display postures have been seen but no courtship display is recorded. The nest is a deep thick-walled, loosely built cup slung beneath a horizontal twig fork 1–3 m above ground, usually below large leaves. The clutch is only one egg, and observations suggest that only one parent incubates as no change-over was seen at the nests. C.B.F.

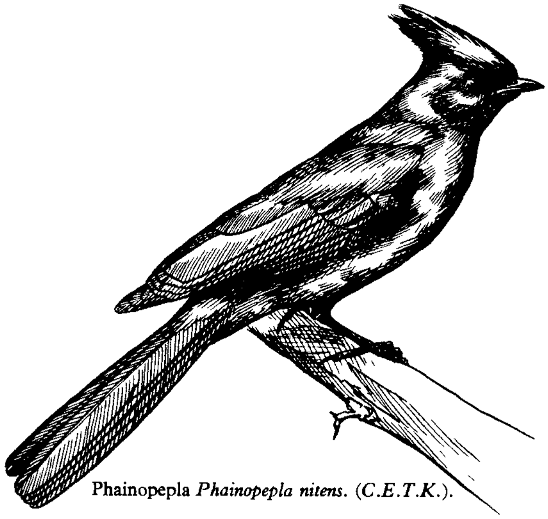
Cottrell, G.W. 1967. A problem species: *Lamprolia victoriae*. Emu 66: 253–266.
Harrison, C.J.O. & Parker, S.A. 1965. The behavioural affinities of the blue wrens of the genus *Malurus*. Emu 65: 103–113.
Heather, B.D. 1977. The Vanua Levu Silktail (*Lamprolia victoriae kleinschmidti*): A preliminary look at its status and habits. Notornis 24: 94–128.
Holyoak, D.T. 1979. Notes on the birds of Viti Levu and Taveuni, Fiji. Emu 79: 7–18.
Olson, S.L. 1980. *Lamprolia* as part of a South Pacific radiation of Monarchine flycatchers. Notornis 27: 7–10.
Watling, D. 1982. Birds of Fiji, Tonga and Samoa. Wellington.

SILKY-FLYCATCHER: substantive name of certain species of the family Ptilogonatidae (Passeriformes, suborder Oscines); in the plural, general term for the family. The relationship of the 3 genera and 4 species, ranging from south-western United States to western Panama, has long been disputed; often they have been classified as a subfamily of the Bombycillidae; but evidence from egg-white proteins, as well as other features, fails to uphold this treatment. Their closest relatives may be the solitaires *Myadestes* (family Turdidae).

Characteristics, habitat and distribution. Silky-flycatchers range from about 17–23 cm in length. They have short, rather broad bills, relatively short wings, and short tarsi. The Phainopepla *Phainopepla nitens*, which ranges from deserts and arid woodlands of south-western United States to the highlands of Mexico, is a slender, long-tailed, crested bird with silky plumage, shining black with white wing patches on the male, grey on the female. The 2 species of *Ptilogonys* are also slender, long-tailed, and prominently crested. The males are grey or blue-grey with yellow flanks and crissum, black wings, and black-and-white tails; the females are similar but more olivaceous. The Grey Silky-flycatcher *P. cinereus* inhabits pine-oak woodlands in the highlands of Mexico and Guatemala. The Long-tailed Silky-flycatcher *P. caudatus*, which has elongated central tail feathers, is confined to the high mountains of Costa Rica and western Panama. The Black-and-yellow Silky-flycatcher *Phainoptila melanoxantha*, with the same range as the Long-tailed, is crestless and more thrushlike in aspect. The male is mostly glossy black, with bright yellow rump, sides, and crissum; the female is more olive.

Food, voice and behaviour. *Phainopepla* and the 2 species of *Ptilogonys* associate in loose, wandering flocks. They perch on high, exposed treetops, from which they make long, spectacular sallies to catch insects. *Phainoptila* lives in pairs amid lower, denser montane vegetation and seizes insects on less spectacular darts. All members of this family eat many berries. *Ptilogonys* and *Phainopepla* use their voices freely but sing sparingly and not brilliantly.

Breeding. The only species that have been carefully studied, the Phainopepla and the Long-tailed Silky-flycatcher, breed in monogamous pairs. Nuptial feeding is frequent. All 4 species build compact open cups in shrubs and trees, often high. Those of the Long-tailed Silky-flycatcher are composed almost wholly of grey beard-lichen *Usnea*; those of the Black-and-yellow largely of green moss; those of the other 2 species of more varied materials. Building is done chiefly or exclusively by the male Phainopepla, but by both sexes of the Long-tailed Silky-flycatcher. *Phainopepla* lays 2–3 (rarely 4) eggs; *Ptilogonys*, 2; and *Phainoptila*, 2 (1 record). The eggs of all 4 species are grey or greyish white, heavily marked with brown or lilac. Both sexes of *Phainopepla* incubate, but only the female *Ptilogonys*. The incubation period of the former is 14–15 days;



Phainopepla *Phainopepla nitens*. (*C.E.T.K.*).

of the latter, 16–17 days. Nestlings have abundant white down, long in *Phainopepla*, in short, compact tufts in *Ptilogonys*. Both sexes feed the young, which remain in the nest for 18–19 days in *Phainopepla*, 24–25 days in *Ptilogonys*. A.F.S.

Bent, A.C. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. Bull. U.S. Natl. Mus. 197: i–vii, 1–411.

Kiff, L.F. 1979. The nest and eggs of the Black-and-yellow Silky-flycatcher (*Phainoptila melanoxantha*). Auk 96: 198–199.

Rand, A.L. & Rand, R.M. 1943. Breeding notes on the Phainopepla. Auk 60: 333–341.

Sibley, C.G. 1973. The relationships of the silky flycatchers. Auk 90: 394–410.

Skutch, A.F. 1965. Life history of the Long-tailed Silky-flycatcher, with notes on related species. Auk 82: 375–426.

SILVERBILL: substantive name of some *Lonchura* spp. (see ESTRILDID FINCH).

SILVER-BIRD: *Empidornis semipartitus* (for subfamily see FLYCATCHER (1)).

SILVER-EYE: name used for some species of Zosteropidae (see WHITE-EYE).

SIMURG: see FABULOUS BIRDS.

SINGING: see VOCALIZATION.

SINGLE-BROODED: laying a single clutch during a breeding season, although a replacement may be laid if the first clutch fails. See CLUTCH-SIZE.

SINUATED: term applied to a feather of which one edge appears as if cut away along a wavy line—not abruptly as when the vane is emarginated.

SINUS VENOSUS: see HEART.

SIRKEER: *Taccocua leschenaultii* (for family see CUCKOO).

SIRYSTES: generic name used as common name of *Sirystes sibilator* (for family see FLYCATCHER (2)).

SISKIN: substantive name of some *Carduelis* (or '*Spinus*') spp.; used without qualification, in Britain, for *C. spinus* (see FINCH).

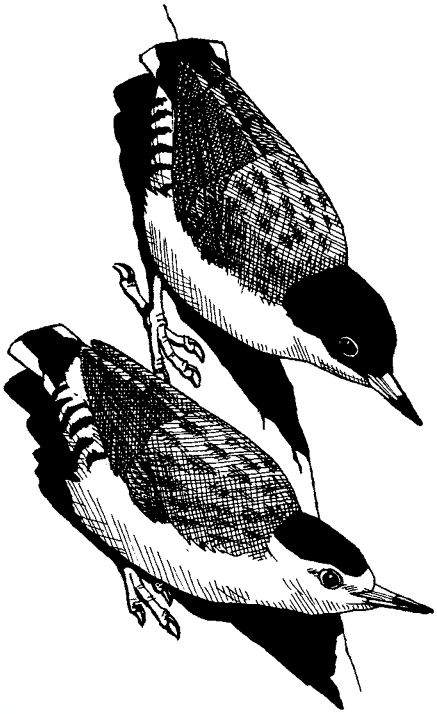
SITE-ATTACHMENT; see TERRITORY.

SITTELLA: alternatively 'treerunner'; in the plural, substantive name for the 3 species of Neosittidae or Daphoenosittidae; (Passeriformes, suborder Oscines). Formerly included in the Sittidae (see NUTHATCH), sittellas differ in leg musculature, bill morphology, plumage, nest type and social structure (Rand 1936; R. Orenstein). They may be most closely related to other Australian Oscine groups such as whistlers and monarch flycatchers (Sibley and Ahlquist 1982).

Characteristics, habitat and distribution. The Varied Sittella *Daphoenositta* (= *Neositta*) *chrysoptera* is a common resident of open *Eucalyptus* or *Acacia* woodland in Australia. It resembles a small nuthatch (10–12 cm) with a laterally compressed, upturned bill and a conspicuous white or orange-buff band across the flight feathers. The possibly conspecific Papuan or Mountain Sittella *D. papuensis*, which lacks the wing-band, is an uncommon New Guinea species of moist mountain forests between 1,075 and 2,450 m. The Black Sittella or Pink-faced Nuthatch *D. miranda*, locally common in Papuan mountain forests between 2,000 and 3,500 m, is a straight-billed, blackish bird with a rose-red face and white wing-band. Sittellas show limited sexual dimorphism, varying among races. Juveniles have whitish spots.

Varied and Papuan Sittellas vary geographically in head colour and, in *D. chrysoptera*, in bill colour, streaking in the plumage, and wing-band colour. The 5 recognized races of Varied Sittella were long considered separate species, but all except, possibly, 2 hybridize extensively where they meet (Ford 1980).

Food. Foraging Varied Sittellas explore branches in a series of rapid, tight spirals, working from their tips towards or on to the trunk, climbing head downwards or on the undersides of limbs. They pry up bark flakes for invertebrates or, rarely, use twigs to probe deeper crevices (Green 1972). Birds may fly long distances between trees; their flight is undulating. The Papuan species behave similarly, although *D. miranda* may be less acrobatic (Diamond 1972).



Varied Sittella *Daphoenositta chrysoptera*, female and male (below). (*N.W.C.*).

Behaviour and voice. Sittellas associate in groups of 3 to 12 or more, males outnumbering females. Members maintain contact with thin, high-pitched calls, louder in flight, and with rapid wing-flicks which expose the wing-band when it is present. The song has a series of 'zitting' notes.

Breeding. *Daphoenositta chrysoptera* breeds between July and March. All group members build the nest, a cup of spider-webs and cocoons, camouflaged with bark and lichen, placed up to 20 m high in a vertical fork. Normally only one female lays and incubates. There are usually 2 or 3 eggs, pale blue or greyish-white with dark spots and blotches. Incubation takes 12 or 13 days. Young birds remain in the nest for 13 or 14 days, fed by all group members, including juveniles from previous broods (Noske 1980). R.O.

Diamond, J.M. 1975. Avifauna of the eastern highlands of New Guinea. Publ. Nuttall Ornith. Club 12: 1–438.

Ford, J. 1980. Hybridization between contiguous subspecies of the Varied Sittella in Queensland. Emu 80: 1–12.

Green, C. 1972. Use of tool by Orange-winged Sittella. Emu 72: 185–186.

Noske, R.A. 1980. Co-operative breeding and plumage variation in the Orange-winged (Varied) Sittella. Corella 4: 45–53.

Rand, A.L. 1936. The rediscovery of the nuthatch *Daphoenositta* with notes on its affinities. Auk 53: 306–310.

Sibley, C.G. & Ahlquist, J.E. 1982. The relationships of the Australo-papuan Sittelas *Daphoenositta* as indicated by DNA-DNA hybridisation. Emu 82: 173–176.

SITTIDAE: a family of the PASSERIFORMES, suborder Oscines (see NUTHATCH).

SIVA: substantive name of some *Minla* spp. (for family see BABBLER).

SIZE: discussions of the evolution of birds are usually concerned exclusively with the radiation of different kinds, emphasizing body shape and posture, plumage colour, bill shape and feeding behaviour or taxonomic affinity. However, it is not so much the kind of bird as the size that has the most dramatic effect on the bird's requirements and ecological opportunities.

There are several measurements for describing the size of a bird. The most satisfactory of these is body weight or mass, primarily because it overcomes the complex variability of linear measurements due to differences in shapes of birds. However, there are considerable seasonal changes in body mass of migratory birds, and of birds such as penguins (Sphenisciformes) which fast during incubation, as well as weight changes due to egg formation and laying. Clark (1979) has provided an excellent review of these problems and bibliography on bird weights.

Range of sizes. The first known bird, *Archaeopteryx lithographica*, was somewhat lighter than a pigeon; its body mass has been estimated at about 270 g. Apparently from a start in this size-range, there evolved a range in sizes from the Bee Hummingbird *Calypte* (*Mellisuga*) *helenae* to the Giant Moa *Dinornis giganteus* and the Elephant Bird *Aepyornis*. The mass of the Bee Hummingbird is variously given as from 1.6 g to less than 3 g, while Amadon (1947) estimated 236 kg for the Giant Moa and 457 kg for the Elephant Bird. The largest living bird, the Ostrich *Struthio camelus*, may weigh 100–136 kg as an adult, 67,500 times as much as the smallest. Including the extinct forms, the class Aves has spanned a 228,500-fold range in body mass. The range in sizes of living land mammals is considerably greater (see Table 1), but in the case of elephants or mammoths, the huge mass is supported by four limbs instead of two. If we limit consideration of the largest mammal representatives to bipedal forms the range is 350,000 to 680,000, about the same order of magnitude as birds.

The avian extremes, hummingbirds and ratites, differ not only in size, but in form, locomotion, habits, and ecological niches. The smallest birds are able to extract a net energy profit from minute droplets of nectar in flowers, taken during an energy-expensive hovering manoeuvre. Energy-balance considerations have made the hummingbird plan seemingly unsuitable at sizes greater than 21 g. The lower size limit for hummingbirds may be related to problems of overnight survival on body energy reserves or the mechanics of the avian method of oviparous reproduction (see Brown *et al* 1978). At the other extreme, the Ostrich's large body size must have conferred benefits such as an opportunity to exploit a grazing niche or reduced vulnerability to attack.

It is more instructive to consider size ranges within some phylogenetic and locomotive subgroupings (Table 1). Within several orders, the range in body mass exceeds 2 orders of magnitude, although there are exceptions to this in the more specialized groups such as penguins, ducks and swifts.

There is an upper limit to flying size (see below and FLIGHT), but the range in body mass for fliers is 10 times that for diving birds. Heat loss to the highly conductive water may limit the smallest size practical for diving, but some warm-blooded mammals dive successfully despite very small sizes: the watershrews *Sorex palustris* or *Neomys fodiens* have one-fifth the mass of the dipper or water ouzel (*Cinclus*).

An important characteristic of flying birds is the wing-loading, or ratio of body mass to the surface area of the wings which provides lift. Analyses by Hartman (1961), Greenewalt (1962) and others have shown that wing-loading increases with body mass; that is, the surface area of the wings was not increased in proportion to body mass increase as larger birds evolved. At any given body size for comparison, gliding and soaring birds have very light wing-loading. Heavy wing-loading is the rule for diving birds that use the wings to swim underwater. They have been limited in wing size because of the greater resistance to movement in water, which has considerably greater viscosity and density than air. Pennycuick (1969, 1972) derived an equation relating characteristic velocities (such as stalling speed, speeds for minimum power consumption or maximum range) to the square-root of wing-loading. Thus to remain airborne a diving bird with relatively smaller wings must fly at a greater speed than a non-diving bird of similar mass.

Allometry. There are no birds weighing more than 13 kg, and still capable of horizontal flapping flight, although it is speculated that some large fossil carinates may have been capable of flight. Pennycuick (1969) provided a theoretical basis for the upper limit to body mass for flight. If a basic body-plan for a bird is scaled up such that its linear dimensions (height, length, width) are each multiplied by a factor of 10, then its volume will be increased to 10 × 10 × 10, or 1,000 times as great. Built of the same materials, the mass to be lifted in flight will be 1,000 times that of the prototype bird. The power required to lift this mass will actually be proportionately greater, about 3,200 times as great as the bird that weighed 1/1,000 as much. The force generated to flap the wings by the pectoralis and supracoracoid muscles is proportional to the cross-sectional area of these muscles. Thus the power available has increased by a factor of only 10 × 10 while power requirements for sustained flight have increased by 32 × 10 × 10. A disproportionate increase in muscle mass to offset the power requirements would require greater oxygen and energy supply. Thus the heart, lungs, and the digestive tract, kidneys, and liver would have to be increased to meet the metabolic requirements for the larger muscles, making the bird still larger and more difficult to lift.

Failure to appreciate the subtleties of scaling has led biologists to a number of erroneous conclusions. It is often stated that birds have faster heart beats and lighter skeletons than do mammals, but compared on an equal-mass basis, this generalization is untrue (Prange *et al* 1979). It is also untrue that larger birds lose less heat than small birds (Calder 1974).

The study of scaling is *allometry* (allos = other; metryon = a measure), first applied to birds in a study of egg size by J.S. Huxley. Contributions of Max Kleiber, Samuel Brody and others have led to a rapidly increasing use of allometric analysis of avian biology. This, in turn, has yielded fundamental understanding of the dimensions of eggs and incubation, the similarity in basal metabolic rates of mammals and birds (except Passeriformes, which are characteristically higher in this regard), the insulative equivalence of feathers and fur, and the longer life spans of birds as compared with mammals. From body mass, we can predict practically any feature of a bird's natural history, its flight speed, territory size, energy requirements and the size of body organs. Note in Fig. 1 that the size-dependent changes are not scaled in the same proportion. Skeletal mass must increase more than heart mass, and the brain mass increases less than either.

Allometric analysis is simple, mathematically. The best fit for the relationship of many biological variables (Y) to body size is an exponential or power function of body mass (M):

$$Y = aM^b$$

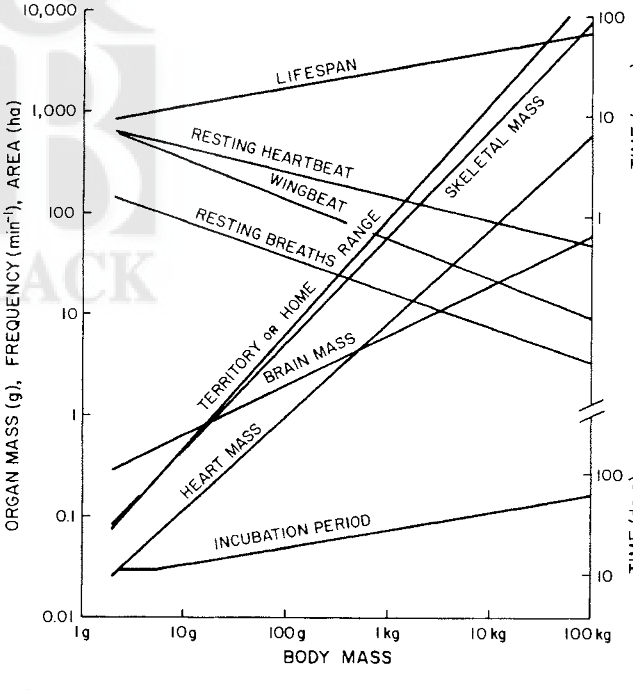


Fig. 1. A sample of avian life history and body construction features which scale as various exponential functions of body mass ($Y = aM^b$; see text). Note that the scales (vertical and horizontal) are logarithmic, which results in straight-line plots, the slopes of which are the exponents b. These lines represent mathematical generalizations; values for actual birds vary above and below the line of statistical best-fit. This shows that, in the evolutionary scale-up, the heart size increases in approximately direct proportion to body size increase while the heart beat, wing beat, and breathing frequency (min^{-1} means per minute) are fast in small birds and slow in large birds. The skeletal mass and territory size increase in greater proportion, while the brain increase does not keep pace with body size increase. Size increase has proportionately the same effect on incubation period and lifespan. (By permission of Harvard University Press).

Table 1: Size ranges in bird groups compared with mammals.

Type of animal	*Smallest species*	*Body M (g)*	*Largest species*	*Body M (kg)*	*Ratio of largest/smallest*
All birds	Bee Hummingbird *Calypte helenae*	2	Ostrich, *Struthio camelus* *Elephant Bird *Aepyornis maximus*	135 457	67,500 228,500
All land mammals	Pygmy Shrew *Microsorex hoyi*	2	African Elephant *Loxodonta africana*	7,000	3,043,478
Bipedal mammals	Little Pocket Mouse *Perognathus longimembris*	8	Gorilla, *Gorilla gorilla*† Man *Homo sapiens*	290 70	35,366 8,537
Ratites	Little Spotted Kiwi *Apteryx oweni*	666	Ostrich *Struthio camelus* *Elephant Bird *Aepyornis maximus*	135 457	203 686
Penguins	Little Penguin *Eudyptula minor*	1,100	Emperor Penguin *Aptenodytes forsteri* *Fossil Penguin *Pachydyptes*	42.5 100‡	39 91
Procellariiformes	Storm Petrel *Hydrobates pelagicus*	28	Wandering Albatross *Diomedea exulans* (wingspan 3.5 m)	12.7	45
Pelecaniformes	White-tailed Tropic-Bird *Phaethon lepturus*	300	Dalamatian Grey Pelican *Pelecanus crispus*	13	43
Anseriformes	White Pygmy Goose *Nettapus auritus*	220	Trumpeter Swan *Cygnus cygnus buccinator*	12.5	57
Galliformes	Painted Quail *Excalfactoria chinensis*	40	Wild Turkey *Meleagris gallopavo*	13	318
Gruiformes	Lark-quail *Ortyxelos meiffrenii*	18	Great Bustard *Otis tarda*	17	933
Trochilidae	Bee Hummingbird *Calypte helenae*	2	Giant Hummingbird *Patagona gigas*	0.021	11
Passeriformes	Flycatcher *Abromis albogularis*	5	Raven *Corvus corax*	1.7	355
Flying birds	Bee Hummingbird *Calypte helenae*	2	Trumpeter Swan, *Cygnus cygnus buccinator*	12.5	6,250
Diving birds	Dipper *Cinclus mexicanus*	50	Emperor Penguin *Aptenodytes forsteri* *Fossil Penguin *Pachydyptes*	43 100‡	850 2,000

* Extinct; body mass estimated.

† Knuckle-walker Quadripedal.

‡ Olson and Hasegawa (1979, Sci. 206: 688) report that the largest fossil plotopterid (Pelecaniformes) may have been larger than any of the giant fossil penguins.

If *b* is 1.0, there is a straight-linear proportionality (i.e. doubling of body mass has involved a doubling of Y, such as a doubling of heart or respiratory system size). If *b* exceeds 1.0 the curve becomes increasingly steep. For example, as bird size increases, the skeleton must be progressively a larger percentage of body mass, and the power requirement for flight grows disproportionately as well. When *b* is a fraction less than 1.0, a doubling of body mass requires less than twice as much of Y, and the graph of the relationship is shallower. Thus a 100 g bird requires less than twice as much (about 1.7 times) food or metabolic heat production as does a 50 g bird. A *b* value of zero indicates that the variable is independent of size of the bird or egg. For example, body temperatures of resting birds are independent of body mass, although the temperature of a hand-held or struggling bird may rise more rapidly the smaller the bird. Birds' eggs, large and small, all lose about 15% of their fresh mass by evaporation during the incubation period. Finally, if *b* has a negative value, the allometric correlate decreases as the body size increases; the heart of a goose beats more slowly than a hummingbird heart, and the wing beat is also much slower.

Plotted on logarithmic scales, these relationships all take the form of straight lines, the exponents becoming slopes of the straight lines, which are fitted by the method of least squares regressions (see BIOSTATISTICS). The plots or equations then provide a basis for comparing birds with mammals in general or for comparing unusual birds with more 'typical' ones (such as the differences in insulation between a ptarmigan *Lagopus* and a bird of more moderate climate). From allometric analysis we can appreciate the complexities of natural selection for larger or smaller birds, and we can predict approximately the requirements or dimensions of the yet unstudied birds. When consistent patterns emerge from the analysis there is strong suggestion of underlying physical constraints which have had a major influence upon the evolution of birds. With this background, one can begin to analyse the structure, physiology, and life history of birds from a fresh perspective.

Birds and mammals compared. We can then make fair comparison of birds and mammals if they are of the same sizes. From Table 2, it may be observed that the basal rates of energy demand by birds and mammals are indistinguishable, as are their skeletal weights. Compared at 1 kg size,

Table 2: A Cpmparison of Birds and Mammals Based Upon Body Size

	1 kg bird	*1 kg mammal*	*Effect of size increase (exponents)*	
			Bird	*Mammal*
Basal metabolic rate (ml O_2/hr)	679	676	0.72	0.75
Energy cost of travel (kJ/km)[a]	49	118	0.77	0.60
Speed of travel (km/hr)[b]	47	6	0.17	0.24
Skeleton mass (g)	65	61	1.07	1.09
Brain mass[c] (g)	7	11	0.51	0.66
Heart mass (g)	9	6	0.94	0.98
Respiratory system volume	161	54	0.91	1.06
Lung mass (g)	13	11	0.95	0.99
Incubation/gestation (da)	28	70	0.17	0.23
Lifespan (yr), in captivity	28	12	0.19	0.20
Heartbeat/min	156	241	−0.23	−0.25
Breaths/min[d]	17	54	−0.31	−0.26

a. Compares flying of birds with running of mammals. 1 kJ = 0.239 kcal or energy in 25 mg fat.

b. Pennycuick, C.J. (1969) Ibis 111: 525, theoretical calculation for minimum power requirements for birds; Heglund, N. *et al* (1974) Science 186: 1112, empirical regression for trot-gallop transition of mammals.

c. Note difference in proportionate effects of size upon brain mass. These relationships predict that birds with body mass under 34 g would have larger brains than mammals of the same sizes, while above 34 g size mammals have progressively larger brains than do birds.

d. Excluding Passeriformes.

birds have smaller brains than mammals, but the smaller scaling exponent translates to the fact that very small birds (<34 g) have larger brains than mice of the same size. Except for small birds and mammals (<34 g) birds have smaller brains. Birds' hearts and respiratory systems are larger, and heart beats and breathing are slower. Time required for incubation of eggs is less than one half of that required for mammalian gestation, but birds' lifespans are more than twice those of mammals of equal size. Birds not only fly faster than mammals can run, but the energy cost for a bird of 1 kg or less to fly a km is less than half the cost for the equivalent mammal to run that distance. The difference in exponents means that size has a greater proportionate influence on birds (0.77) than on mammals (0.60). The relative advantage is reduced to 63% of mammalian running cost at the maximum body size for flying birds. From this energy comparison it is obvious why migration is more common in birds than in mammals. Amongst the mammals, long distance migration is limited to the larger terrestrial mammals, to bats and to marine mammals.

Having compared these two classes of 'warm-blooded' vertebrates, consider the details of scaling within the class Aves. As noted above, with the evolution of larger birds, the margin between power available and power required for flight decreased until flight was no longer feasible. Similarly the 'dead weight' of the skeleton must increase out of proportion to body size increase. This is slightly offset by the fact that the brain need not increase in linear fashion to coordinate the bird's physiology. Organs basic to life support, such as heart, lungs, respiratory system, gut mass, and blood volume are increased in an approximately direct linear proportion to body mass increases (Calder 1974; 1984). The exponent 0.94 for heat mass as a function of body mass may reflect more than statistical scatter in its departure from strict linearity (1.0). This may be attributed to the fact that the largest birds are not fliers and do not experience as intense demands for oxygen, hence can manage with hearts that are proportionally somewhat smaller than those of smaller birds.

Heart rate bears an inverse relationship to heart mass, the smaller heart beating more rapidly. This is seen not only within Class Aves, but in the comparison with Mammalia, noted above. A 1 kg bird has a heart 1.48 times as heavy as that of a 1 kg mammal, while the mammal's resting heart rate is 1.55 times as fast as the heart of a 1 kg bird. From more limited data, there appears to be no significant difference in ratios of active to resting heart rate between birds (2.6 ± 0.75 s.d.), eutherian mammals (2.13 ± 0.945 s.d.), and marsupial mammals (2.24 ± 0.35 s.d.), nor is there any size-related trend to the variability within these groups. Similarly, breathing rates decrease as respiratory system volume increases with body mass in both birds and mammals. At a comparable 1 kg body mass, the breathing rate of the mammal is 3.1 times that of the bird, while the RESPIRATORY SYSTEM of the bird has 3 times the volume of that of the mammal.

Body size and environment. Within many species or genera, body size increases with increasing latitude or altitude, increases which are associated inversely with temperature. These empirical trends are established beyond argument, but their interpretation has been controversial (James 1970).

The smaller the bird, the greater the ratio of surface area ($\propto M^{2/3}$) to volume ($\propto M^1$). Since heat is produced by the volume or mass of tissues but lost by the surface, the higher surface:volume ratio is taken to indicate a greater liability for heat conservation. While it is true that the metabolic cost per gram is higher in smaller birds, the total heat loss from a large bird is greater than from a small bird.

Body size and temperature. The body temperatures at which birds live are size-independent, 40 ± 1.5°C when resting, 43 ± 0.5°C when heat-stressed or highly active. The heat production which supports the body temperature (T_b) is a by-product of metabolism. The basal (minimal) metabolic rate is proportional to $M^{3/4}$. When the environmental temperature (T_e) is below a critical lower limit (T_{lc}) this metabolic rate is insufficient to maintain the body at 40°C, and shivering commences in proportion to the difference ($T_b - T_e$) and is inversely related to the amount of insulation contributed by the plumage, a resistance (R) to heat flow.

Consideration of the plumages of a goose and a tit tells us that the larger the bird, the thicker its insulation. The thermal insulation R is generally proportional to the square-root of body mass, $M^{1/2}$, that is to say it does increase with size, but not as much as body mass or body surface ($M^{2/3}$). Consequently, the goose produces more heat and loses more heat than does a tit, and a big tit loses more heat than a little tit. A male Black-capped Chickadee *Parus atricapillus* in Alaska weighing 11.1 g exposed to 0°C would lose heat at a rate of 0.66 watts, while at the lower latitude of Ohio, USA, the chickadee weighs 10.0 g and exposed to 0°C, loses heat at a rate of 0.63 watts (Calder 1974).

How then can the size increase that is correlated with lower environmental temperature be interpreted? The amount of energy reserves a bird can store as fat and in the crop and gut contents is at least a linear function of body mass, that is to say, amount of energy $\propto M^{1.0}$. The rate of their depletion during a fast imposed by blizzards or ice-storms is proportional to the metabolic rate, rate $\propto M^{3/4}$. Endurance time equals amount/rate, $M^1 \div M^{3/4} = M^{1/4}$. This positive fractional exponent says that the larger tit will survive longer.

Ecological consequences of size: lifespan. The larger the bird, the longer its lifespan ($M^{0.2}$, Lindstedt and Calder 1976 (see also AGE)). The allometry of maximum longevity data from birds indicates that birds survive 61% longer in captivity than in the wild (bird-ringing records). The difference between wild and captive longevities must reflect the effects of disease, predation, and (or) uncertainties of food supplies in natural environments. In captivity, birds have maximum lifespans well over twice those of mammals of the same body size. If fertile lifespan was a similar proportion of total lifespan in both classes, the birds would have a greater opportunity for successful reproduction.

Ecological consequences of size: reproduction. The larger the bird, the larger the egg ($\propto M^{0.77}$) and the longer the incubation period ($\propto M_{body}^{0.17}$ or $M_{egg}^{0.22}$). Compared on a body mass-equivalent basis, incubation of bird eggs is considerably more expeditious than gestation in mammals, requiring only 41% as much time. This perhaps reflects a natural selection that reduced the period of exposure to predation.

Ecological consequences of size: territory. Both territory and home range increase with increasing body size. When food habits were not considered, Schoener (1968) found that both territory ($\propto M^{1.09}$) and home range ($\propto M^{1.16}$) increased in greater proportion than body mass. Treated separately, territory and home range of birds consuming animal food increased even more disproportionately with body mass increase ($\propto M^{1.31}$, $M^{1.39}$, respectively), while territories of omnivores and herbivores increased in a less than linear fashion ($\propto M^{0.35}$, $M^{0.70}$, respectively).

Obviously, on a given amount of land of suitable habitat, there will be more small birds with small territories than large birds with large territories. Thus, the larger the bird, the fewer its numbers. This would mean that other things being equal, larger birds would be generally more vulnerable to extinction, and large carnivores would be especially vulnerable. To this effect may be added the previously mentioned correlation of long incubation period with large bird size, which could increase the vulnerability. Certainly many birds listed as extinct, vanishing, or endangered were or are large, absolutely or within their taxa: moas, elephant-birds, Dodo, Arabian Ostrich, Whooping *Grus americana* and Japanese Cranes *G. vipio*, the bustards Otididae, Takahe *Notornis*, California Condor *Gymnogyps californianus* and Ivory-billed Woodpecker *Campephilus principalis*.

Other considerations. There are sex differences in size (see SEXUAL DIMORPHISM). Full size is attained before fledging of altricial species or by the time of replacement of down by feathers in precocial species (see GROWTH; YOUNG BIRD). The consequences of body size extend to all aspects of avian biology. W.A.C.

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SKEIN: see ASSEMBLY, NOUN OF.

SKELETON, POST-CRANIAL: the internal framework (endoskeleton) of the body which, along with the SKULL protects and supports its soft structures. Together with the muscular system (see MUSCULATURE), it forms an integrated system for exerting force and movement (see LOCOMOTION, TERRESTRIAL; FLIGHT).

Nature and development. The skeletal system is composed of bone, cartilage, and ligaments. Bone is a living tissue composed of an inorganic mineral (hydroxyapatite: $Ca_{10}(PO_4)_6(OH)_2$), laid down in an organic matrix (collagen fibres). Together these substances form fibrils. In lamellar bone the fibrils lie parallel to each other, whereas in woven bone they are tangled more or less at random. The composite structure of bone makes it more rigid than collagenous fibres, more flexible and resistant to fracture than mineral, and more versatile in the kinds of loads it can withstand than either of its components alone. The red marrow found within bones is the primary blood-forming organ in the adult (see BLOOD), and bones may serve as storage areas for calcium and phosphorus.

Most bones have a complex organization (Fig. 1). On the outside is a tough fibrous membrane (periosteum). Mature bone is composed of an outer layer of dense, ivory-like, compact bone and an inner network of thin sheets of bone (trabeculae) and intercommunicating spaces (cancelli) which together form spongy bone. The spongy bone often has a hollow central cavity which contains marrow or fat or outgrowths of the air sacs (see PNEUMATIZATION OF BONE; RESPIRATORY SYSTEM).

The greater part of the skeleton is first laid down in the embryo (see DEVELOPMENT, EMBRYONIC) as a cartilaginous framework and later converted into bone by the process of ossification. Most bones thus ossify in cartilage and are called cartilage bones. Some, however, ossify directly without going through a cartilaginous stage, and these are known as membrane bones; except for the clavicle, they are confined to the SKULL, where they make up the roof, parts of the side walls, and most of the jaws and palate. In the adult, cartilage is found mainly as articular pads which serve as shock absorbers and to reduce friction between bones.

Bones begin to appear early in embryonic development, but many of them are not completely ossified until maturity. The ossification of a cartilage bone, such as a limb bone, begins in the middle of the shaft, the ends remaining cartilaginous for a time. The bone grows longer as the result of the proliferation of cartilage near the ends and, as new cartilage is formed, it is progressively converted into bone.

In addition to growing in length, a bone also grows in thickness as new material is deposited beneath the periosteum. As the entire structure increases in size, it is remodelled so that it retains its shape, bone tissue being added in some places and removed in others. A bone and its internal structure will develop normally only under the influences of the surrounding muscles and soft tissue.

Two types of ligaments have been reported in birds: collagenous-fibre ligaments, which are highly elastic and noncompliant, and yellow elastic ligaments, which are elastic and relatively compliant. Little is known of the properties and distribution of yellow elastic ligaments; they are known from the avian neck and may be found in the wings of some birds.

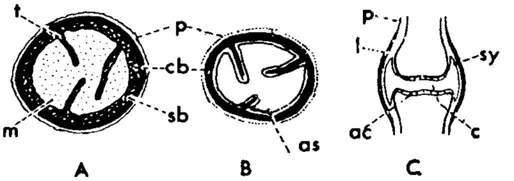

Fig. 1. A, B. Transverse sections through mid-shaft of femur (A) not pneumatized, and humerus (B) pneumatized, of fowl *Gallus*. The thickness of the bone wall, and the relative thickness of the compact and spongy bone, varies in different specimens, especially in the femur. (Partly based on data from A. S. King.)
(C) Diagram showing structure of synovial joint.
ac. articular cartilage; **as.** air sac; **c.** cavity of joint; **cb.** compact bone; **l.** ligament of joint capsule; **m.** marrow; **p.** periosteum; **sb.** spongy bone; **sy.** synovial membrane; **t.** bone trabecula.

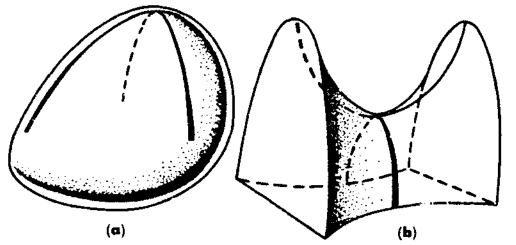

Fig. 2. Two fundamental geometric types of articular surfaces. (a) Ovoid, which may be convex (male) or concave (female). Note that the solid body presents ovoid profiles in two planes at right angles and that the curvatures of the two may be different. (b) Saddle-shaped surfaces, which are concave-convex. In practice both types of surfaces may vary from only slightly to highly curved. Thus ovoid surfaces may be 'almost flat' or 'almost spherical', but the majority show intermediate grades of curvature, and much variation in change of radius from place to place. (Courtesy of Williams & Warwick, 1973, and Longman Group Ltd.)

Most avian ligaments are collagenous-fibred bands between bones; articular ligaments and linkage ligaments are the two main kinds. Articular ligaments bind the bones of the skeleton together; they prevent the articulations from being disrupted under stress and fix the type and extent of movement between two bones at an articulation. Linkage ligaments are known only from the head; they span two or more articulations and limit or couple the movement of the bones they join.

The joints between bones differ greatly in their structure and mobility. The arrangement of a typical freely moving joint is shown in Fig. 1c. Contact between the two bones is made by cartilaginous surfaces on their ends. The surfaces have a low coefficient of friction and are lubricated by the viscous synovial fluid. The joint is enclosed in a fibrous capsule, lined by the synovial membrane and usually strengthened with ligaments. Sliding, angular, circumductional, and rotational movements at joints may be combined to produce an almost infinite variety of movements. Two fundamentally different articular surface shapes, ovoid and saddle-shaped (Fig. 2), make these movements possible. Ovoid surfaces are either convex in all directions (male ovoid) or concave in all directions (female ovoid) whereas saddle-shaped surfaces are convex in one plane and concave at right angles. In addition to allowing motion between bones, articulation, along with ligaments and muscles, reduces stress and redistributes forces within the skeleton.

Factors influencing form and structure of bones. The shape of bones and joints and their internal structure are adapted to the functions which they have to perform and the strains to which they are subjected in life. The degree to which this is the result of hereditary factors or of use during embryonic or later life has been extensively studied. A femur of relatively normal shape will develop from isolated fragments of limb bud removed from the embryo and grown in a tissue culture, despite the absence of muscles and of the possibility of movement. In cultures of limb-bud material the skeleton will differentiate into the elements of the thigh and leg, and joint rudiments will appear at the appropriate places. On the other hand, the finer details of the normal skeleton do not develop perfectly. The rudimentary joints tend to fuse, although they can be made to develop more normally if the bones are artificially moved.

The shape of bones and the amount of bony material present in a skeletal bone depend to a great extent upon the magnitude of the forces acting upon the skeleton. For example, the surface markings of bones reflect the shape of the attached connective tissue structures: depressions (fossae) are produced by fleshy muscular attachments; elongated (crista), pointed (process), or rounded (tuberosity, tubercle, or trochanter) elevations are usually associated with the attachment of tendons. The thickness of the wall of bones and the arrangement of the internal trabeculae are readily modified by changes in stress patterns. Bone apposition by osteoblasts and bone resorption by osteoclasts are in balance under normal conditions. Under greater-than-normal strains bone apposition will predominate; under decreased stresses bone absorption will predominate. Weak but steady compression may cause erosion; a steady tension may cause the appearance of bony processes at muscle attachments, ossification of collagenous tissue, and formation of sesamoid bones; and new articulations may develop when two bones contact one another and continue to rub together. The arrangement of the internal trabeculae has been shown to correspond to the lines of force acting on the bone. When local stresses are applied, trabeculae may undergo a corresponding condensation and reorientation.

The evidence thus indicates that the major features of the skeleton's architecture are determined by heredity, but many of the finer details that appear later in the embryo or after hatching depend for their proper development on environmental factors such as movement and mechanical stress. Skeletal structure is also affected by diet and by the action of chemical substances (hormones) secreted into the bloodstream by certain ductless glands such as the pituitary, parathyroids, and sex glands (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM). Adequate supplies of calcium and of vitamins such as A and D are necessary for normal ossification and growth, and (as in mammals) rickets and other deficiency diseases will occur in their absence.

Changes in the composition of the adult skeleton are associated with physiological processes accompanying such activities as moulting and egg laying. In chickens and pigeons, additional bone tissue (medullary bone) is laid down in the marrow spaces of limb bones before the eggs are laid, and this is subsequently reabsorbed and the calcium thus liberated used in the formation of the eggshell. A similar condition may be artifically induced in male or immature female birds by the use of hormones.

Evolutionary history. The skeleton of birds most closely resembles that of reptiles, especially that of members of the subclass Archosauria (e.g. dinosaurs, pterosaurs, crocodiles). Birds share the following skeletal characteristics with reptiles:

1. The skull and atlas are articulated by a single occipital condyle.
2. The lower jaw is composed of several elements and is hinged on a movable quadrate bone.
3. The ear has a single ossicle, the columella (or stapes).
4. The ribs have uncinate processes, a characteristic found elsewhere in only a few reptiles.
5. The ankle is formed by an intertarsal joint.
6. The pubic bone slants backward as in some dinosaurs.

Until recently it was generally accepted that birds arose from the pseudosuchian thecodontians, a group of primitive archosaurian reptiles. Recent reevaluation of the fossil record strongly indicates that the immediate ancestor of birds was among the small coelurosaurian theropod dinosaurs (see EARLY EVOLUTION OF BIRDS).

The Jurassic bird *Archaeopteryx* possessed a remarkable combination of reptilian and avian features (see ARCHAEOPTERYX). There is great diversity in the form of avian skeletons, which is evident when the skeletons of ratites, penguins, or hummingbirds are compared with those of typical songbirds. Many of our ideas about the relationships of the higher categories of birds are based on characteristics of the skeleton. Most of these ideas were developed at the turn of the century, after which morphological studies generally declined. Recently systematists have shown renewed interest in using skeletons for a variety of taxonomic and evolutionary ecological studies. Skeletons offer a wider variety of measurable characteristics than do skins for those interested in variation among and between populations and a host of qualitative characters for those interested in phylogenetic studies. Unfortunately, few such studies have considered the physiological adaptations of bone mentioned above. Thus, similarities between species which use similar environments, such as grebes (Podicipedidae) and divers (Gaviidae), or flamingos (Phoenicopteridae) and avocets (Recurvirostridae), are as likely to be the result of adaptations as they are to be the result of common ancestry. Current museum skeletal collections are grossly inadequate for the work which needs to be done.

Special avian features. Most of the striking features of a bird's skeleton are associated with its two independent and specialized methods of locomotion, flying with the forelimbs and walking with the hind ones. In typical birds, both fore and hind limb girdles are stoutly built, since each has to support the whole weight of the body alone when the bird is, respectively, flying or walking. The shoulder (pectoral) girdle and sternum form a unit that is firmly (although not immovably) attached to the ribs, and the pelvic girdle is rigidly fastened to a long segment of backbone. Birds have forelimbs with highly modified skeletons in which the arm, forearm, and hand all play a part in supporting the wing (see WING, COMPARATIVE ANATOMY OF).

The hindlimb is also specialized. Some of the metatarsals, which actually belong to the foot, are fused and lengthened so that the leg, like those of certain dinosaurs and running mammals, appears to contain an extra segment. The vertebral column, except for the neck region, is comparatively immobile, and many of the vertebrae are fused. As in pterosaurs, the skeleton of many birds is lightened by extensive pneumatization.

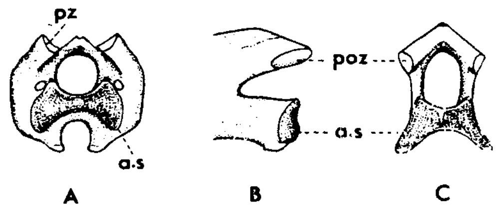

Fig. 3. Neck vertebra of bird: (A) from in front, (C) from behind; (B) shows hind part of vertebra from the side.
as. articular surface; **pz, poz.** pre- and post-zygapophyses.

Vertebrae and ribs. The vertebral column of birds is usually subdivided into cervical (neck), thoracic (chest), lumbar (loins), sacral (hip), and caudal (tail) regions. The total number of vertebrae varies between about 40 and 60; most of the difference is due to variation in the number of cervical vertebrae. The joint surfaces of most of the unfused vertebrae are heterocoelous (saddle-shaped) (Fig. 3), but in penguins, waders or shorebirds (Charadrii), and parrots some of the thoracic vertebrae may have opisthocoelous (hollowed out behind = ovoid) joints. The first two cervical vertebrae (atlas and axis) differ in structure from the rest; in the hornbills (Bucerotidae) they are fused into a single bone. Some of the

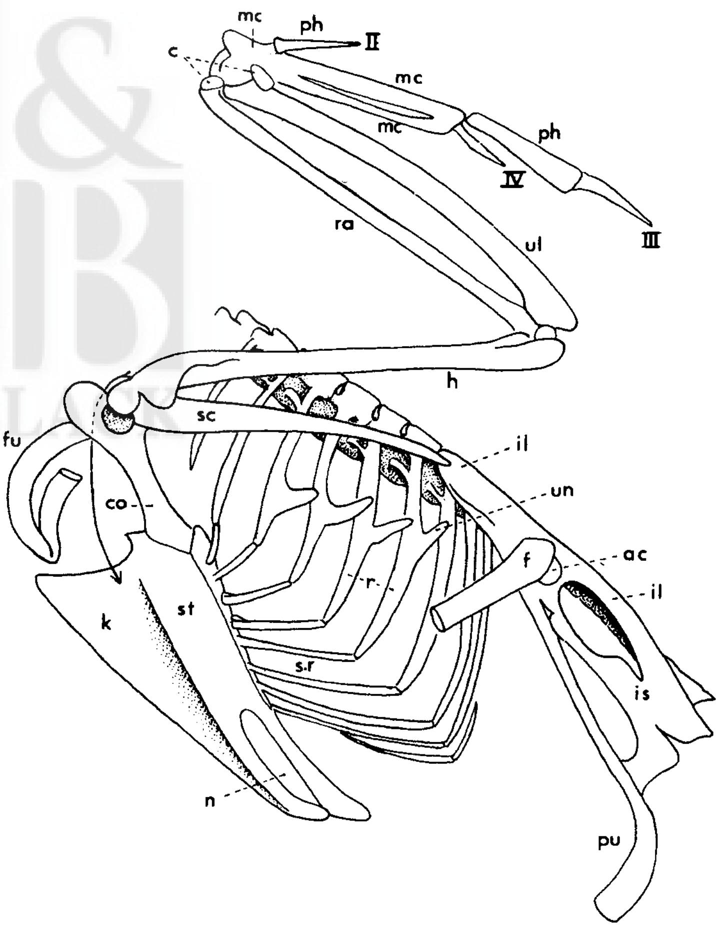

Fig. 4. Skeleton of trunk of goose *Anser* sp. (After Kingsley, Comparative Anatomy of Vertebrates, 1917).
ac. acetabulum; **c.** carpals; **co.** coracoid; **f.** femur; **fu.** furculum; **h.** humerus; **il.** ilium; **is.** ischium; **k.** sternal keel; **mc.** metacarpals; **n.** sternal notch; **ph.** phalanges; **pu.** pubis; **r.** ribs; **ra.** radius; **sc.** scapula; **sr.** sternal ribs; **st.** sternum; **ul.** ulna; **un.** uncinate process; **II, III, IV,** digits. Curved arrow shows direction of pull of pectoralis secundus muscle.

neck vertebrae are highly modified in the darters (Anhingidae), most cormorants (Phalacrocoracidae) and herons (Ardeidae), in which the neck is permanently kinked but can be partly straightened suddenly to capture fish. The rib-bearing thoracic vertebrae have little movement, and some of them may be fused. The ribs articulate with the vertebrae by two heads and are divided into dorsal (vertebral) and ventral (sternal) segments which are jointed together (Fig. 4). The sternal segments are bony, unlike the corresponding costal cartilages of mammals; possibly their ossification, although it also occurs in ratites, is an adaptation to the stresses of flight. Most of the ribs have uncinate processes, each bound by ligaments and muscles to the rib behind, which help to strengthen the chest.

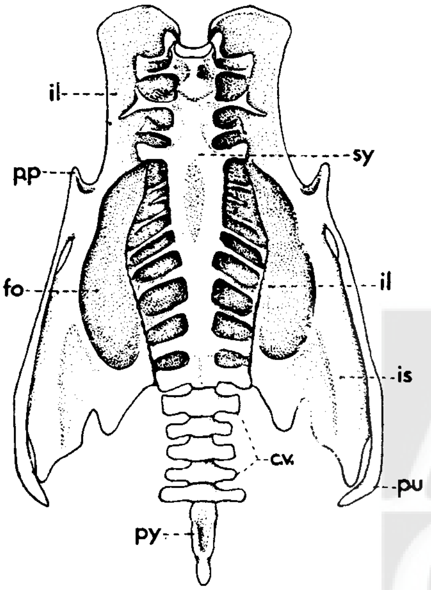

Fig. 5. Pelvis and synsacrum of fowl, seen from below.
cv. caudal vertebrae; **fo.** fossa for part of kidney; **il.** ilium; **is.** ischium; **pp.** pectineal process; **pu.** pubis; **py.** pygostyle; **sy.** synsacrum.

A number of posterior thoracic, lumbar, sacral, and anterior caudal vertebrae are fused together to form the synsacrum (Fig. 5). This is ancylosed or at least very firmly attached to the pelvic girdle, so that the weight of the body when borne by the legs is widely distributed along the backbone.

Behind the synsacrum are a number of movable tail vertebrae and then a structure composed of several fused elements known as the pygostyle (plough-share bone). This bone carries the tail feathers, and its movements are important to flight.

Sternum. The sternum or breastbone has a well-developed keel (carina) in modern flying birds (carinates), to which are attached the strong pectoral muscles. Its posterior end varies in shape, having one or two notches or holes (fenestrae), or one of each, on each side in many species (Fig. 4). In swans (*Cygnus* spp.) and some cranes (Gruidae) it is hollowed in front to contain folds of the trachea. There is no sternal keel in ratites; the sternum is flat ('raft-like') or slightly bossed.

Pectoral girdle and wings. The pectoral girdle (Fig. 4) consists, on each side, of the scapula, coracoid, and clavicle. The scapula is very long and firmly attached to the ribs by muscles and ligaments; the coracoid extends down from the front of the scapula to the sternum. The glenoid cavity, with which the head of the humerus articulates, is situated at the junction between scapula and coracoid. It is shallow, allowing the limb free mobility. Each clavicle articulates with the front of the coracoid and scapula so that a hole, the foramen triosseum, is enclosed between the three bones. The tendon of the supracoracoideus muscle passes through this hole and, curving backwards, is attached to the head of the humerus; this muscle gives the wing power on its upstroke (see FLIGHT).

The two clavicles are usually fused in the midline forming the furcula ('wishbone' or 'merrythought'). The angle of the furcula is generally widest in birds with strong flight, the bone acting as a curved strut to brace the wings apart. The clavicles are much reduced in a few flying birds (e.g. some parrots). Reduction or loss of the clavicles is also seen among certain ground-living birds; these include the ratites, in which the two bones do not even approach one another in the midline. In ratites the forelimb as a whole is reduced, especially in the kiwis (Apterygidae) and the giant extinct moas (Dinornithidae); in the latter the skeleton of the arm and hand seems to have been entirely absent.

The head of the humerus is expanded and has crests for muscle attachments. Its outer end articulates with the radius and ulna. The latter is the stouter of the two forearm bones and often bears a row of quill knobs where the secondary flight feathers attach. The relative lengths of the wing segments (arm, forearm, manus) vary widely among birds, the functional significance of which needs more work; they are said to be correlated with the type of flight. Generally, in strongly flying birds (e.g. swifts) the forearm and hand are longer than the humerus; in soaring birds (e.g. albatrosses Diomedeidae) the reverse is true.

The carpal bones of the wrist are reduced in the adult to two (radial and ulnar complexes), although others occur in the embryo and later either disappear or fuse with each other or with the metacarpal (to form a carpometacarpus). Only three of the fingers are present; whether these represent the I, II, and III or the II, III, and IV digits of the series is in dispute. (The II, III, and IV convention is used here.) Each digit is represented by a metacarpal and one or more phalanges. Metacarpal II is fused with the base of III, and III and IV are partly fused. The II digit has some power of independent movement and carries the bastard wing (alula). In a few birds one or more of the digits are clawed. The nestling Hoatzin *Opisthocomus hoazin* uses these for scrambling about after leaving the nest. (See also WING.)

Pelvic girdle and hindlimbs. As in other vertebrates, the pelvic girdle

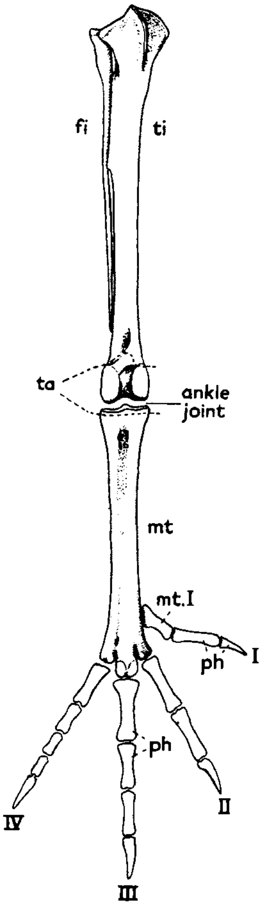

Fig. 6. Right leg and foot of fowl, seen from in front.
fi. fibula; **mt.I.** first metatarsal; **mt.** fused metatarsals; **ph.** phalanges; **ta.** tarsal contribution to tibiotarsus above and tarsometatarsus below shown between the interrupted lines. **ti.** tibia. **I-IV**, digits.

is formed, on each side, by the ilium, ischium, and pubis, which are partly fused. The pubis has a most unusual orientation, found elsewhere only in some dinosaurs: it lies parallel to and beneath the ischium (Figs 4, 5). Except in the Ostrich *Struthio camelus*, the pubic bones do not meet to form a symphysis enclosing the pelvic outlet; this condition may be related to the size and hardness of the bird's egg. The acetabulum, into which the head of the femur fits, lies at the junction of the three pelvic bones and is perforated. Behind it there is usually a large ischiatic foramen. The proximal end of the femur has a prominent process (trochanter) to which muscles are attached. Many species have a kneecap, or patella.

The condyles of the femur articulate with the tibia and fibula at the knee. The tibia, the inner of these bones, is much the larger. In most birds the fibula ends as a thin splint about two-thirds of the way down the tibia (Fig. 6), though in a few (e.g. penguins) it may reach the ankle (intertarsal joint).

A bird's ankle is constructed very differently from that of a mammal. In most vertebrates a series of small bones, the tarsals, is arranged in two rows between the bones of the leg and those of the foot. In birds, however, some of the tarsals of the proximal row have disappeared while others have fused with the lower end of the tibia. Thus the tibia referred to in the previous paragraph should, strictly speaking, be termed the tibiotarsus.

Similarly, some of the bones of the distal tarsal row have become fused with the metatarsus. Consequently, the ankle joint is actually situated between the proximal and distal rows of tarsals, instead of between the proximal tarsals and the leg bones as in man. These observations have been derived mainly from the study of embryos and cannot be verified from adult skeletons.

Most birds have 4 toes, each represented by a metatarsal element and a number of phalanges. The fifth toe is normally absent. The metatarsals of the second, third, and fourth toes are very long and fused; some of the tarsals are fused with their proximal ends. The result is a single bone known as the tarsometatarsus; its compound nature is apparent at its distal end, where it divides into three pulley-shaped processes or trochleae, each corresponding with one metatarsal (Fig. 6). In penguins the metatarsals are less closely fused than in other birds; this is no longer regarded as a primitive feature, since it has been shown that the fusion was often more complete in fossil than in living forms.

The second, third, and fourth toes each articulate with the appropriate metatarsal pulley and generally point forward. They contain 3, 4, and 5 phalanges, respectively, the distal one being clawed. In many birds there is also another toe, the first (hallux), which is short and points backward. Its metatarsal is small and attached to the back or side of the tarsometatarsus; it contains at most only 2 phalanges. Since it is opposed to the other toes, it may be an important aid in perching. It tends to be reduced in birds that do not perch and may be elevated some distance above the other toes. In ratites (except kiwis) it is absent. The Ostrich is peculiar in having only 2 toes, probably the third and fourth. Special modifications of the feet in various birds are described in LEG.

Pneumatization. Some of the bones in birds contain extensions from the nose and middle ear (in the case of the skull bones) or from the air-sacs that originate from the lungs (see RESPIRATORY SYSTEM). During the process of pneumatization, which begins in the late embryo and is not completed until some time after hatching, these extensions grow into the bones. The holes through which they enter may be seen in the dry skeleton; in the humerus, for example, there is a large pneumatic foramen on the inner aspect of the proximal end. The number of bones that become pneumatized varies greatly, but accurate data on the extent of pneumaticity are available for only a few species (see PNEUMATIZATION OF BONE). J.G.S.

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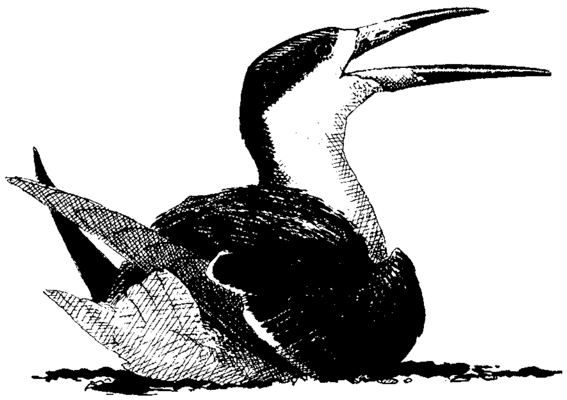

Black Skimmer *Rynchops niger*. (*B.P.*).

SKIMMER: substantive name of the 3 species of the family Rynchopidae (Charadriiformes, suborder Lari); also called shearwater, sea dog, or scissorbill. The Indian Skimmer *Rynchops albicollis* inhabits India, Pakistan and Burma; *R. flavirostris* is African; and the Black Skimmer *R. niger* has several races in eastern North, Central and South America.

Characteristics. Skimmers, *c.* 40 cm long, are brownish-black above with white underparts, face and forehead. Their bills are yellow or red with black or yellow tips, and their small, moderately webbed feet are also red. Similar in body weight to a medium-sized tern or small gull, they appear deceptively large because of their relatively long, pointed wings and long, deep, laterally compressed bill. Females resemble males but are markedly smaller, averaging 250 g as opposed to 350 g for males of North American *niger*. Juveniles differ from adults in having dark bills and feet and the upper parts streaked with brown and buff. Skimmers are unique among birds in that the pupil closes to a narrow, vertical slit in bright light. Anatomical and behavioural studies show affinities with gulls, terns, and skuas, and suggest an early departure of the skimmer line from the ancestral Lari.

Habitat. In South America and the Old World skimmers frequent lakes and rivers, breeding on sand bars exposed during the dry season. When rivers run high during the rainy season they move to estuaries and the coast. Perhaps because high river water coincides with the breeding season of North American skimmers, they are exclusively coastal,

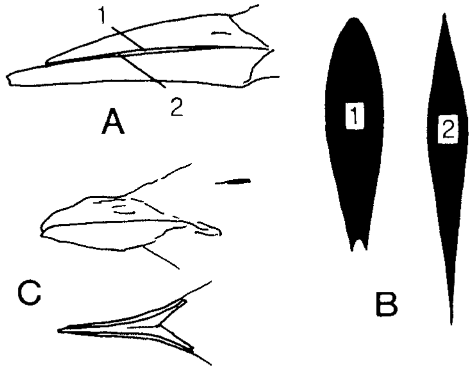

Fig. 1. Bill of the Black Skimmer *Rynchops niger*.
(A). Lateral view of adult. 1 and 2 are planes of sections shown in (B).
(B) Oblique sections of upper (1) and lower (2) mandibles.
(C). Bill of 87 g chick in lateral and ventral views. (*R.L. Zusi*)

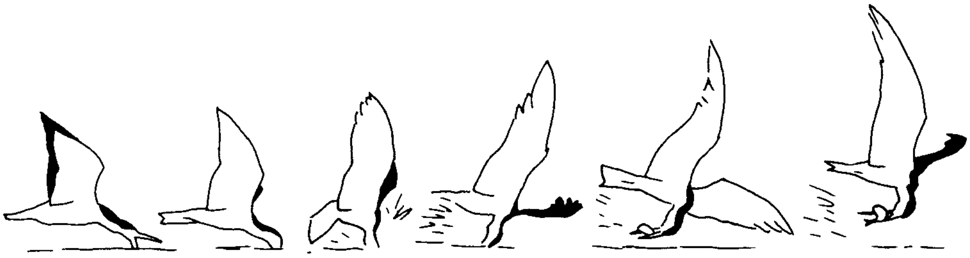

Fig. 2. Black Skimmer *Rynchops niger* catching fish. Drawn from selected frames of a single motion picture sequence. (*R.L. Zusi*)

breeding on barrier islands and dredge banks. The more northerly and southerly populations of *niger* perform north–south migrations.

Food. In bill structure and feeding behaviour *Rynchops* is unique. The lower mandible is laterally flattened like a knife blade and it protrudes well beyond the upper, which itself is narrow and oval in cross section (Fig. 1). A skimmer can raise its upper jaw about 45° above the closed position while depressing the lower jaw. Skimmers catch their prey (fish and shrimps) by flying low over the water with the upper jaw raised and the lower jaw open and immersed. When the sharp edge of the lower mandible strikes prey the head doubles under the body of the flying bird and the jaws snap shut (Fig. 2). The prey is drawn out of the water while the bird's head faces back or down, and is swallowed in flight or after the bird alights. Motion of the head cushions the shock and enables the shorter upper mandible to reach prey struck beyond its grasp. With the upper jaw raised during skimming, the lower jaw cuts the water unobstructed and the chance of striking prey is increased. The oft repeated statement that fish slide up the inclined edge of the lower mandible is incorrect.

Usually skimmers feed in shallow water containing high concentrations of prey. Flying in ones or twos, or sometimes in loose flocks, they cut a straight path apparently without seeing individual prey, but the birds are attracted to surface disturbances caused by swarms of fish. Their essentially tactile method of foraging permits them to feed also at night, which they do even under the darkest conditions. The lower jaw of a foraging bird may strike submerged obstacles or the muddy bottom, and the head then doubles under the body. Breakage and abrasion at the tip of the rapidly growing rhamphotheca of the lower jaw control its length. Fishing rates in the Black Skimmer have been measured under various conditions at one fish per half minute (rarely much faster) to one per 6 minutes of skimming. Sometimes a catch is lost through kleptoparasitism by gulls.

Behaviour. When not feeding, skimmers typically preen, bathe, or rest in a dense flock facing into the wind.

The Black Skimmer exhibits a variety of displays associated with aggression, pair formation and maintenance, territorial defence, and copulation. These show little correspondence to displays of the black-capped terns, but resemble those of noddies *Anous*, gulls, and skuas. Only with the latter do they share a distraction display when the young are threatened.

Voice. The voice of *niger* is a short or protracted *arp*, *arp* . . ., and of *albicollis* a nasal *kap*, *kap* . . . recalling the yapping of young fox hounds; that of the smaller *flavirostris* is a sharp *kik kik* . . ., or a harsh, tern-like *kreeep*.

Breeding. Skimmers nest in loose colonies, generally on open sand or shell, but *niger* occasionally nests on seawrack in salt marsh with terns, or even on gravel roofs. Colonies vary in size from only a few birds to many hundreds or several thousands. In mixed colonies Common Terns *Sterna hirundo* usually outnumber the Black Skimmer and are more aggressive, affording the skimmers protection from predatory gulls. The African Skimmer, however, is known to mob and chase away such predators as Sacred Ibis *Threskiornis aethiopicus*, herons, monitor lizards, and crocodiles. Mortality of eggs is caused by sudden rain squalls, and some colonies are subject to destruction from storm tides. Skimmers are single-brooded but they will lay again after destruction of eggs during a period of about 2 months in eastern North America.

The nest is a hollow maintained by kicking sand back while the bird squats or incubates. Eggs are creamy white marked with an endless variety of brown, black, and lilac spots and blotches. In North America clutches are usually 4 (2–5); in Africa and Asia usually 3 or less (1–4). Both sexes incubate and care for the chicks. Incubation begins with the first egg and lasts about 3 weeks. One study of *niger* showed a hatching success of about 80%, but 10 of 11 surviving fledglings were the first hatched of the brood, which pecked and chased younger siblings at feeding time. It is stated of *flavirostris* that the first chick wanders off within a day of hatching and the remaining eggs are abandoned. Parents are known to wet their feet and belly feathers while flying over water before returning to incubate or brood, presumably to promote cooling of the eggs or young; out of the breeding season wetting of these parts probably serves to wash off mud (see BELLY SOAKING). Chicks, difficult to see in their cryptic down, squat and dig into a hollow in the sand, sometimes kicking sand on to their backs. They are offered freshly-caught fish or shrimps carried from the feeding ground crosswise in the adults' bills. The mandibles of chicks are of nearly equal length, permitting them to take food from the adult or from the ground (Fig. 1). Young begin to fly at about 5 weeks and at this time the differentiation in mandible lengths is under way. Fledged young continue to beg from their parents or other adults, but they also engage in skimming. A young bird flying with its parents probably learns quickly the most auspicious places in which to forage. R.L.Z.

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SKIN: the protective and containing integument of the body, consisting of an underlying dermis and an overlying epidermis. The dermis is relatively thick and highly organized, being supplied with muscles, blood vessels, and nerves. The thinner and simpler epidermis consists of layers of cells, renewed by proliferation from the basal (Malpighian) layer as the outer layers die and become horny (keratinized). The epidermis of birds is notable for the special external structures to which it gives rise and by which it is almost wholly covered—especially the feathers, but also the horny sheathing of the bill, legs, and feet, with the claws on these last (see FEATHER; BILL; LEG). Correlated with the presence of this covering is the almost complete absence of skin glands; the exceptions are a few small glands within the external auditory meatus and the oil gland on the rump (see OIL GLAND). The skin of birds thus does not perform the function of sweating, which has an important physiological role in mammals, and does not produce a sebaceous secretion for lubrication of its surface or outgrowth; nor can it play a great part in heat transmission (see HEAT REGULATION). The skin is, however, supplied with tactile nerve-endings or 'Herbst's corpuscles' (see TOUCH). Its blood vessels give the skin, at least in some instances, the capacity of exhibiting transient colour changes (flushing), visible on bare patches or even through the horny covering of bill and legs (see HERON; OSTRICH). In some birds there are such appendages as spurs, wattles, combs, lappets, sacs, or pouches (see INTEGUMENTARY STRUCTURES). For care of the body surface generally see under COMFORT BEHAVIOUR.

'Skin' is also the term applied to the usual unmounted study specimen of a bird (see MUSEUM).

SKUA: substantive name, especially in British usage, of all members of the Stercorariidae (Charadriiformes, suborder Lari); in the plural, general term for the family. Usage in North America and elsewhere prefers the name 'jaeger' (German word meaning 'hunter') and restricts

Great Skua *Stercorarius* (*Catharacta*) *skua*. (*B.P.*).

'skua' (from Icelandic word 'skufr') to *Catharacta*. The family contains 2 genera, *Catharacta* (not recognized elsewhere in this work) and *Stercorarius*; the latter has 3 species, all northern: the Arctic Skua (or Parasitic Jaeger) *S. parasiticus*, the Pomarine Skua (or Pomarine Jaeger) *S. pomarinus*, and the Long-tailed Skua (or Long-tailed Jaeger) *S. longicaudus*. *Catharacta*, formerly considered to be a superspecies with one boreal representative and several forms in the far south, is now divided into 3 species. (1) *C. skua* comprises 4 allopatric sub-species distinguished by plumage and measurements: *C. s. antarcticus* (Falkland Skua), *C. s. lönnbergi* (Brown or Subantarctic Skua), *C. s. skua* (Great Skua), and *C. s. hamiltoni* (Tristan Skua). (2) *C. maccormicki* (South Polar or McCormick's Skua) breeds on the Antarctic continent, overlapping *C. s. lönnbergi* with limited hybridization on the Antarctic peninsula. (3) *C. chilensis* (Chilean Skua) overlaps with *C. s. antarcticus* in Patagonia, also with some hybridization.

Characteristics. The skuas are sometimes treated as a subfamily of the Laridae. They are similar to gulls in size (lengths 50–58 cm) but have dark plumage, and a faster, stiffer wingbeat. They are widely known for their habit of chasing other seabirds in flight until they disgorge food (see PIRACY). Like gulls, they are chiefly associated with the sea, but may breed far inland.

In *Stercorarius*, adult plumage varies between a light phase, with the underparts and collar creamy or almost white and the head conspicuously dark-capped, and a dark phase with the whole plumage almost uniformly dark (see POLYMORPHISM). The dark phase is very rare in *S. longicaudus* and possibly does not occur in adult plumage; in the other 2 species the proportion of light and dark birds varies from area to area. In Shetland less than one fifth of the Arctic Skuas are light, but further north the proportion is generally higher, up to almost 100% in Svalbard and arctic Canada. In *Stercorarius* the primary shafts and bases are always white, but less prominent than in *Catharacta*; the 2 central rectrices are much elongated—pointed and fluttering in *S. longicaudus* but twisted through 90° and appearing clubbed in *S. pomarinus*. The bill is gull-like, unusually soft in its basal half, where a pair of separate thin plates overlie the nostril area, but hard and rather strongly hooked towards the tip. The feet are gull-like also, but with more strongly curved, sharp claws. Juveniles of all *Stercorarius* species are barred below. Barring may be retained in immature plumage and is found in a very small proportion of breeding adults. During winter adults may become somewhat barred below, apparently due to partial moult of body feathers. Among *Catharacta*, only juveniles of *C. chilensis* show any barred plumage, and this is confined to the back and scapulars. In *Catharacta* the plumage is generally brown, with conspicuous white wing patches at the base of the primaries. *C. maccormicki* is dimorphic, with light phase birds increasing in frequency at higher latitudes. The wings appear a characteristic velvety-black, contrasting with the body colour. *C. chilensis* adults are decidedly rufous in body colour, have cinnamon under wing coverts and the head has a markedly capped appearance. *C. s. lönnbergi* is a large, heavy form with a fairly uniform medium brown plumage, *C. s. antarctica* relatively small with a stubby deep and powerful bill, while *C. s. hamiltoni* is intermediate in appearance between *C. s. lönnbergi* and *C. s. skua*; adults of the latter can be identified by their conspicuously streaked plumage.

Habitat. All skuas are marine outside the breeding season, but probably frequent areas less than 50 km from coasts, although they remain entirely independent of land. *Catharacta* breeds socially, although nest dispersion varies greatly between and within species. Colonies are often adjacent to bird cliffs or penguin rookeries, on open ground. The Arctic Skua nests in colonies on moorland in association with seabird communities in Scotland, the Faeroes, Iceland and elsewhere, but also nests in well dispersed territories on arctic tundra. Pomarine and Long-tailed Skuas are exclusively tundra nesters.

Distribution. The 3 *Stercorarius* species are northern circumpolar breeders. Their ranges overlap widely. *S. longicaudus* generally extends furthest north. The breeding of all 3, but especially *S. pomarinus* is influenced by local fluctuations in lemming *Lemmus* abundance. The 3 species exclude each other from their territories. *S. pomarinus* is highly nomadic and moves to areas of lemming abundance. In years when it breeds, it excludes the 2 smaller species from the area. *Catharacta skua* is notable for having a bipolar distribution. *C. s. skua* is confined to the North Atlantic, nesting in Shetland, Orkney, Caithness, Sutherland and the Outer Hebrides, the Faeroes, Iceland, and has recently colonized Bear Island, Svalbard and north Norway. Non-breeders may appear anywhere in the North Atlantic, from Svalbard to Brazil. *C. s. hamiltoni* nests only on Gough and Tristan, *C. s. antarctica* nests on the Falkland Islands and adjacent coast of South America, and *C. s. lönnbergi* nests on part of the Antarctic peninsula, and on subantarctic islands all round the continent. *C. maccormicki* nests on the Antarctic continent. *C. chilensis* nests along the west and south coasts of South America south of 35°S, and on the east coast between Puerto Deseado and Puerto Gallegos.

Populations. On the edge of its range, in Scotland, numbers of Arctic Skuas have increased a little this century, lately to around 2,400 breeding pairs, but in the Faeroes numbers have declined considerably in recent years. In the Arctic, numbers of the 3 *Stercorarius* species are unknown, but presumably large. *C. s. skua* has a total population of 12,000 breeding pairs, half nesting in Britain, with the largest single colony of 3,000 pairs on Foula (Shetland). *C. s. hamiltoni* numbers less than 6,000 breeding pairs, *C. s. antarctica* between 3,000–5,000 pairs, *C. s. lönnbergi* about 20,000 pairs, *C. maccormicki* about 7,000 pairs and *C. chilensis* at least 10,000 pairs. In addition, each population contains large numbers of immature birds, perhaps about equal to the number of breeding pairs.

Movements. *Stercorarius* spp. are all long-distance migrants. *S. pomarinus* has a well-marked winter concentration off the highly productive coast of West Africa between 25° and 5°N, and non-breeders occur there in summer also. *S. parasiticus* winters further south, commonly on the continental shelves of southern Africa and Australia, but dark phase birds apparently move less far south than light phase individuals, indicating a leap-frog migration. Fledglings of *C. s. skua* migrate to south-west Europe in winter, with most ringing recoveries off the coast of Iberia, while some move as far as Brazil, Guyana and the Cape Verde Islands. In summer the immatures move northward again, many 2 to 4 year old immatures visiting high latitudes between Greenland and Svalbard. A high proportion of adults remain in British waters throughout winter. Icelandic birds show similar movements to the British population but with a large number of birds migrating down the west coast of the Atlantic, where very few British Great Skuas are found.

Food. *S. pomarinus* feeds largely on lemmings in summer and by predation on small seabirds (notably phalaropes) in winter, less regularly by fishing or piracy. *S. longicaudus* lives on lemmings, insects, berries, small birds and eggs in summer and by piracy, chiefly on terns, in winter. In arctic tundra areas *S. parasiticus* feeds on insects, berries, small birds and eggs and only to a limited extent on rodents. In coastal areas, such as Orkney and Shetland, it subsists largely by piracy on terns, auks and Kittiwakes *Rissa tridactyla*, similarly in winter. *C. s. skua* variously splash-dives for surface fish, preys directly on seabirds and terrestrial mammals, robs gulls, auks and Gannets *Sula bassana* of food and scavenges, e.g. behind fishing boats. Southern *Catharacta* have a similar range of feeding habits; *C. s. lönnbergi* is particularly associated with penguin rookeries, but *C. maccormicki* survives largely by catching food for itself at sea.

Behaviour. Skuas are normally monogamous and pair for life. In *C. s. skua* a few exceptional cases have been recorded where a male paired with 2 females which layed in the same nest; in *C. s. lönnbergi* colonies on islands off New Zealand and on Marion Island, such trios have also been found to occur regularly, as have others comprising 2 males and 1 female, although this social system is not found in any of the other *Catharacta*. Distances between skua nests vary from the extreme spacing on arctic tundra, where nests are often 2 km or more apart and skuas defend at least 1 sq km against congenerics (hunting over some 3 sq km), down to a spacing of nests only 5 m apart, in rare cases within colonies on small islands off north Scotland. On Foula, 306 pairs of Arctic Skuas bred in a colony occupying 1.7 sq km, or approximately the area defended by a single pair breeding on arctic tundra. A partial explanation for the variation lies in the fact that the birds nesting in Shetland do not obtain a significant amount of food within the territory, but feed at sea. There have been detailed studies of the behaviour of each species of skua. Most exhibit the same display patterns, although only the smaller species use a 'distraction display' as well as diving on intruders near the nest. Whether standing, swimming or flying, *Catharacta* typically display their white wing patches by stretching their wings vertically upwards, back to back, an advertisement posture found in less intense form in the Pomarine Skua, but not found in Arctic or Long-tailed Skuas.

Voice. Skuas are very vocal at their breeding places, but are usually silent elsewhere. *Stercorarius* spp. make high-pitched cat-calls and harsh, deeper notes. *Catharacta* spp. have a short grunting call and a long display call which is used in mate-greeting and indicating ownership of territory or food items.

Breeding. As skuas have only two brood patches, birds with 3 eggs usually fail to hatch any. Clutches of 2 are normal with about 10% laying only 1 egg. Although hatching success of skua clutches is normally high, in *Catharacta* colonies, where food is short, usually only one chick is fledged by each successful pair; the second-hatched chick, younger by one or 2 days, is often killed by its sibling. *S. parasiticus* begins to breed (on Fair Isle) at between 3 and 6 years of age (most at 4), but apparently at a younger age in arctic Russia. *C. s. skua* begins to breed (on Foula) at between 5 and 10 years of age (most at 7 or 8), but a year earlier in the small colony on Fair Isle between Orkney and Shetland.

See photos AGGRESSION; PIRACY. R.W.F.

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SKULL: the bony and cartilaginous elements of the head, housing the brain and special sense organs, and providing a rigid framework for the feeding apparatus (jaws and hyoid). The remainder of the bird's skeleton is treated separately (see SKELETON, POSTCRANIAL). General topography and nomenclature of parts are considered first, followed by a review of mechanical properties. The positions of most of the skull bones (the majority paired, occurring on each side) are shown in Fig. 1, and only a few are named in the text. On the whole, they are similar to those of reptiles, although certain reptilian bones such as the postorbital are absent, and the temporal region is much modified. The skull is light, and often extensively pneumatized (see PNEUMATIZATION OF BONE), with a compact, rounded braincase. It is pierced by various foramina which transmit cranial nerves and blood vessels. Usually, the cranial sutures

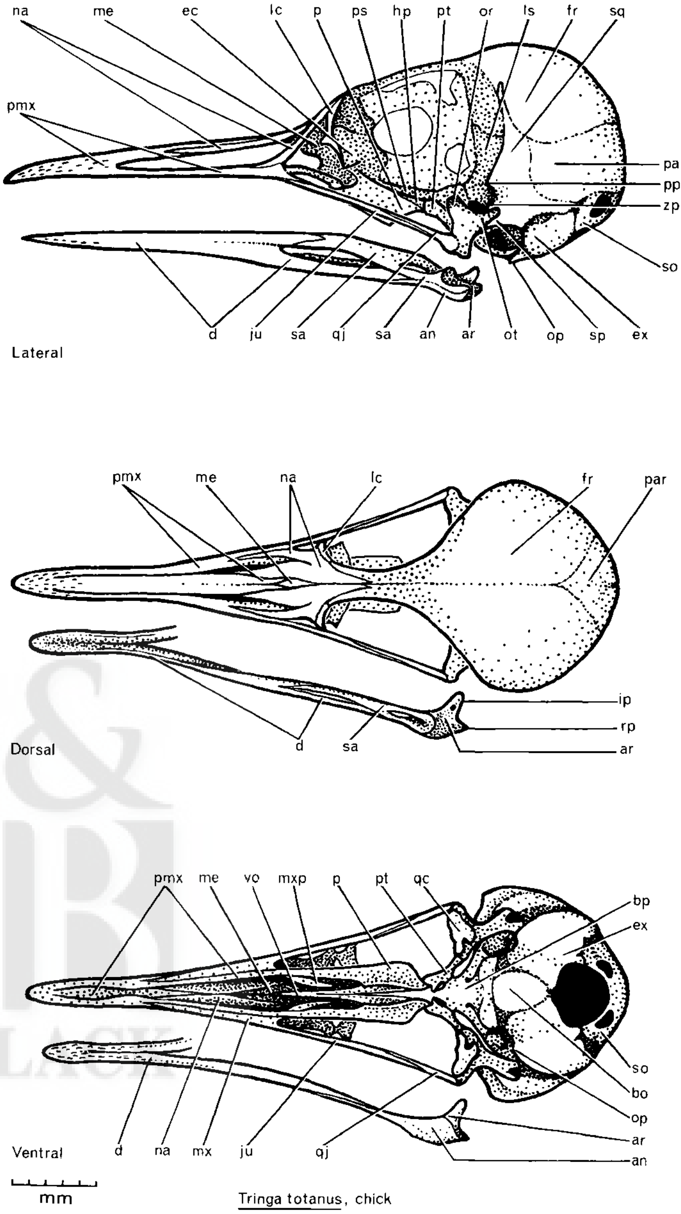

Fig. 1. Skull of Redshank *Tringa totanus* chick, a few days old, to show bones of the skull and important features referred to in the text. At this age, sutures between cranial bones are still clearly visible. This skull is rhynchokinetic, with bending zones in the upper jaw well forward of the craniofacial hinge—contrast with the prokinetic skull of *Ara* in Fig. 2.

an	angular	**or**	orbital process of quadrate
ar	articular	**ot**	otic process of quadrate
bo	basioccipital	**p**	palatine
bp	basitemporal plate	**par**	parietal
d	dentary	**pp**	postorbital process
ec	ectethmoid	**pmx**	premaxilla
ex	exoccipital	**ps**	parasphenoid
fr	frontal	**pt**	pterygoid
hp	hemipterygoid	**qc**	articular condyles of quadrate
ip	internal process		
ju	jugal	**qj**	quadrato-jugal
lc	lacrymal	**rp**	retroarticular process
ls	laterosphenoid	**sa**	surangular
me	mesethmoid	**so**	supraoccipital
mx	maxilla	**sp**	suprameatic process
mxp	maxillo-palatine	**sq**	squamosal
na	nasal	**vo**	vomer
op	opisthotic process	**zp**	zygomatic process

close early in life, so that identification of the various bones in the adult may be difficult. Articulation with the atlas is by a single occipital condyle.

Orbits and nares. The orbits are usually very large, and, except in a few forms such as parrots, are not completely ringed by bone. They are separated from each other by a vertical plate known as the interorbital septum or mesethmoid bone; this is generally incomplete, the gaps being filled in life by connective tissue or cartilage. In the kiwis *Apteryx*, which have (for birds) very small eyes, this septum is absent, and the orbits are separated mainly by the very large nasal cavities; this is a specialized condition associated with the great development of the organs of smell (see SMELL).

The external nostrils are set back near the base of the bill, except in the kiwis where they are at its tip. In some birds, e.g. gannets *Sula* spp., the nostrils become closed by the growth of the surrounding bones (see RESPIRATORY SYSTEM). The nasal cavities, which are lined by mucous membrane, and the cartilaginous nasal capsule that invests them, are situated inside the bones of the bill. Each nasal cavity opens in front at the external nostril and on the palate at the internal nostril; it is separated from that of the opposite side by a cartilaginous septum. Turbinal cartilages project into each nasal cavity from its outer wall, increasing the area of mucous membrane. In some birds, the nasal capsule and septum are poorly ossified.

Upper jaw and palate. The skeleton of the upper jaw is formed mainly by the premaxillae, which in life are sheathed by the horny rhamphotheca. The attachment of the upper jaw to the skull is flexible, so that, as in many reptiles, it is able to move relative to the braincase; this property, known as cranial kinesis, is discussed further below. Key elements in kinesis are the quadrates, which articulate with the cranium at the rear of the orbit. Their lower ends in turn articulate with the jugal bars (jugal and quadratojugal), and with the pterygoids, which rostrally articulate with the palatines. Other elements of the palatal complex and their variations are treated separately (see PALATE).

Lower jaw. The lower jaw, on each side, is usually made up of 6 bones, the front one being the dentary (generally the largest) and the rear one the articular. The latter may be produced backwards as a retroarticular process, giving increased attachment area and leverage for M. depressor mandibulae. This increases the force of jaw opening—a feature of birds which excavate for food by 'gaping', i.e. inserting the closed jaws into a substrate, then opening them. Articulation with the rest of the skull is between the quadrate and the articular. The two halves of the lower jaw meet in a symphysis of varying length rostrally. In several groups, lateral flexion can occur along the free ramus on either side, permitting the gape to be widened, a mechanism discussed further below. Teeth are unknown in any recent bird, though some workers have claimed to identify rudimentary tooth-germs in bird embryos.

Hyoid skeleton. The tongue is supported by a median bone, the entoglossum; this is often partly cartilaginous, and may take the form of paired bones linked by cartilage or ligament, as in many parrots. It articulates with another median element (the basibranchiale) from the caudal end of which arise the paired cornua or hyoid horns, each consisting of a ceratobranchiale anteriorly, articulating with the epibranchiale posteriorly. The horns curve out, then round the posterior end of the mandible to lie near the occipital region of the cranium. In WOODPECKERS, the entoglossum itself is tiny, but the basibranchiale and horns are greatly elongated, giving them the ability to protrude the tongue for great distances; at rest, the horns extend round the top of the skull, in some species even entering a nostril or curving far round the orbit.

Ossicles. As in amphibians and reptiles, there is only a single bone, the columella (stapes), for conducting sound vibrations from the eardrum to the inner ear; the form of this ossicle has some value as a taxonomic character (see Feduccia, 1980). The extra 2 mammalian ear ossicles, the incus and malleus, are represented in birds by the quadrate and articular respectively. In some owls, the bony ear region is asymmetrical on the two sides of the head, a condition probably associated with their highly developed ability to locate sound sources.

The sclerotic coat of the eye is cartilaginous, and the front of the eyeball is reinforced by a series of usually 16 to 18 small, overlapping bony plates known as scleral ossicles. They assist in the process of visual accommodation (see VISION). In some birds there is also a small horseshoe-shaped bone (os opticus) in the sclera, surrounding the optic nerve as it enters the back of the eyeball. Sesamoids are present at the quadrate/mandible articulation in many birds, and are exceptionally highly developed in the Kokako *Callaeas cinerea* of New Zealand.

Cranial kinesis. Despite claims that have at times been made that some birds have akinetic upper jaws, it appears that the ability to move the upper jaw relative to the braincase is of universal occurrence throughout the class. For detailed accounts of the mechanism of kinesis, see Bock (1964) and Bühler (1981). Compared with the condition in which only the lower jaw moves, as in mammals, kinesis confers several advantages, viz:

(a) Maintenance of the primary axis of orientation. When the jaws are opened, the position of their long axis changes relatively little in position, in contrast to the situation in a mammal, in which it is considerably displaced as the lower jaw moves downward. This property may have great value when fast moving prey has to be captured.

(b) In general, cranial kinesis permits a wider gape when the jaws are opened—a feature of special significance in some specialized methods of feeding.

(c) Maintaining the mandible in the closed position. Coupling of upper and lower jaws (see below) permits a considerable reduction of the muscular effort needed to hold the jaws closed; if the upper jaw is heavier than the lower, this effort will in fact be nil.

(d) Faster closing jaws.

(e) A shock absorbing mechanism for all forces acting on the jaws, permitting a lighter skull construction than in mammals. Lightness is also aided by the wider spread of jaw muscle attachments in the kinetic skull, which reduces stress per unit area.

Two main types of kinesis are usually recognized. In *prokinesis*, exhibited by the majority of birds, the whole upper jaw moves about its articulation with the cranium. The articulation is usually formed by a narrow strip of flexible bone though, in large parrots, a set of synovial joints is present instead. Force to raise and lower the upper jaw is provided mainly by muscles attached to the palatines, pterygoids and quadrates (see MUSCULATURE), and is transmitted to the upper jaw via the palatines and jugal bars. In *rhynchokinesis*, the musculature and palatal complex function in essentially the same way, but the base of the upper jaw is rigid, and bending takes place further forward along the jaw. To make this possible, the upper jaw is separated for much of its length into a median dorsal bar, and paired ventral bars. Backward or forward movement of the ventral bars is permitted either by a flexible nasal bar, or (as in ratites and tinamous) a gap in the nasal bar. Rhynchokinesis occurs in the Gruidae, Charadriiformes, and Trochilidae, and in ratites and tinamous. It reaches its most sophisticated level of development in long-billed sandpipers, such as Snipe *Gallinago gallinago* or Curlew *Numenius arquata* (Burton 1974). The bending zone in such species is situated very far forward, enabling the distal region only of the jaws to be opened to grasp subterranean prey while probing. Alternatively, retraction of the upper jaw in highly rhynchokinetic species enables its tip to move backwards relative to the lower, a facility which can be used in shifting food towards the mouth, or in manipulating awkward objects.

Lower jaw movements. The simplest and most basic lower jaw movement is depression, in which the whole jaw is rotated downwards about the quadratomandibular articulations. In some birds, notably parrots and finches, these articulations also permit gliding movements, so that the jaw can additionally be moved backwards and forwards. More complicated is the action of lateral spreading, in which the mandibular rami are bowed outwards to enlarge the gap between them. This action is possible only in birds possessing two pairs of flexion zones within the mandibular rami, and is seen in various groups which regularly have to swallow large objects (e.g. many fish-eating birds, gulls and fruit pigeons *Ptilinopus*) or as an adaptation to special feeding methods (e.g. nightjars, pelicans). Spreading of the mandibles is achieved in most cases by the action of part of the pterygoideus muscle, which pulls the medial process of the lower jaw forwards, causing the rear part of the mandibular ramus to swing outwards. In gulls, this action is also aided by a guiding effect of the quadratomandibular articulation, and in barn owls *Tyto* is entirely produced by this means, taking place automatically as the lower jaw is depressed. An excellent detailed account of lower jaw structure and mobility is provided by Bühler (1981).

Jaw coupling. It is possible for the actions of upper and lower jaws to be coupled, that is to say, mechanically linked so that elevation of the upper jaw cannot occur without depression of the lower. Typically, such coupling is effected by the postorbital ligament, when loaded by muscle

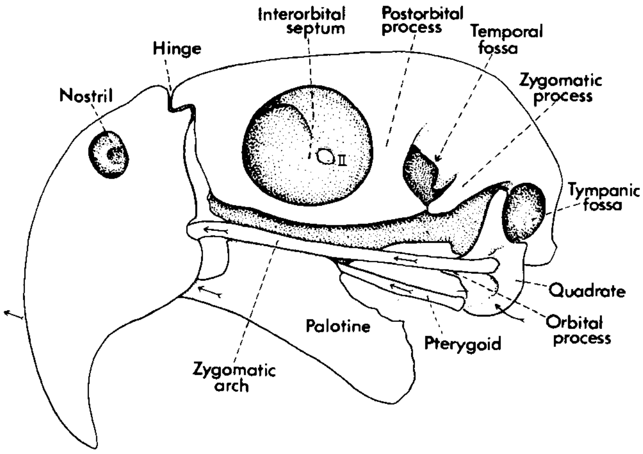

Fig. 2. Skull of Macaw *Ara* sp. showing mechanism of kinesis. Arrows indicate direction of bone movement.

action. (In ducks, its function is complemented or even replaced by a lacrimomandibular ligament, rostral to the orbit.) If the pattern of muscle contraction leaves the ligament unloaded, the jaws are able to move independently. Coupling is important where complicated actions of jaw and tongue have to be integrated with perfect precision, as in the straining actions of ducks (Zweers 1974) or seed opening by finches. Independent jaw action, on the other hand, is necessary if the jaws are to vary their angle relative to one another for manipulative purposes. This is especially so if the upper jaw is to be depressed past its normal closed position. Independence is also necessary, for instance, when both jaws are lowered simultaneously, as occurs during the mandibular spreading of gulls. The majority of birds probably have the option of either coupled or uncoupled jaw action, but this is not so in groups (e.g. various procellariiforms and ciconiiforms) which achieve coupling by means of a specialized form of quadrato-mandibular articulation. This arrangement is best seen in the Shoebill *Balaeniceps rex*, in which the lower jaw is so securely locked on to its articulation that even in a dried skull it is impossible to depress it by hand.

Stops and guides. In a complex and delicate system of bony levers such as that seen in avian jaw structures, some inbuilt safety devices might be expected. Fisher (1955) who examined those in a few easily obtained species concluded that most limitation on movement was imposed by soft parts of the head. However, protraction stops (e.g. orbital process of the quadrate abutting against the orbital wall) and retractor stops (e.g. nasal process abutting against lacrimal) are present in many birds. Some other features which may act as guides or constraints on movement are less well understood. The basipterygoid processes, which form a short region of contact between the basitemporal region of the skull and the pterygoids, are a case in point. Though they are undoubtedly of primitive origin, their form in many birds indicates that they are more than mere relics; in the Oilbird *Steatornis* for example, the pterygoid bears a clasp-like device enclosing the basipterygoid process. Many birds, however, including all passerines, fulfill a wide range of jaw actions without them. The os uncinatum, interposed between the lacrimal and jugal in the Musophagidae and some other families, is another example of a presumed bony guide whose function is not well understood (Burton 1970).

Secondary jaw articulations. First described in the Black Skimmer *Rynchops niger* in which it is well developed, a secondary articulation of the mandible occurs in a wide range of birds. These have been listed by Bock (1960), who referred to this articulation as the 'medial brace' of the mandible. It is between the tip of the medial process of the mandible and the basiparasphenoid bone, and is termed Artc. mandibulosphenoidalis in the *Nomina Anatomica Avium*. Another secondary articulation (Artc. ectethmo-mandibularis) occurs between the ectethmoid and the dorsal border of the mandible in honeyeaters (Meliphagidae). A description of this, and a functional discussion of both secondary articulations is provided by Bock and Morioka (1971). P.J.K.B.

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SKYLARK: *Alauda arvensis* (see LARK).

SLEEP: a state of immobility accompanied by high arousal thresholds and eyelid blinking (Amlaner and McFarland 1981). This state occurs especially during ROOSTING. Most birds spend approximately one-third of the 24 hour cycle engaged in some form of loafing (see ROOSTING) and/or roosting behaviour, the duration varying greatly between species, and also with season, breeding condition, latitude, and other factors. A comprehensive review of sleeping in wild birds has been conducted by Amlaner and Ball (1983).

In the sleep posture, the bird sits, stands or perches (on one leg or two) or floats, with—often depending on species—its bill pointed backwards, tucked under the scapulars, under folded wings, resting on the back, or straight forward. The bill may be hooked behind the wing if the scapulars are indistinct, as in penguins. Most birds perch horizontally when sleeping, but woodpeckers and treecreepers cling vertically, while *Loriculus* parrots hang upside down like bats.

In the typical sleeping state, the eyelids usually blink slowly, but during a disturbance birds will keep them open, i.e. 'pseudo-sleep', a state of wariness. In the similar-looking rest-sleep posture, the bird again sits, stands, perches or floats, but with its head drawn into the breast and bill pointing forwards. Head and bill are lowered below the horizontal.

In the head-on-ground posture the bird lies with its head and neck extended along the ground. The feet may be tucked under the body or stretched behind the bird. This posture is normally assumed by young birds and by large flightless species, e.g. Rhea *Rhea americana* and Ostrich *Struthio camelus*.

Sleeping on narrow perches is facilitated by a special mechanism which automatically locks the toes in a gripping position. As the leg muscles relax and the tarsal joint flexes, the flexor tendons are automatically stretched and tightened. In addition, the under-surface of some portion of the flexor tendons is ridged, and corresponding ridges on the tendon sheaths in the region of the metatarso-phalangeal joint, where the body weight presses the joint against the perch, mechanically 'lock' the tendon in position.

Evidence for sleeping on the wing is inevitably circumstantial as, for example, the suggestion that the pelagic Sooty Tern *Sterna fuscata* may sleep aerially since it quickly becomes waterlogged on the water surface. Rheinwald (1975) found that House Martins *Delichon urbica* descended to the breeding colony early in the morning from great heights; he concluded that they were unlikely to roost elsewhere than on the wing. Evidence from eye-witnesses and from radar observations exists to suggest that Swifts *Apus apus* can sleep on the wing, a view strongly endorsed by Lack (1956) and others. Against this, it has been argued that the birds may descend after observations cease and that radar identification is not unequivocal. Certainly Swifts do also roost in their nest sites.

The 'quality' of sleep may be inferred from rates of eyelid blinking (i.e. the duration and frequency of eyelid closure). Hamerstrom and Janick (1973) assumed that a Barred Owl *Strix varia* slept when its eyes remained closed and 'dozed' when its eyes were 'partly closed'. Herring Gulls *Larus argentatus* do not close their eyelids completely for more than about 60 seconds, but there does appear to be a difference in the quality of sleep depending on whether they tuck their bill under the scapulars or place it forward (Amlaner and McFarland). Sleeping while standing or sitting is also a means of determining quality of sleep—deeper perhaps when sitting, and lighter and more vigilant when standing. Duration of sleep bouts, as determined by length of continuous eyelid closure, has been reported to be up to 2–3 hours (Klima 1966) or to last from only a few seconds to several minutes (Hamerstrom and Janick).

Birds may sleep by day, by night, or both by day and night. For discussion of the timing of roosting and sleep, see ROOSTING. Bird activity in Arctic and Antarctic summers of continuous daylight has been reviewed by, e.g. Armstrong (1954) and Cullen (1954). Nearly all workers agree that birds have a period of inactivity but not all that birds sleep during this time. Birds that do sleep spend fewer hours asleep than their counterparts at lower latitudes (Pohl and West 1978); for example Eiders *Somateria mollissima* slept for 3–5 hours in the arctic summer, but for 7 hours during the day and most of the night further south in Norway. Most species studied in continuous light conditions had an inactive period slightly after midnight, e.g. Wheatear *Oenanthe oenanthe*, Meadow Pipit *Anthus pratensis*, Lapland Bunting *Calcarius lapponicus*, while a few had sporadic sessions of inactivity throughout the 24 hours (e.g. Arctic Tern *Sterna paradisaea*).

Little is known about the development of sleep in wild birds. Herring Gull chicks appear to sleep longer than adults but not in the same postures. Gull chicks sleep in the head-on-ground posture. Only when several weeks old do they attempt to place their bills on their backs.

Delius (1970) likened sleep to a displacement activity such as grooming or pecking. He suggested that the origin of this association was obvious because much of an animal's other behaviour can be assumed to have high priority and require a high degree of responsiveness to stimuli. Sleeping, on the other hand, many not be so dependent on precise timing, and consequently might have a low priority; it could therefore be postponed until higher priority activities like feeding and drinking had taken place.

Tinbergen (1951) suggested that sleeping should be regarded as instinctive. This concept is central to the immobilization theory (Meddis 1975) which suggests that sleep acts mainly to preserve inactivity and does not necessarily conver any unique physiological benefit. Sleep reduces the wastage of energy by ensuring that the animal is unaware of surrounding stimuli which might provoke action. The sleep instinct enables an animal to choose a site which is well protected from inclement weather and will conserve energy. The sleeping posture is also chosen to reduce energy waste. Torpor (see TORPIDITY) occurs during sleep and is a significant means of reducing energy consumption.

The study of sleep in birds poses several problems. First, knowledge has hitherto been derived mostly from laboratory studies, using environmental factors inferred from the literature. Furthermore, sleep is not a mutually exclusive behaviour; while asleep, birds may, for example, also digest food or sit in their territory, thus complicating functional interpretations. Lastly, sleeping animals are difficult to observe and are easily disturbed if approached.
C.J.A.

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SMELL: a sense for which the receptive surface is the sensory lining of the nasal passages. The olfactory organs of birds are well developed and are situated in the paired nasal cavities that open by the nostrils (external nares) at the base of the bill (see BILL; NARIS; SKULL). The nasal cavities are separated by a median partition, the nasal septum, and they communicate posteriorly with the roof of the mouth by paired openings, the internal or posterior nares (or choanae). Each cavity is divided into three distinct regions or chambers whose walls are enlarged by the formation of folds from the lateral walls (the nasal conchae). Generally, each region contains one concha. The surface area in many species is further increased by the coiling of the conchae, or by the development of longitudinal furrows as in the Ostrich *Struthio camelus*.

The first two chambers appear to serve only respiratory functions and are of importance in warm-blooded animals, since they act as an air-conditioning apparatus (see RESPIRATORY SYSTEM). The lining epithelium has a rich blood supply and the removal of dust particles from the inhalant airstream is effected here, probably with the aid of the secretions of the nasal glands, which open into the first chamber. These glands are small in terrestrial species, but are well developed in marine birds and play a part in the elimination of excess salt (see EXCRETION, EXTRARENAL).

Only the third (dorsal) chamber is lined by olfactory epithelium. Its concha is usually a prominent tubercle, but in some procellariiform birds and the Turkey Vulture *Cathartes aura* it is developed into a turbinal system. In the nocturnal kiwis *Apteryx* spp. the concha of the olfactory chamber consists of about 5 transverse folds which are greatly enlarged in comparison with the size of the remaining respiratory area. Avian olfactory receptors are usually distributed on the epithelial surface of the posterior concha, the nasal roof and the upper septum. The olfactory epithelium is similar to that found in mammals; the olfactory receptors contained in it are pigmented and are long, narrow, columnar cells surrounded by columnar supporting cells. Information gathered by the olfactory receptors is carried to the brain by the olfactory nerve, non-medullated fibres of which form a plexus in the olfactory mucosa.

The size of the olfactory bulbs in the brain is extremely variable when compared with the size of the forebrain (see NERVOUS SYSTEM). They are largest in the Apterygiformes, Procellariiformes, Podicipediformes, Caprimulgiformes and Gruiformes, perhaps denoting a well-developed olfactory sense in these groups, and smallest in the Pelecaniformes, Piciformes, Passeriformes and Psittaciformes. Bang and Cobb (1968) for example suggested that the large and well innervated nasal organs of the Turkey Vulture, the Oilbird *Steatornis caripensis* and the albatrosses *Diomedea immutabilis* and *D. nigripes* indicate that these species have a good sense of smell.

However, although birds apparently possess adequate olfactory organs, early experiments produced conflicting evidence concerning the sense of smell in birds and it was not until about 1965 that a clear picture began to emerge. These more recent studies include detailed electrophysiological and behavioural investigations.

Tucker (1965) recorded electrically the nervous impulses travelling in the primary olfactory nerve of a number of different species of birds, ranging from those with small olfactory bulbs, such as the House Sparrow *Passer domesticus*, to the Black *Coragyps atratus* and Turkey Vultures with relatively large olfactory bulbs. Nervous activity was recorded in all species when presented with amyl acetate and other, unspecified, odours. Recordings from single olfactory units (as distinct from the whole nerve) in vultures have produced more detailed results; the sensory thresholds vary between units and, whilst in some units the rate of firing increases with the intensity of the stimulus, other units respond by a reduction in frequency when the concentration of the odour is raised.

Wenzel and Sieck (1972) have used electrodes implanted in the olfactory bulb of the brain to test the sense of smell in a number of species (pigeon *Columba livia*; chicken *Gallus gallus*; Mallard *Anas platyrhynchos*; Manx Shearwater *Puffinus puffinus*; Black-footed Albatross *Diomedea nigripes*) and all, irrespective of the relative size of the olfactory bulb, showed the bursts of nervous activity on inspiration of odours that are typical of vertebrates. They responded to such artificial stimuli as pyridine, methyl salicylate, octanol and amyl acetate, but not if the olfactory nerves were cut or the nostrils plugged.

Walter (1943) obtained entirely negative results in a series of investigations with pigeons, using the technique of conditioned reflexes. More recently, however, the heart rate of pigeons and the pattern of respiration of Greylag Geese *Anser anser* have been reported to change consistently in response to various odours in carefully controlled experiments; and similar results of behavioural changes have now been reported with a range of species. Both the trigeminal and olfactory nerves have been shown to be involved in the detection of the odours in these experiments.

Other behavioural studies (although they have been criticized and some workers have not achieved the same results in similar experiments) have demonstrated that certain species (pigeon; Bobwhite Quail *Colinus virginianus*; chicken) can use olfactory stimuli as cues for learned responses. For example pigeons have been trained to respond differentially to an airstream that was bubbled through distilled water or an artificial odorant. On balance, the evidence suggests that under careful experimental conditions some species can form associations between olfactory stimuli and specific responses, although they probably do this less readily than to visual and auditory stimuli.

Certain avian species (all with large olfactory bulbs) have long been believed to locate either their food or nest site by their sense of smell, and carefully controlled experiments with these birds under natural conditions are of particular interest. Turkey Vultures were seen to collect above upcurrents of ethyl mercaptan released from hidden sites in a canyon. Kiwis *Apteryx australis* readily and accurately distinguished between dishes that contained food and those containing only earth, although the birds had to break through stiff netting covering the containers to reach the food, this procedure ensuring that visual, tactile and gustatory discrimination was not possible. Leach's Petrels *Oceanodroma leucorhoa* walk upwind to their burrow and, in a Y-maze, captive birds chose an air current coming from their own nest material in preference to one from similar materials collected from the forest floor. The same birds, however, did not respond positively in the Y-maze to air currents from their own stomach oil or preen gland oil. Petrels taken from their burrows did not return within a week if their external nares were plugged or if their olfactory nerves were transected, although they did return if only sham-operated (Grubb 1974). Petrels and shearwaters have also been reported to make positive responses to airborne odour trails from sponges soaked in cod liver oil. Papi (1974) and his colleagues suggest that olfaction plays a part in the navigational ability of pigeons, the birds learning the odour prevailing in the area of the loft.

Finally, the olfactory system may have other physiological roles. Pigeons have been trained to detect X-rays, although they require higher doses and longer training than mammals; birds that learned to respond lost the ability after section of the olfactory nerves. Removal of the olfactory bulbs or sectioning of the olfactory nerves of pigeons also has an effect on the ability of the birds to learn operant procedures. They are slower to adapt to new situations and it has been suggested that the olfactory system may serve a wider function than simply processing information about odorous stimuli.

Wenzel (1971) has concluded from anatomical and electrophysiological studies that the avian olfactory system is broadly comparable to that of reptiles and mammals, and it is certain that many species can detect a variety of odours. However, so far, the sense of smell has been shown to be important in the lives of only a few species and in all (except perhaps the kiwis) it is probably of much less importance than vision and hearing.

For smell in its other meaning see ODOUR. C.J.D.

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SMEW: *Mergus albellus* (see DUCK). See photo DISPLAY.

'SMOKE-BATHING': term used, often uncritically, for a variety of reactions by birds to smoke and hot air rising from chimneys, etc. In the Rook *Corvus frugilegus* and a few other passerines, aberrant ant-application behaviour (see ANTING) seems to be involved at times but in most cases the behaviour appears to be a type of thermo-regulatory heat-basking akin to sun-basking (see SUNNING) performed mainly in cold weather. Any function in feather maintenance (see COMFORT BEHAVIOUR) remains to be demonstrated. K.E.L.S.

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(For further references, see ANTING and SUNNING.)

SNAKE-BIRD: alternative substantive name of species of Anhingidae (see DARTER); also a popular name in Britain for the Wryneck *Jynx torquilla* (see WOODPECKER).

SNIPE: substantive name (commonly unchanged in the plural) of species of *Gallinago* (*'Capella'*) and allied genera, and also sometimes misapplied to the dowitchers *Limnodromus* spp. (see under SANDPIPER; for other families see PAINTED SNIPE and SEEDSNIPE).

See photos COMFORT BEHAVIOUR; FACILITATION, SOCIAL.

SNOWCAP: *Microchera albocoronata* (for family see HUMMINGBIRD).

SNOWCOCK: substantive name of *Tetraogallus* spp. (see PHEASANT).

SOARING: see FLIGHT. See photo FLIGHT.

SOCIAL DISPLAY: see FLOCKING; LEK.

SOCIAL FACILITATION: see FACILITATION, SOCIAL.

SOCIAL NESTING: see COLONIALITY.

SOCIAL ORGANIZATION: see AGGRESSION; COLONIALITY; DISPLAY; DOMINANCE (2); FLOCKING; RECOGNITION; TERRITORY; VOCALIZATION; also CROW (1); PENGUIN; ROOSTING.

SOCIETIES, ORNITHOLOGICAL: see ORNITHOLOGICAL SOCIETIES.

SOCIOBIOLOGY: on Edward O. Wilson's definition, the systematic study of the biological basis of all social behaviour. Biologists had been studying the basis of social behaviour for several decades before the word 'sociobiology' was shot into our everyday vocabulary by the publication of Wilson's *Sociobiology* in 1975, but the word has come to refer not to a scientific discipline but to a particular set of ideas about the evolution of behaviour. In a more popular context, sociobiology means the application (and misapplication) of biological, particularly evolutionary, ideas to explain human behaviour.

Evolutionary ideas. A series of theoretical developments in the 1960s and early 1970s revolutionized evolutionary explanations of social behaviour. The new theory applies with renewed vigour the Darwinian principle that behaviour must be explained by its benefit to no larger entities than individual organisms. Group selection, which explains traits by their benefit to groups, was criticized both for being implausible in theory (for it requires unnaturally high rates of group extinction) and superfluous. Traits such as altruism, territoriality, reproductive rates and dominance were reconciled with natural selection by the work of W.D. Hamilton, J. Maynard Smith, R.L. Trivers, G.C. Williams and others; this theoretical reconciliation provides the stuff of sociobiology.

The systematic comparative studies of mating systems, started by J.H. Crook and David Lack on birds, provide the other principal component of sociobiology. These studies explain evolutionary trends of convergence and divergence in social behaviour by the species' ecology.

Human sociobiology. Superficially, it looks as if the sociobiological ideas could help to understand human behaviour, and indeed many arguments have been made about how human behaviour might be adaptive. An acerbic 'sociobiology controversy' has been inspired by several confusions on the part of both critics and advocates. Human sociobiology can only describe and explain human adaptations; but it has been criticized for (and sometimes unscientifically advocated as) morally upholding the inegalitarian social order. Similarly, evolutionary arguments often posit a certain kind of 'selfishness', in that the effects of behaviour benefit the organism's genes. Sociobiology has been criticized for the claim that humans are fundamentally selfish in motivation. The kind of selfishness that features in sociobiological explanation, when correctly understood, is not one of motivation, and is quite compatible with humans being fundamentally unselfish. M.R.

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SOFT PARTS: see BARE PARTS; INTEGUMENTARY STRUCTURES. For care of, see under COMFORT BEHAVIOUR.

SOFTTAIL: substantive name of *Thripophaga* spp. and allies (see OVENBIRD (1)).

SOFTWING: substantive name sometimes used for *Malacoptila* spp. (see PUFFBIRD).

SOLAN GOOSE: former alternative name (misnomer) for *Sula bassana* (see GANNET).

SOLITAIRE: substantive name of 2 species of the extinct family Pezophapidae, previously Raphidae (see under DODO); and, in America, of *Myadestes* spp. (for family see THRUSH).

SOMATERIINI: see DUCK.

SOMITE: see DEVELOPMENT, EMBRYONIC.

SONAGRAM: see VOCALIZATION.

SONAGRAPH: a machine which produces on paper a visual representation of a sound (sonagram), with time on the horizontal axis and frequency on the vertical axis; regularly used in the analysis of bird VOCALIZATIONS.

SONG: see VOCALIZATION.

SONGBIRDS: term often used for the suborder Oscines (see PASSERIFORMES).

SONG FLIGHT: display flight involving song.

SONGLARK: substantive name of *Cinclorhamphus* spp. (see WREN (2)).

SONG PERIOD: the part of the year during which the song of a particular species can be heard.

SONG-SHRIKE: sometimes used, in the plural, as a general term for the CRACTICIDAE.

SORA: name, alternatively 'Sora Rail', of *Porzana carolina* (see RAIL).

SOUND RECORDING: one of the more recently evolved methods of collecting information about birds.

History. The earliest bird recording known still to exist is that of a captive Common Shama *Copsychus malabaricus* made in Germany in 1889 by Ludwig Koch on an Edison wax cylinder. The earliest reference in ornithological literature to the reproduction of a bird sound is in the account of the 16th Congress of the American Ornithologists' Union in 1898, which mentions a 'graphophone demonstration of a Brown Thrasher's song'. The first recordings of wild birds made anywhere are probably those of Cherry Kearton, who in England in about 1900 captured on wax cylinders a few Song Thrush *Turdus philomelos* notes and the song of the Nightingale *Luscinia megarhynchos*.

The earliest recordings of wild birds in the Nearctic and Afrotropics were made in 1929, in the Australasian region in 1931, in the Antarctic in 1934, in the Orient in 1937, and in the Neotropics in the early 1940s.

At least one sound has been recorded (up to mid 1982) from over half the world's 9,000 living bird species. The approximate figure is 5,000 species. The recordings are housed, usually on tape, in the collections of national institutions, universities, broadcasting organizations and private individuals. The total number of individual recordings may be of the order of 100,000.

Published recordings. Recordings of about 2,500 species have been published on about 1,160 gramophone records and cassettes, 1910–1982. The earliest 'bird' gramophone records (issued from 1899 onwards) were of human imitations of birds (see HUMAN IMITATION OF BIRD SOUNDS).

Between 1910 and 1913 recordings were made of captive Nightingale *Luscinia megarhynchos*, Thrush Nightingale *L. luscinia*, Canary *Serinus canaria* and others at the Karl Reich aviary at Bremen and published on HMV gramophone records. The first publications to present selections of recordings of wild birds were Brand and Keane's 'Bird Songs recorded from Nature' which appeared in the USA in 1931, Weismann's set of 5 discs produced in Denmark in 1934 and Heinroth and Koch's 'sound book' published in Germany in 1935. These were followed by many more selections of commoner wild species. A few discs have been devoted to individual species—one as early as 1931 to the Lyrebird *Menura novaehollandiae*, 4 to the Mocking-bird *Mimus polyglottos* (most recently Grimes' 1979 LP on which mockers copy 86 other species), one to the Great Northern Diver *Gavia immer* (1980), and so on. The first attempt at faunistic treatment—195 species on thirteen 78s—was that of North and Simms: '*Witherby's Sound-Guide to British Birds*' (1958). This was closely followed (1959) by Kellogg and Allen with their '*Field Guide to Bird Songs of Eastern and Central North America*' (305 species on two LPs), and Kellogg's (1962) western Nearctic album (515 species on three LPs), both issued by the Laboratory of Ornithology, Cornell University. The largest such treatment is the European '*Field-guide*' (1981) which gives 612 species on 16 cassetttes; it is published by the Swedish Broadcasting Corporation. A record by Borror and Gunn introduced, in 1958, the specialized treatment of individual variation in song; '*Warblers*' gives songs by 150 individuals of 38 species of parulid. The first attempt to present the species' repertoires of the birds of a country was Victor Lewis's '*Bird Recognition: an Aural Index*' published in Britain in 1966. In the 1970s a number of records appeared which had the more serious educational purpose of presenting the biology of bird sound communication: Borror's '*Bird Song and Bird Behavior*' (1972), a quartet of small German discs devised by Thielcke and Bergmann (1973–78) called '*Biologie der Vogelstimmen*'; and Jellis's '*Bird Sounds and their Meaning*' (1977), an LP accompanied by a book. There is a Russian disc (about 1976) designed to scare off unwanted species, and in contrast a cassette by Gibson from Canada the purpose of which is to lure species into birdwatchers' ken. Since the first in 1971 more and more bird recordings have been published on tape cassettes. The most recent development is electronically enhanced human mimicry as an aid to field identification—a British record/cassette called '*Big Jake Calls the Waders*' offers almost unbelievable verisimilitude. The most prolific publishers have been the Laboratory of Ornithology at Cornell in the USA and Jean-Claude Roché in France. The best selling birdsong discs are almost certainly Veprintsev's first three in his '*Voices of Nature*' (1960–62) series each of which had sold over 250,000 copies (mainly within the USSR) by 1982.

Sound libraries and collections. The number of scientifically significant collections is about 50. The oldest and largest, the Library of Natural Sounds at Cornell University Laboratory of Ornithology, Ithaca, in the USA, established in 1931 by Allen and Kellogg, had accumulated by 1982 approximately 35,000 recordings of about 3,750 bird species. The Americas and eastern Africa are particularly well represented at Cornell. The largest personal collection must be that of Claude Chappuis of France who by 1980 had made 12,000 recordings of about 2,000 species in 40 countries. The British Library of Wildlife Sounds in London, inaugurated in 1969, contained by 1982 tape recordings of about 1,600 bird species. The Soviet equivalent was started in 1973 by Veprintsev at Puschino, near Moscow, and by 1982 had 450 species on tape. Sizeable other Palearctic collections also exist in Britain (BBC), France (Chappuis, Roché), Estonia (Jüssi), Denmark (Bondesen), Sweden (Astrom), East Germany (Wallschläger), Austria (Jilka), Hungary (Szöke) and Japan (Nakatsubo, Kabaya). In the Nearctic there are a number of notable sound libraries besides Cornell's: W.W.H. Gunn's in Ontario, the Borror Laboratory of Bioacoustics in Ohio, the Florida State Museum Bioacoustic Archives, and others in Berkeley, Los Angeles, Ottawa, San Francisco and St Johns. In Australasia, the CSIRO in Australia and the Wildlife Service in New Zealand have good archives. Major Neotropical collections include those of L.I. Davis (from Central America and held in Louisiana), T. Davis (from Suriname, held in New York), Coffey (northern Neotropics and held in Tennessee), Schwartz (Venezuela and held at Cornell), Parker (Peru and Bolivia and held at Cornell), Reynard (Caribbean and held in New Jersey), Vielliard (taped and held in Brazil), and Straneck (taped and held in Argentina). In the Orient there is Roberts' Pakistan collection and Scriven's at the University of Malaya, Kuala Lumpur. Large Afrotropical collections include those of North (held at Cornell, copy in London), Chappuis, Stjernstedt and McVicker. In South Africa there is the Fitzpatrick Bird Communication Library at the Transvaal Museum (800 birds on tape). Two archives (Cornell and Borror) have computerized data.

Numbers of Bird Species whose Voices have been Recorded

Region	*Total*	*Published*
Palearctic	850	800
Nearctic	800	600
Australasian	600	250
Neotropical	1,650	550
Afrotropical	1,500	650
Oriental	450	125
Antarctic	50	15

Note: no totals are given because some species will have been recorded in more than one region.

Technique. The earliest recordings were made on wax cylinders, later superseded by wax discs. These were followed by magnetic wire (very occasionally), optical sound film (much used in the 1930s by Cornell), acetate discs, and finally—and most important of all the modern developments—magnetic tape, which was first used for bird-sound recording by Palmér in Sweden in 1946. Most recordings have been made on 6.25 mm wide tape recorded reel-to-reel; but 4 mm wide tape cassette recordings can now also be technically acceptable. The parabolic reflector, which acts like a great mechanical ear, enables the recordist to work at distances from the singing bird up to 40 times as great as would be necessary with an open microphone. Dynamic microphones are still widely used, but transistorized condenser microphones—'gun mikes'—which incorporate a directional effect otherwise achieved by the parabolic reflector, are being used more and more. The parabolic reflector was first tried by the Cornell workers in 1932 and is now regarded as an indispensable tool. Brand and Kellogg of Cornell were also the first workers to transmit the sounds of a bird by short-wave radio for the purpose of recording them; this was in Canada in 1936. Later, this method was used by Weismann in Denmark in 1947, by Palmér in Sweden in the same year, and by Simms in England in 1954. The earliest stereo recordings of birds were made in about 1959 and a number have been published, the first selection on Wahlström's disc in 1963. Wahlström also designed and used the first stereo parabolic reflector.

In addition to the use of the reflector and short-wave transmitter, field techniques include hiding the microphone near known singing places or the nest, and playing back in the field to territorial and other species recordings of advertising sounds in order to stimulate a reply and lure the birds within range of the microphone (see PLAYBACK).

Purposes. The ultimate scientific aim must be to record the full vocabulary, vocal and instrumental, of every species, with all the major individual, seasonal, and geographical variations. With the ever-increasing likelihood of extinctions, the taping of, for example, tropical rain forest species becomes more important. The uses of recordings are many and varied. They are employed for purposes of personal pleasure, education and identification; also in studies on bird behaviour, ontogeny, learning ability, heredity, and taxonomy. For the use of the sound sonograph in technical analysis see VOCALIZATION. Sound sonagrams have now found their way into a field guide, monographs and two regional handbooks, and they are a central feature of a specialist bird voice field guide (Bergmann and Helb 1982).

The Puerto Rican Whip-poor-will *Caprimulgus noctitherus*, thought for over 40 years to be extinct, was rediscovered in 1961 by means of a sound recording of its voice. The recordings also have mundane applications, as for example, in scaring gulls *Larus* spp. from airfields and Starlings *Sturnus vulgaris* from orchards and buildings (see SCARING).

For the production of sound by birds, see VOCALIZATION and MECHANICAL SOUNDS. For musical use of bird recordings see MUSIC, BIRDS IN.

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SOUNDS: see ECHO-LOCATION; HEARING AND BALANCE; MECHANICAL SOUNDS; MIMICRY, VOCAL; VOCALIZATION.

SOUND SPECTROGRAPH: term no longer generally used for SONAGRAPH.

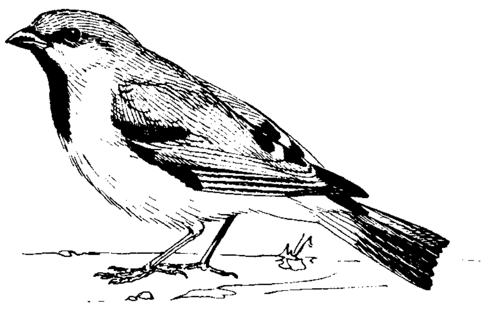
SPADEBILL: substantive name of *Platyrinchus* spp. also called 'flatbills' (see FLYCATCHER (2)).

SPARROW (1): substantive name for most species of Passeridae (Passeriformes, suborder Oscines); in the plural, general name for the family. The Passeridae show affinities both to the finches (Fringillidae) and the weavers (Ploceidae), though how far these are genuine and not adaptive is not agreed. Until the relationship has been resolved it seems better to treat the sparrows as a separate family (Voous 1977). The family can be conveniently placed into 3 genera: the true sparrows, genus *Passer*, in which 16 species have been recognized, though recent investigations (Hall and Moreau 1970) suggest that one of the African species, the Grey-headed Sparrow *P. griseus*, may be a superspecies of 5 different species exhibiting some sympatry in their ranges, thus bringing the total to 20; the rock (or bush) sparrows, genus *Petronia*, 6 species, and the snow finches, genus *Montifringilla*, 7 species. The SPARROW-WEAVERS AND SCALY-WEAVERS, comprising 10 species in 5 genera, *Plocepasser*, *Histurgops*, *Pseudonigrita*, *Philetairus* and *Sporopipes*, are included in this work in the subfamily Plocepasserinae of the Passeridae. The true sparrows appear to be a comparatively recent family and studies by R.F. Johnston and R.K. Selander have shown changes suggesting that measurable evolution has occurred in the House Sparrow *Passer domesticus*, in the 100 or so years since the species was introduced to America (see Johnston and Klitz 1977).

Characteristics. The species are small (10–20 cm long with one exception) and—except for the white on the snow finches—have plumage mainly of brown and grey hues, but sometimes with black and, in a few species, yellow. *Montifringilla* and *Passer* share the characteristic that the bill of the male changes from horn-coloured to black during the breeding season. The main feature distinguishing the sparrows from the weavers is that the first primary is much reduced and placed dorsally; in this and a number of other characteristics they resemble the finches. In the structure of the palate, form of nest and social behaviour they are closer to weavers. The rock sparrows, snow finches and about half of the Afrotropical sparrows are monomorphic. In the remaining Afrotropical sparrows the males have characteristically a black throat and chin with some black on the head; this pattern occurs in all the Palearctic and Oriental sparrows and in one species, the Tree Sparrow *P. montanus*, it has been adopted by both sexes.

Habitat. The sparrows are mainly birds of open country, ranging from high mountains in the case of the snow finches, which are among the highest-living birds, nesting from 2,000 to 4,500 m, through rocky semi-arid country to light scrub in the case of the rock sparrows, to cultivated and even highly urbanized areas with the true sparrows. The true sparrows, more than any other group of birds, have colonized man's urbanized habitat. In the House Sparrow the extent of this adaptation is quite remarkable, not only is it found in the centre of extensive built-up areas, but even inside large buildings such as railway stations, factories and stores, and recently some birds that became trapped in a coal mine not only survived for some years 600 m below the surface, but a pair actually bred successfully in this alien environment.

Distribution. The sparrows, apart from recent introductions (see below), are restricted to the Afrotropical, Palearctic and Oriental Regions, and probably have an Afrotropical origin. The rock sparrows are all found in Africa, but 3 extend to Asia and one, the Rock Sparrow *Petronia petronia*, occurs in southern Europe as well. The greatest



Desert Sparrow *Passer simplex*. (*C.E.T.K.*).

concentration of *Passer* species occurs in the Afrotropical Region; the Golden Sparrow *P. luteus*, is predominantly African, but extends into Arabia; the Desert Sparrow *P. simplex* is found in the Sahara and Asian deserts. The remaining 7 species are found in the Palearctic and Oriental Regions, the House Sparrow and Tree Sparrow being very widely distributed, the Spanish Sparrow *P. hispaniolensis* being mainly western but extending to Afghanistan and Turkestan; in contrast the remaining species have rather restricted, widely separated distributions in Asia, though they all overlap with one or more of the 3 widespread species. In comparatively recent times (since 1850) the ranges of 2 of the already widespread species have been extended by introductions to other parts of the world. The House Sparrow has been extremely successful in this, taking over the otherwise unoccupied urban niche, and is now probably the most widespread species of land bird, being found in all major settled areas with the exception of China and Japan; the Tree Sparrow has been less successful, but is established in the USA, Australia, and may also have been introduced to, rather than spread to, Borneo, Sulawesi and the Philippines. The House and Spanish Sparrows bear an interesting relationship to each other. In Europe and Asia where they occur together they behave as good species, ecologically separated, the House Sparrow living in towns and villages, the Spanish Sparrow in the surrounding countryside with a preference for moister conditions: in Morocco the same situation occurs, but in eastern Algeria and Tunisia the species interbreed, producing a complete range of intermediates. The Italian Sparrow *P. d. italiae*, a well-differentiated form occurring in Italy and Crete, appears to be a stabilized intermediate between House and Spanish Sparrows and stable populations, very similar in appearance, are also found at the isolated southern Algerian oases (Johnston 1969). The snow finches inhabit high mountainous country from the Pyrenees to Mongolia.

Population. Within their ranges some of the sparrows are among the more common birds, so that they reach pest proportions in those species that inhabit cultivated land, though not to the extent of some of the highly gregarious weavers. Population density has been most closely studied in the House Sparrow; it ranges from about 0.05 birds per ha in open farmland to over 1 bird per ha in highly cultivated land and built-up areas.

Movements. As a general rule the sparrows are mainly sedentary, though most of the Palearctic species make minor seasonal movements: the snow finches to lower ground and most of the true sparrows some southward extension of range in the winter, though the Spanish Sparrow is a regular winter visitor to the Nile valley, eastern Arabia and north-western India. The House Sparrow throughout most of its range is extremely sedentary, the majority of individuals spending their lives within a compass of a few km. At high latitudes and altitudes it builds winter nests, where it roosts protected against long cold nights.

Food. The sparrows are largely seed-eaters, with the *Passer* sparrows showing a marked preference for cereals. House and Tree Sparrows living in the more built-up surroundings exist mainly on such 'unnatural' foods as bread and household scraps; the young nestlings are fed at first principally on insects, but they are regularly given bread and it is a major part of the diet of some young born in highly urbanized districts.

Behaviour. There is a widespread tendency in the sparrows to form extensive foraging flocks, frequently involving 2 or more species and often in association with finches. In many cases large communal roosts are formed. A characteristic of *Passer* is the tendency to associate with man; at least 10 (13 if 20 species are recognized) of the species regularly nest in the eaves of inhabited buildings. This trait is so marked in the House Sparrow that it can be fairly described as a commensal of man and it is to be found breeding away from man only in exceptional circumstances. The Tree and Spanish Sparrows fill the same niche in those parts of their ranges where the House Sparrow is lacking. Despite their close association with man, sparrows are extremely wary birds; they are not easily tamed and do not readily settle down and breed in captivity.

Voice. The members of the genus *Passer* are somewhat noisy birds using a variety of rather harsh chirping calls. There is no true song, though the chirping notes are strung together to serve in this function. The other members of the family have rather more varied songs, but their calls tend to be somewhat harsh.

Breeding. Many of the sparrows are gregarious and breed in colonies although, in general, the nests are discrete and not communal structures such as are found with some of the weavers. The Spanish Sparrow is the most social; colonies of several hundred nests of this species have been found in a few trees or bushes. Nests are found in a variety of situations, but most frequently in holes in rocks, banks, buildings and in trees. In *Passer* the nests are typically bulky, domed and made of dried grasses and lined with feathers; in the other 2 genera, however, the nest may be reduced to a mere pad of grasses, although again lined with feathers. The clutch ranges from 2–7. Both sexes co-operate in nest building and care of the young. With the hole nesters the same hole is regularly used from year to year and, provided they survive, by the same pair. The incubation periods average 12–14 days; nestling periods range from *c.* 15 days in the House Sparrow to as many as 24 days in the Cape Sparrow *Passer melanurus*. See photo PARENTAL CARE. D.S.-S.

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SPARROW (2): substantive name used in America for many species of Emberizinae found there (see BUNTING).

SPARROW (3): name applied or misapplied to some other birds than those comprised in the two groups dealt with above, e.g. the Hedge-sparrow (or Dunnock) *Prunella modularis* in the family Prunellidae (see ACCENTOR), and the Java Sparrow *Padda oryzivora* and other species of Estrildidae (see ESTRILDID FINCH; and CAGE BIRD).

SPARROWHAWK: *Accipiter nisus*, a widespread small hawk of the Palearctic region. The same name, usually spelt as two words, was formerly used for *Falco sparverius*, a small falcon widespread in the New World, now usually known as the American Kestrel.

SPARROW-WEAVER AND SCALY-WEAVER: general terms for members of the subfamilies Plocepasserinae (Sparrow-weavers) and Sporopipinae (Scaly-weavers) of the Passeridae, Passeriformes, suborder Oscines (see WEAVER). They are endemic to the Afrotropical Region and placed in 5 genera; *Plocepasser* with 4 species, *Pseudonigrita* with 2 species, *Histurgops* and *Philetairus* with one species each, and *Sporopipes* with 2 species. They differ from the true sparrows (*Passer*) in tongue structure (Bock and Morony 1978).

Characteristics. All but one of the species are 12–15 cm long, the exception being the Rufous-tailed Weaver *Histurgops ruficauda* (20–23 cm). They are drab-coloured birds, brown above and white below, with species-specific markings confined mainly to the head and wings. The Rufous-tailed Weaver, besides its relatively longer tail, is greyer, and has a heavy scaly pattern over all of its underparts. The sexes are alike in all species. All are notably gregarious.

Habitat and distribution. All are found in the dry regions of Africa. The most widespread species is the White-browed Sparrow-weaver *Plocepasser mahali*, ranging from Ethiopia southwards to northern Cape Province. Its range in Ethiopia overlaps with that of the Chestnut-crowned Sparrow-weaver *P. superciliosus*, which occurs across the whole of the savanna belt north of the Equator, but appears to prefer higher altitudes than *mahali*. In Kenya the range of *mahali* completely overlaps that of Donaldson-Smith's Sparrow-weaver *P. donaldsoni* which, however, prefers a drier habitat.

The Grey-capped Social Weaver *Pseudonigrita arnaudi* and the Black-capped Social Weaver *P. cabanisi* are confined to north-eastern Africa, the Rufous-tailed Weaver to a small area of northern Tanzania and the Sociable Weaver *Philetairus socius* to the drier regions of south-western Africa.

Movements. No movements from the home range take place; the birds of a colony reside in one tree the year round, sleeping in their nests, and forage within a few km of the tree.

Food. All species forage on the ground for seeds and insects. In the Social Weaver adults depend more on insects (80% of food intake) than seeds and feed their young entirely on insects.

Behaviour. The White-browed Sparrow-weaver forms small colonies of 5–7 birds which defend a group feeding territory. They build several nests communally in which they sleep separately. Both of the *Pseudonigrita* species form colonies, ranging in size from a few to 50 or more nests in one tree. Birds from different colonies forage together in large flocks on communal feeding grounds; this behaviour occurs also in the Sociable Weaver. Nests of the Grey-capped Social Weaver are sometimes closely packed, with 10 or more nests clumped together, and are often used for roosting by more than one bird at a time.

All members of a new colony of Sociable Weavers join in the initial construction of the nest chambers. After some days, each bird restricts its activity to a few chambers only. During the breeding season only the breeding pair maintains the nest chamber, whereas any bird in the colony may repair any part of the superstructure of the nest mass. The number of birds per colony is highly variable, but may be as high as 500.

Voice. Only a few details are known. The male White-browed Sparrow-weaver gives a pleasant canary-like song from an elevated position, often singing after dark. A wide variety of calls are used by the Sociable Weaver and consist of staccato chipping notes, somewhat metallic in quality. The male's short, melodious song advertises ownership of a nest chamber and attracts a mate.

Breeding. All species build roofed nests that are thatched, rather than woven, from grass stems, the nest chamber being lined with softer materials. The nests of all species, except the Sociable Weaver and the scaly-weavers have two openings, one of which is closed when eggs are laid and opened again when the young fledge.

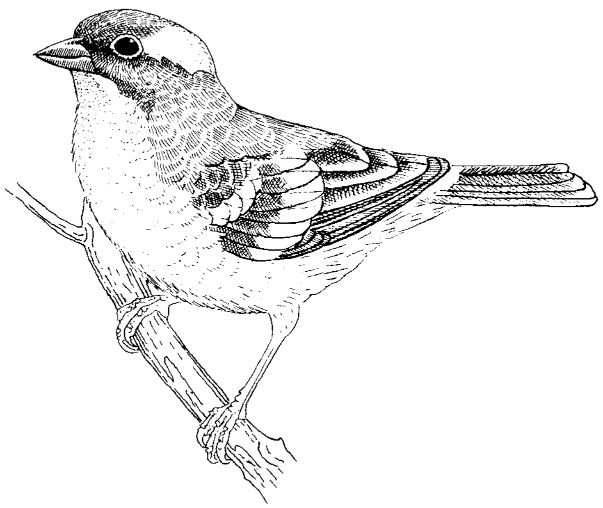
In a colony of the White-browed Sparrow-weaver there is only one brood nest, and one female incubates, although all or most members of a group will help feed nestlings. In contrast to this, a breeding colony of Grey-capped Sparrow-weavers may contain several breeding groups in the same tree. Only the pair incubates, but young of preceding broods help feed the nestlings.

The nest of the Sociable Weaver is the largest nest of any passerine; it may be as much as 9 m in length and 1.5 m high, and contain over 100 individual nest chambers. Small twigs are added to the thick dome-shaped roof which helps shed rain, gives shade from the hot sun, and protection from predators other than cobras. The larger the nest mass the more stable is its internal temperature. These colonial nests persist from year to year; one camelthorn acacia was known to have contained a colony for 100 years. The species is monogamous; both sexes incubate and feed nestlings which are also sometimes fed by young of previous broods hatched in the same breeding season.

The clutch-size in *Plocepasser* species is usually 2, the eggs are cream or pinkish white, and usually speckled with red and grey, forming a ring at the large end; in *superciliosus* the eggs are more heavily blotched. Clutch-size in *Pseudonigrita* species is in the range 2–5; the eggs are usually white or pinkish spotted with brown. The most frequent clutch-size of the Sociable Weaver is 4; the eggs of *Histurgops* are pale blue with scribblings and a few blotches of reddish-brown; its clutch-size is 3. Incubation takes 13–14 days in the Sociable Weaver and its young leave the nest 21–24 days after hatching.

Scaly-weavers. The 2 species of scaly-weavers *Sporopipes* are of uncertain systematic position. They have been considered to be a link between the true weavers (Ploceidae) and the waxbills (Estrildidae); their nest construction is similar to the sparrow-weavers'. Both species are endemic to the Afrotropical region, inhabiting the dry belt south of the Sahara (Speckle-fronted Weaver *S. frontalis*) and south-west Africa (Scaly-fronted Weaver *S. squamifrons*). They breed either singly or in small loose colonies in thorn trees, sometimes under the eaves of houses.

N.E.C. (L.G.G.)



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SPATULETAIL: *Loddigesia mirabilis* (see HUMMINGBIRD).

SPECIATION: the process whereby new biological species are evolved (see EVOLUTION; SPECIES). Speciation is believed to proceed as follows: an existing species becomes subdivided by some extrinsic factor, the isolated populations diverge genetically, and finally some form of intrinsic isolation, such as sexual isolation or genetic incompatibility, evolves among the populations. The newly separated populations can then evolve independently and may achieve ecological compatibility, allowing invasion of each other's geographic ranges without extirpation or extinction. Three modes of speciation are theoretically possible: allopatric, parapatric, and sympatric (Bush 1975, Endler 1977, Mayr 1963, White 1978). These modes differ primarily in the geographic relationships among the differentiating populations. Allopatric populations are geographically disjunct, parapatric populations are in contact along a common boundary, and sympatric populations overlap over most of their area. There is a great deal of controversy about the relative frequency of the various modes of speciation, and in some ornithologists' opinion only the allopatric mode has occurred.

Sympatric speciation involves the splitting up of different groups of individuals even though they are physically close enough to interbreed. This mode of speciation depends on assortative mating, or the tendency for individuals to mate more often with others of the same variety than those which differ. There is evidence for assortative mating within species, for example in the Blue—Snow Goose complex *Anser caerulescens—hyperborea*. Such mate preference is never complete nor continuous enough to allow intense genetic differentiation and full speciation without some additional factor; the 'wrong' matings still take place at a significant frequency. The only evidence for sympatric speciation comes from insects, and seems to involve a very strong host-plant specificity. A new species may be formed when a group of individuals invade a new host-plant species. This yields perfect assortative mating and complete isolation because mating normally takes place only on the host species that the parents ate as larvae. It is only where one finds strong microhabitat segregation associated with assortative mating that sympatric speciation seems to be possible. Birds are not nearly so microhabitat specific; therefore it is unlikely that sympatric speciation has played any role in the generation of bird diversity.

Allopatric and parapatric speciation involve geographical separation among the diverging populations, and differ only in the amount of physical restriction to movement among populations. Physical restriction to dispersal is complete in allopatric speciation and weak or absent in parapatric speciation. There are many intermediates between the two modes, and they collectively can be called geographic speciation.

In allopatric speciation the ancestral species is divided into two or more populations by a complete geographic barrier such as a mountain range, ocean, or extremely unsuitable habitat. This may happen by geological or climatic changes, or by dispersal across barriers. Dispersal of a small group of individuals, with (by chance) a genetic composition different from the ancestral species, may result in rapid divergence of the newly isolated population. This may be a more common mode of differentiation than the addition of a physical barrier to an existing species range (Mayr).

In parapatric speciation a complete physical barrier is not necessary because there is isolation by distance. Very few species are so geographically restricted in the breeding season that all the individuals meet with each other and can mate at random. Most species have a sufficiently large breeding area so that individuals from a given place are more likely to mate with those from the same area than with others further away. Even in migratory birds such as the Guillemot *Uria aalge*, it has been shown by ringing studies that matings between birds born in nearby sites are considerably more frequent than those between birds born in nests separated by long distances. The average nett distance travelled from birth to reproduction may be called the gene flow distance because it is proportional to the average distance traversed by genes per generation. If this distance is large relative to the size of the geographic range of a species, then there is no isolation, and speciation cannot occur. A good example is the Long-tailed Duck *Clangula hyemalis*, which often breeds thousands of kilometres from its birthplace. But, except for ducks, individuals of most species breed within a few kilometres of their parental nest; the gene flow distance is relatively small. In the latter case, many hundreds or even thousands of generations may be required for genes from one population to move into another. For example, populations of Asian Wheatears *Oenanthe oenanthe* are effectively isolated from the European populations, even though their ranges are continuous. Thus in parapatric speciation the barrier is one of time and distance rather than the physical obstruction to dispersal of allopatric speciation (Endler, White).

In general, the earth's surface is heterogeneous in climate, physiography, flora and fauna, and it is more likely than not that each population will be subject to different factors of natural selection. If selective factors vary geographically, and there is not a high rate of intermixing of genes from widely different habitats, then populations can diverge. There is extensive and convincing evidence for this (see Mayr, and DISTRIBUTION, GEOGRAPHICAL). In allopatric speciation, breeding sites are completely isolated, so there is no intermixing at all. In parapatric isolation, intermixing between populations in different environments proceeds so slowly that the groups isolated by distance can diverge nearly as much as if they were completely isolated. In the latter case the amount of differentiation is determined by the degree of environmental differences between populations and the gene flow distance (Endler). If this distance is small, then differentiation can proceed rapidly. If genes move a long distance every generation, then differentiation proceeds more slowly. Thus it is not surprising that there are many subspecies and species of sparrows *Zonotrichia* etc., there are relatively fewer geographic variants of geese, and ducks are the least differentiated geographically; these 3 groups illustrate increasing distance from fledging to breeding. Another example is the Australian bird fauna; sedentary species show more geographic variation and subspecies than migratory or vagrant species.

Geographic divergence can have a variety of causes. Habits and morphology may vary in relation to climate, available foods, or the presence or absence of other species. For example, in Germany, where 2 nightingales *Luscinia megarhynchos* and *L. luscinia* are found together, one keeps to drier woods and the other to wetter, although each is widespread in moist woods outside the area of overlap. Geographically, varying foods are associated with variation in bill size and shape in DARWIN'S FINCHES *Geospiza* spp. Predation appears to affect the colour patterns in relation to habitat in the Song Sparrow *Melospiza melodia*. Such differentiation may evolve rapidly; since their introduction into North America a century ago, various populations of the House Sparrow *Passer domesticus* have evolved a significantly different morphology in response to varying climate.

When two populations have diverged but remain geographically separate, it is not possible to decide with any certainty whether they are species or only subspecies. For example, Scrub Jays *Aphelocoma* are distributed throughout western North America, but are not found east of the Rocky Mountains except in southern Florida. These disjunct populations are morphologically similar but significantly different in behaviour. When a barrier is removed, so that the two populations actually meet in the wild, a definite conclusion may be possible. The two populations may (i) fuse together into a single hybrid swarm, (ii) there may be only a limited zone of hybridization, or (iii) they may remain distinct as breeding populations. Respectively, examples are (i) the flickers *Colaptes cafer* and *C. auratus*, (ii) the Hooded and Carrion Crows *Corvus corone* and *C. cornix*, and (iii) the ladder-backed woodpeckers *Picoides nuttalli*, *P. scalaris*, and *P. borealis*. In the first case they cannot be regarded as separate species; we find a broad zone of intergradation. In the second the process of speciation has advanced considerably further; the zone of intergradation is restricted to a narrow band, but sexual isolation has not evolved. The presence of all degrees of intermediate forms in the zone of contact indicates that species status has not been reached. In the third example there are 3 parapatric 'good' species, though of course we do not know whether they originated in allopatry or in parapatry. See Short (1969) and HYBRIDIZATION, ZONE OF SECONDARY for a discussion of contact zones and taxonomic decisions.

If there is only a limited degree of hybridization, and the hybrids are definitely inferior to either parental form (in the wild), then there will be selection against mating between the forms (Dobzhansky 1970, Endler). Those individuals which mate preferentially with their own kind will leave greater numbers or more vigorous progeny than those mating with the other kind. For this reason natural selection results in the continual improvement of sexual discrimination between the two forms. This has been verified experimentally with fruit flies *Drosophila* and crop plants. Eventually this can eliminate hybridization between the two forms. When this happens, the two forms (now 'good' species) have evolved isolating mechanisms specifically against each other.

In parapatric speciation, differentiating populations are separated initially by populations which are intermediate between them. As two populations become more and more different from each other, interbreeding may result in genetic incompatibility. Eventually the accumulation of genetic differences is great enough so that interbreeding results in fewer or weaker offspring, and specific isolation mechanisms can easily evolve. Of course, if genetic differences are not sufficient or appropriate, intrinsic isolation may not evolve; this may be the case in the European *Corvus*. From experiments we know that sexual isolation can evolve in less than 100 generations, so we are unlikely to see intermediate stages in parapatric speciation. Even so, ring-species are known in birds and other organisms and provide some support for this speciation mode. Ring-species exhibit a continuous series of differentiated parapatric subspecies, but the end forms overlap without interbreeding (see RING-SPECIES). An example is found in the Herring and Lesser Black-backed Gulls *Larus argentatus* and *L. fuscus*.

In allopatric speciation, two populations evolving in complete isolation from one another (e.g. on two different islands) cannot build up an isolating mechanism specifically against each other. In the course of time they may diverge sufficiently so as to be unrecognizable to each other as the same species if they come together. The results of hybridization among such populations may be a complete failure owing to accumulated genetic differences. Such differences may not necessarily evolve in allopatry, and are fortuitous by-products of differentiation in isolation. Because they result from chance differentation, it is also possible that any sexual isolation which evolves in allopatry may be asymmetrical. For example if one of two isolated populations loses some male behavioural elements needed in the courtship ritual, then males of that population will not be accepted by females of the other population, whereas mating may be normal in the reciprocal cross. For these reasons, mechanisms which specifically isolate populations from one another are not as likely to evolve in allopatry as they are in parapatry. Of course if a physical barrier disappears, then sexual isolation can evolve rapidly.

Specific isolating mechanisms can only evolve between two groups if they interbreed, if such hybridization does not result in 'swamping' of one set of genes by another, and if the hybrids are inferior in some way. 'Swamping', or overwhelming of one population by the genes from another, will only occur if there is a large gene flow distance. If this distance is small, 'swamping' is prevented by the long time required for genes from one population to invade the other. But if populations are never in contact there is no opportunity for natural selection to promote sexual isolation, and speciation can only occur by the fortuitous development of genetic, morphological, or behavioural incompatibility. Thus, although morphological differentiation can evolve rapidly in allopatry, parapatry or sympatry are more likely to favour the evolution of species-specific isolating mechanisms. Perhaps the most rapid way new species can be generated is by allopatry followed by parapatry. We cannot test this hypothesis because the biogeographic and genetic patterns produced by this sequence would not be different from that produced by 'pure' allopatric or 'pure' parapatric speciation (Endler).

The presence of sexual isolation between species has an important consequence, at least in bisexually reproducing organisms such as birds. Each species is a separate line of evolution, and does not exchange genes with any other species to any important degree. A species consists of an array of geographically and genetically definable populations that either do actually interbreed freely or would be expected to do so should they ever meet in the wild (see SPECIES). Sexual isolation does not necessarily mean that there are huge genetic differences among the isolated populations; genetic or sexual incompatibility and morphological differentiation may evolve more or less independently. Intrinsic isolating mechanisms may be present with minimum morphological differentation, as in sibling species. Examples are the Reed Warblers *Acrocephalus palustris*, *A. scirpaceus*, and *A. dumetorum*, the Chiffchaff and Willow Warbler *Phylloscopus collybita* and *P. trochilus*, and the Black-capped and Carolina Chickadees *Parus atricapillus* and *P. carolinensis*. Alternatively, sexual isolation may be as strong as morphological differentiation, for example the Blue-winged and Golden-winged Warblers *Vermivora pinus* and *V. chrysoptera*. Even morphological differentiation is no guarantee of sexual isolation; although *V. pinus* and *V. chrysoptera* are very distinct in appearance, they hybridize in disturbed habitats in certain parts of eastern North America.

Speciation is a continuing process, and we can find most stages of speciation in nature. This makes it difficult to decide whether two geographically isolated but nevertheless related populations should be considered as two subspecies of the same species, two semispecies, or as two species of a superspecies. Semispecies are populations which are just about to break apart into 'good' species, and superspecies are arrays of geographically replacing forms, some of which are too different to be regarded as the same species. Ring-species are a nuisance to a taxonomist, as it is necessary to make an arbitrary decision about the status of the various populations which contradicts a minimum of facts. But, biologically, ring-species are simply stages in geographic divergence of populations and may be an intermediate stage in the speciation process.

At any one place it is rarely difficult to distinguish the separate species, but difficulties appear when the same criteria are applied to large areas. One possible reason for this may be competition, which favours divergence in morphology, habits, and ecology among forms living together, but not among those living apart (see COMPETITION). Competition may directly favour divergence and speciation because hybrids between parental forms will be more similar to the parental species than the parents are to each other. Competition intensity is proportional to similarity, so hybrids will be at a disadvantage, favouring sexual isolation. Ecological factors act on a local scale, are unlikely to be uniform over large areas, and are therefore an additional factor promoting geographic differentiation and speciation. If two sister species evolve under different ecological conditions, then they may eventually diverge sufficiently to achieve ecological compatibility, making coexistence possible. This may result in the invasion of each other's geographic ranges without local extirpations or the extinction of one of the species.

The prime characteristic distinguishing species from differentiated populations is the presence of intrinsic isolating mechanisms. Once speciation is complete, physical or distance barriers between the species become relatively unimportant to genetic interchange, the populations may invade each other's geographic ranges, and further evolution and divergence can continue more rapidly. Speciation is important because the genetic independence of the new lineages allows rapid diversification and the invasion of new habitats. J.A.E.

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SPECIES: in simple terms, a 'kind' of bird (or other organism). The word has a variety of technical meanings and this has caused much confusion in the literature. To most biologists, species are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1969). This is the biological species definition. The term has several other meanings, depending on the use to which it is put, and the way in which the entities are distinguished.

The biological species concept has two important properties. It treats species as cohesive and interacting units independent of other such units, and it treats them logically as individuals rather than as a class. Another definition of the biological species is: the most extensive units in the natural economy such that reproductive competition occurs among their parts (Ghiselin 1974). Mayr's definition emphasizes their reproductive independence from other such groups, and Ghiselin's emphasizes the fact that species are a closed system. The most important property of species is that they represent an evolutionarily independent entity.

To a naturalist working in a particular place, it is rarely if ever difficult to distinguish between species; they are distinctly different kinds of animals, with characteristic morphology, habits, and habitat, which remain constant from year to year (Mayr). Their most characteristic attribute is that they are separated from other species by gaps in the normal variation among individuals. One can always tell a Blackbird *Turdus merula* from a Song Thrush *T. philomelos* and both from a Mistle Thrush *T. viscivorus*. It is possible that such gaps in variation are caused by COMPETITION, or the genetic and developmental limits to adapting to a specific niche (see ECOLOGY), but we actually do not know the reason for this phenomenon.

A rather different way to explain the observed variation pattern is the typological species concept. This originated with Plato and Aristotle and regards species as representing some ideal form or *eidos*, and individual variation as merely the imperfect expression of the ideal form. Thus, by the typological definition, a species is a class of objects which represent to varying degrees the ideal type. This definition applies to inanimate objects (such as minerals) as well as organisms. It is very convenient for identification of objects whose characters are determined by purely physical and chemical events and independent of history. It is entirely inappropriate for organisms because they are influenced by genealogy as well as physics and chemistry. The typological species concept has virtually disappeared from current usage (Mayr). As a vestige of the typological species concept (used by Linnaeus), a bird is identified with reference to a TYPE SPECIMEN and a TYPE LOCALITY. In present usage these serve as signposts to the entity we call a species, and in fact a given bird may be quite different from the type specimen and still obviously be a member of the same species.

There are several empirical species concepts which are based upon gaps in variation, and some of these have typological overtones. The morphological species is a group of individuals that resemble each other in most of their visible characters, sex for sex and variety for variety, and such that adjacent local populations within the group differ only in variable characters that intergrade marginally (Simpson 1961). This can be interpreted as an empirical method for distinguishing species, but has also been used in a typological sense (see Sneath and Sokal 1973). Species can also be separated by physiological and molecular techniques. Such methods can be useful as clues to variation, but must be used with caution. Note that all the empirical species concepts treat the species as a class of individuals with defining properties, and they ignore the effects of common descent. They therefore suffer from the same problems as the typological species concept.

Typological and empirical species definitions depend upon physical resemblance and are part of a classification system which is based upon a hierarchy of similarity. This is adequate for classification of inanimate objects, where a particular degree of similarity reflects the effects of the same degree of similarity in the processes which formed the objects. Quartz is the same in Europe as in North America, but 'blackbirds' are not. Organisms belonging to the same species share a common ancestor. Variation in rates of evolution may result in marked CONVERGENCE among unrelated species, divergence within species, and closely related species may or may not resemble each other in appearance. For example, birds are often found which are quite different from the main population in morphology or habits (perhaps due to POLYMORPHISM or age differences), yet they are clearly part of the same species. In addition, sibling species may hardly differ from another in morphology, yet never interbreed, and are clearly separate entities. One of the purposes of modern taxonomy is to form a classification which reflects phylogeny rather than mere similarity of appearance (see TAXONOMY). Only the biological species concept is appropriate in this case.

An additional problem with the naturalist's typological and empirical species definitions is that they all break down when one attempts to apply them over a broad geographic range, or over geological time. Species are not constant in space or time, they change in morphology, behaviour, and habitats. Such changes in space are called CLINES, are a normal part of the differentiation process, and may occur in SPECIATION. For example, Flickers *Colaptes cafer* have yellow tail and wing linings in eastern North America, but this grades into red and orange in the west and southern parts of the continent. Individuals from different parts of the geographic range are sufficiently different to look like different species and in fact there has been much argument about the status of the forms. The naturalist's typological and empirical species definitions cannot accommodate such variation as they require the species to be a class with defining properties rather than an integrated unit or individual in the logical sense. The biological species concept avoids this problem.

With respect to taxonomy, species are quite different from other categories. Species are the only category which represents a functional unit. Lower categories (subspecies, races, etc.) may not evolve independently of each other and their boundaries may be arbitrary. Higher categories (genera, families, orders, etc.) consist of a number of independent entities and are therefore classes with defining properties, yet they attempt to reflect the degree of relatedness among their component parts (see TAXONOMY, GENUS, NOMENCLATURE). Like species, higher taxa are historical units.

The most important property of a biological species is that it is a separate line of evolution, with little or no exchange of genes with other species. This allows more rapid evolution than would be possible if all organisms exchanged genes, because it allows genetic adaptation to local conditions and to new habitats. The biological species definition is not intended to provide an infallible criterion. There will always be a residue of borderline cases for which the decision will be arbitrary. This difficulty comes from the species being not fixed but evolving (Dobzhansky). Species change in time, and can give rise to new species. It is the intermediate stages in speciation which cause the most difficulty in classification and identification, just as during cell division it is a matter of opinion whether there is one cell or two (see SPECIATION; HYBRIDIZATION, ZONE OF SECONDARY; RING-SPECIES; SEMI-SPECIES; SUPERSPECIES). The non-existence of borderline cases would mean only that evolution had run its course and was no longer happening (Dobzhansky).

J.A.E.

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Sneath, P.H.A. & Sokal, R.R. 1973. Numerical Taxonomy. San Francisco.

SPECIES DIVERSITY INDEX: a mathematical index which describes, in somewhat abstract terms, the numbers and relative abundances of bird species in a habitat. A large number of equally common species yields a much higher index of diversity than a small number of species dominated by one very common form, and several rare ones. Intermediate levels of abundance and/or dominance yield intermediate values. Several alternative indices with these properties have been proposed, of which the most widely used in the ornithological literature is the Shannon-Wiener index (H'):

$$H' = -\sum_{i=1}^{i} p_i \log p_i$$

where $p_i = N_i/N$
N_i = Number of individuals in the i^{th} species
N = Total number of individuals of all species

SPECIES GROUP (1): with reference to the ranks of taxa, term embracing the categories species and subspecies (see NOMENCLATURE).

SPECIES GROUP (2): in taxonomy, a group of closely related species, less definite than a subgenus and not constituting a formal taxon for purposes of nomenclature. See also SUPERSPECIES.

SPECIES PAIR: two very closely related and very similar species.

SPECIES SPECIFIC: confined to one particular species.

SPECIFIC: in taxonomic terminology, appertaining to a species, e.g. 'specific name' (see TAXON); more generally (in one of the everyday senses), characteristically peculiar to some mentioned category. The two meanings are combined in the expression 'species specific', i.e. specific (in the second sense) for a species.

SPECIFIC ACTION POTENTIAL: 'the state of the animal responsible for its readiness to perform the behaviour patterns of one instinct in preference to all other behaviour patterns; this specific readiness diminishes or disappears when the consummatory act of the charged instinct has been performed' (Thorpe 1951). The term has fallen into disuse because of its association with the outdated concept of 'specific drives'.

SPECIFIC NAME: see NOMENCLATURE.

SPECKLE-BELLY: a name in North America for the Whitefronted Goose *Anser albifrons* (see under DUCK).

SPECTACLE-BIRD: name used for some species of Zosteropidae (see WHITE-EYE (1)).

SPECTROGRAPH, SOUND: obsolete term no longer generally used for SONAGRAPH.

SPECULUM: a patch of distinctive colour on the wing, in some plumage patterns, especially the metallic patch seen in dabbling ducks.

SPEEDS OF FLIGHT: see FLIGHT, SPEEDS OF.

SPEIROPS: substantive name sometimes used for the 3 species of *Speirops*, a genus of white-eyes confined to the islands of the Gulf of Guinea and Mt Cameroon (see WHITE-EYE (1)).

SPERMATOZOON: (plural 'spermatozoa') or 'sperm', a male germ-cell (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; and GENETICS). Also called 'spermatozoid' in the free-swimming stage, e.g. when in the female reproductive tract after copulation and before union with an ovum.

McFarlane, R.W. 1963. The taxonomic significance of avian sperm. Proc. XIII Int. Orn. Congr., Ithaca, N.Y., 1962: 91–102.

SPHENISCI; SPHENISCIDAE: see below.

SPHENISCIFORMES: an order, alternatively 'Sphenisci', comprising only the family Spheniscidae (see PENGUIN); the group is placed by Wetmore in a superorder, Impennes, of its own, but this view has been abandoned by most authors and their possible relationship with the Procellariiformes stressed. They are marine birds, with wings modified as flippers, and restricted to the Southern Hemisphere.

SPIDER-HUNTER: substantive name of *Arachnothera* spp. (see SUNBIRD).

SPINAL CORD: see NERVOUS SYSTEM.

SPINEBILL: substantive name of *Acanthorhynchus* spp. (see HONEYEATER).

SPINETAIL: substantive name of Synallaxinae spp. (see OVENBIRD (1)); also sometimes used (Africa) as an abbreviation of 'spine-tailed swift', substantive name of species in more than one genus (see SWIFT).

SPINIFEXBIRD: *Eremiornis carteri* (see under WREN (2)).

SPLITTER: a taxonomist who prefers a nomenclature that recognizes fine distinctions between taxa—in contrast to a LUMPER.

SPOONBILL: substantive name for the 6 species of Plataleinae in the Family Threskiornithidae (Ciconiiformes, suborder Ciconiae).

Characteristics and distribution. Spoonbills are long-legged water birds, about 70–85 cm in length, with a distinctively long and flattened, spatulate bill. They fly slowly, with outstretched necks, and can both glide and soar; and they occasionally swim. They are rather silent, except for low grunting sounds uttered at their nesting colonies. Spoonbills occur primarily in the warmer regions throughout the world. All 5 Old World species of spoonbills are in the genus *Platalea*, and are similar in that each has a mostly white plumage and a nuchal crest during the breeding season. The most conspicuous physical difference between adults of these 5 species is in the colour of the bill, legs and unfeathered facial region, which are predominantly red in the African Spoonbill *P. alba*, yellow in the Yellow-billed Spoonbill *P. flavipes* of Australia, black in both the Royal Spoonbill *P. regia*, occurring from Australia to Indochina, and the Black-faced Spoonbill *P. minor*, found from eastern China and Cambodia to the Philippines, and black and yellow in the Eurasian Spoonbill *P. leucorodia*. The one New World species, the Roseate Spoonbill *Ajaia ajaja*, occurring from the southern United States to northern Argentina, is primarily vivid pink with red upper wing and tail coverts, bare-headed, and has a tuft of elongate feathers on the lower neck. Adults and juveniles of the 5 *Platalea* species, as well as juvenile Roseate Spoonbills, have mostly feathered heads.

Habitat. Spoonbills are birds of coastal and freshwater wetlands, often nesting and roosting in large and remote, permanently flooded marshes or swamps, which are located adjacent to lake or river shorelines or in estuarine regions. Several *Platalea* species typically nest in expansive thickets of rushes and reeds, or in patches of dense, woody vegetation encompassed by marshes, while the Roseate Spoonbill and Black-faced Spoonbill more often nest in coastal regions, including for the former such diverse habitats as mangrove swamps and scrub-clad islands. All species feed in shallow flooded, calm or slow moving water, where aquatic and emergent vegetation is sparse or absent.

Populations and movements. Although numbers of Eurasian Spoonbills have fluctuated during recent decades in some parts of their range, possibly due to regional differences in water levels between years, this species has declined in numbers throughout much of its range due principally to habitat losses and direct human disturbance. In parts of the south-eastern United States the Roseate Spoonbill has shown a continuing recovery of numbers and reoccupation of former range following the cessation of plume-hunting and disturbance to nesting colonies. Spoonbills show regular, short-range dispersals following nesting, mainly by younger birds, and occasionally wander for long distances. Populations that breed in more temperate regions are migratory, including the Eurasian Spoonbill which leaves many parts of its breeding range between August and October, and returns in March and April. Its wintering areas are in southern Asia, the Mediterranean region and tropical Africa. The winter-nesting population of Roseate Spoonbills in southern Florida arrives at the nesting colonies during October and November, and departs in March and April.

Food. Spoonbills feed by actively wading through shallow water, sweeping the bill, which is held almost vertical and partly open, from side to side through water and silt. Food consists of aquatic insects and insect larvae, small fish, and small crustaceans, and to a lesser degree aquatic snails, frogs, tadpoles, worms and possibly some plant material.

Behaviour. Spoonbills are gregarious in much of their activities. They nest either in single species colonies or with other colonial nesting water birds. Spoonbills often fly in flocks, and may feed individually or in groups depending upon food densities. Temporary, monogamous pair bonds are established and maintained through each breeding season.

Breeding. Both members of the pair share building the nest, commonly a platform of sticks in a tree or bush, but also among reeds or even on the ground, incubation, care of the nestlings and defence of the immediate nest site. Clutches usually contain 2–5 eggs, most frequently 3. Incubation lasts between 21 and 25 days, and young fledge 40–50 days after hatching. Spoonbills become fully mature at 3 to 4 years of age. J.C.O.

Allen, R.P. 1942. The Roseate Spoonbill. Research Report 2, Natl. Audubon Soc., New York. 142 pp.

Brouwer, G.A. 1964. Some data on the status of the Spoonbill, *Platalea leucorodia* L., in Europe, especially in the Netherlands. Zool. Meded. 39: 481–521.

Cramp, S. & Simmonds, K.E.L. (eds.). 1977. The Birds of the Western Palearctic, vol. 1. Oxford.

Spoonbill *Platalea leucorodia*. (*R.G.*).

SPORT, BIRDS IN: a subject not, in general, covered by this work; but see FALCONRY; GAMEBIRDS; UTILIZATION BY MAN; WILDFOWL.

SPOTBILL: *Anas poecilorhyncha* (see DUCK).

SPOTTED CREEPER: see CREEPER, SPOTTED.

SPRAYS, AGRICULTURAL: see TOXIC CHEMICALS.

SPREO: sometimes used as substantive name of African glossy starlings of the genus *Spreo* (see STARLING).

SPRIG: a name in North America for the Pintail *Anas acuta*, a drake of the species being known to some American sportsmen as a 'buck sprig' (see DUCK).

SPRING: see ASSEMBLY, NOUN OF.

SPROSSER: German name often used as English (in preference to the fabricated 'Thrush Nightingale') for *Luscinia luscinia* (for subfamily see THRUSH).

SPSHING: see SQUEAKING.

SPUR: see INTEGUMENTARY STRUCTURES; LEG; WING.

SPURFOWL: substantive name of *Galloperdix* spp., and in Africa of *Pternistis* spp. (for family see PHEASANT).

SQUAB: an unfledged nestling, particularly of pigeons (Columbidae).

SQUACCO: or Squacco Heron, *Ardeola ralloides* (see HERON). See photo FEEDING HABITS.

SQUAMOSAL: a paired bone of the SKULL.

SQUAW, OLD-: the American name of the long-tailed Duck *Clangula hyemalis* (see DUCK).

SQUEAKER: popular alternative name for *Strepera versicolor* (see under CURRAWONG).

SQUEAKING: the practice of attracting passerine birds close to the observer by repeated squeaks.

STAGEMAKER: alternative name of *Scenopoeetes dentirostris* (see BOWERBIRD).

STANDARD DEVIATION: see BIOSTATISTICS.

STANDARD DIRECTION: see MIGRATION (Distances and directions).

STANDARD ERROR: see BIOSTATISTICS.

STANDARD METABOLIC RATE: the rate of energy production measured in a resting, post-absorptive animal at any stated ambient temperature. In endotherms like birds SMR is equivalent to the Basal Metabolic Rate within the Thermoneutral Zone (see METABOLISM), but it increases both at lower ambient temperatures to compensate for increased heat loss (but decreasing in torpor) and under heat stress above the thermoneutral zone (see also ENERGETICS; HEAT REGULATION).

STANDARDWING: substantive name of *Semioptera wallacei* (see BIRD-OF-PARADISE).

STAPES: the ear ossicle (see SKULL).

STARCHY: *Nesocichla eremita*, the endemic THRUSH of the Tristan da Cunha group in the South Atlantic.

STARFRONTLET: substantive name of some *Coeligena* spp. (for family see HUMMINGBIRD).

STARLING: substantive name of many species of Sturnidae (Passeriformes, suborder Oscines); used without qualification (Britain) for the common Palearctic species; in the plural, general term for the family. The name has also been used for other birds similar in appearance to starlings or once believed to be allied to them, e.g. the Military Starling (or Red-breasted Blackbird) *Leistes militaris* (see ORIOLE (2)). The 2 African tickbirds or OXPECKERS of the genus *Buphagus* are aberrant and have been assigned to a separate subfamily of their own (Buphaginae). By origin, the name starling belongs to the European *Sturnus vulgaris*, which ranges across Europe and the Middle East to Asia as far as Mongolia. The family comprises about 110 species, in 25 genera, restricted to the Old World except for human introductions.

Characteristics. Starlings are of small to medium size (16–45 cm in length). Usually heavily built, they have strong legs and bill. Many are blackish but often with iridescent plumage; in the glossy starlings (in the genera *Aplonis*, *Lamprotornis* and *Spreo*) the iridescence may be highly developed with vivid greens, blues, purple and orange in the plumage. Many of the African starlings are among the most beautiful of the family. The Superb Starling *Spreo superbus* of East Africa is iridescent blue and glossy orange and the Emerald Starling *Lamprotornis iris* of West Africa is brilliantly metallic green. The Long-tailed Glossy Starling *L. caudatus* has a flowing purple and blue tail that may attain 35 cm in length in the male. The Rose-coloured Starling *Sturnus roseus* has a glossy black head and wings and a pale pink body. Other species have areas of bare skin around the eye, lappets, wattles, or bristly feathers on the head and some have erectile or permanent crests. Towards the breeding season, the Wattled Starling *Creatophora cinerea* loses the feathering of the head and long wattles grow, while in the non-breeding season the wattles are resorbed and feathers grow anew: these properties have been used in research on cancer and on cures for human baldness respectively. In many species the sexes are indistinguishable while in others females are duller; in some, females and juveniles are markedly different from the iridescent adult males. Many of the tropical species are largely arboreal but some starlings, especially *Sturnus* and *Acridotheres*, are equally at home on the ground where they walk rather than hop. In the round-winged arboreal species flight is direct, but it is faster in the inhabitants of open ground with their more pointed wings.

Habitat. The mainly arboreal species frequent tropical forest edges, while others inhabit temperate grasslands which have been made more extensive by man's activities.

Superb Starling *Spreo superbus*. (*D.A.T.*).

Distribution and movements. The starlings are entirely Old World and primarily tropical, although a few reach Europe, China and Japan. Part of the population of the Shining Starling *Aplonis metallica* migrates from New Guinea to breed in Queensland, the only incursion into Australasia. The family is well represented in Africa but the greatest diversity occurs in the Oriental zoogeographical region. One genus, *Aplonis*, is widely spread in Polynesia and had reached even Tahiti, although it is now extinct there. Four species, 2 from the Mascarene islands and 2 from Polynesia, have become extinct in the last 200 or so years, and Rothschild's Mynah *Leucopsar rothschildi*, from the Indonesian island of Bali, is classed as 'endangered'. Other starlings are eminently successful, and the European Starling, with a huge breeding area in Eurasia and populations established elsewhere by introductions, is now one of the world's most numerous species of bird.

Most starlings are resident but some undertake local movements, while others are obligate or partial migrants. An interesting Afrotropical species is the nomadic Wattled Starling, immense flocks of which search for concentrations of migratory locusts. When locusts lay their eggs in an area where rains have led to abundant grass growth, Wattled Starlings also nest and later feed their young on the flightless immature 'hoppers'. In such circumstances, each tree in an area may contain several nests of the Wattled Starling. Another species that establishes breeding colonies where locusts abound is the Rose-coloured Starling. It winters in India and breeds in central Asia and eastern Europe, but since its breeding distribution is dependent upon a good supply of locusts, an area which held a large colony one year may be deserted the next.

Several of the starlings, including the European Starling and the Indian Mynah *Acridotheres tristis*, have established a more or less commensal relationship with man. In countries where it has been introduced, the European Starling has become not only an agricultural pest but also a serious competitor of native birds, such as the bluebirds *Sialia* spp. in North America. In New Zealand, however, the European Starling is encouraged, by the provision of nest boxes, on account of its consumption of an insect pest of grassland. In the north of its ancestral range, the European Starling is regarded as beneficial, but on migration and in its wintering areas it is a serious pest of vineyards, olive groves, cherry orchards and cattle feeding areas. The Indian Mynah has been introduced to many tropical islands, ostensibly to control locusts, but this species has also usually become a pest in these areas.

Food. Starlings are omnivorous, with most eating fruit and insects, while some take pollen, nectar and seeds; some are important pests of cultivated fruit and cereals.

A contributory factor to the European Starling's success may have been the evolution, notably in the genera *Creatophora*, *Acridotheres* and *Sturnus*, of a feeding method called 'prying' or 'open-bill probing'. In these genera the muscles that open the bill, the protractors, have become well developed in comparison with those in the frugivorous and insectivorous, mainly arboreal species. This enables the bill to be forcibly opened after it has been pushed into the soil surface, thereby exposing soil organisms.

Behaviour. Most starlings nest in colonies, feed in flocks and roost communally: winter roosts of the European Starling may contain over a million birds.

Voice. None has a really accomplished song but many utter a variety of pleasing whistles. Some mimic other species and the Hill or Talking Mynah *Gracula religiosa* can imitate human speech (see MIMICRY, VOCAL).

Breeding. Most species nest in holes, especially in trees, but holes in cliffs and buildings may also be used, as may holes bored by other species like woodpeckers and barbets. Within the cavity a bulky nest is built. The Bank Mynah *Acridotheres ginginianus* digs its own burrows in river banks and the Woodpecker Starling *Scissirostrum dubium*, of Sulawesi, bores holes in dead trees like woodpeckers, except that these starlings are highly colonial so that a tree may be riddled with nest holes. Some species, like the Superb Starling, build domed nests and the Shining Starling builds pendulous nests like those of weavers (Ploceidae). Two to 6 eggs are laid, with tropical species generally laying smaller clutches. The eggs are generally pale bluish-green with brownish spots, but in *Sturnus*, *Acridotheres* and *Creatophora* the eggs are unspotted. Both sexes usually incubate for 11–18 days, but the female takes the greater share, and both parents usually feed the young, which fledge in 18–30 days. In the European Starling polygyny is quite frequent and mates may be changed between nesting attempts within a breeding season, while some females are parasitic, laying eggs in other European Starlings' nests. Co-operative breeding has been documented in several African starlings in the genera *Cosmopsarus* and *Spreo*: in the Chestnut-bellied Starling *S. pulcher* a breeding pair may be assisted by as many as 12 non-breeding or immature birds.

See photos FEEDING HABITS; ROOSTING; TAIL. C.J.F.

Amadon, D. 1943. The genera of starlings and their relationships. Amer. Mus. Novitates, No. 1247: 1–16.
Amadon, D. 1956. Remarks on the starlings, Family Sturnidae. Amer. Mus. Novitates, No. 1803: 1–41.
Amadon, D. 1962. Family Sturnidae. *In* Mayr, E. & Greenway, J.C. (eds.). Check-list of Birds of the World, vol. 15. Cambridge, Mass.
Beecher, W.J. 1978. Feeding adaptations and evolution in the starlings. Bull. Chicago Acad. Sci. 11: 269–298.
Feare, C.J. 1984. The Starling. Oxford.
Wilkinson, R. 1982. Social organization and communal breeding in the Chestnut-bellied Starling (*Spreo pulcher*). Anim. Behav. 30: 1118–1128.

STARRING: see HATCHING.

STARTHROAT: substantive name of *Heliomaster* spp. (for family see HUMMINGBIRD).

STATISTICAL POPULATION: term used to denote the universe of objects (birds, eggs, nests, etc.) from which some sample under study has been drawn. See BIOSTATISTICS.

STATISTICAL SIGNIFICANCE: the probability that the observed result of a statistical test has arisen by chance, in the absence of causal effects. See under BIOSTATISTICS. If this probability is low enough—conventionally below 0.05 (whence the notation $P < 0.05$)—the presence of a biological effect is more believable than is the null hypothesis. For example, statistical calculation predicts that an unbiased coin tossed 5 times will yield 5 heads in 3 of every 100 such series, but most people would suspect a coin to be biased on seeing it come up with 5 heads in a row.

STEAMER-DUCK: substantive name of 2 species of ducks of the genus *Tachyeres*, confined to southern parts of South America and the Falkland Islands. The smaller species, *T. patachonicus*, occurs on both inland waters and along the coasts and can fly; the larger species, *T. pteneres*, is confined to coastal waters and is flightless. Three species are sometimes recognized (see DUCK).

STEAMING: term applied to the mode of progression of steamer-ducks *Tachyeres* spp. (see DUCK; FLIGHTLESSNESS).

STEATORNITHES; STEATORNITHIDAE: see under CAPRIMULGIFORMES; OILBIRD.

STEGANOPODES: see PELECANIFORMES.

STENOECIOUS: occupying a narrow range of the habitats available in an area, i.e. showing 'narrow habitat tolerance'—contrasted with EURYOECIOUS.

STENOTOPIC: more or less equivalent to STENOECIOUS (see above).

STEPPE: treeless uncultivated plain, usually as found in Central Asia.

STERCORARIIDAE: see under CHARADRIIFORMES; SKUA.

STERNIDAE: see CHARADRIIFORMES, suborder Lari; TERN.

STERNUM: the breast-bone (see SKELETON, POST-CRANIAL; and CARINATE; RATITE).

STIFFTAIL: substantive name of the White-headed Stifftail *Oxyura leucocephala*; in the plural, general term for the Oxyurini (see DUCK).

STILT: substantive name of some species of Recurvirostridae (see under AVOCET).

STIMULUS: see RELEASER; SIGN STIMULUS.

STINT: substantive name (in British rather than American usage) of certain small sandpipers assigned to the genus *Calidris* or to '*Erolia*' (see SANDPIPER).

STITCHBIRD: *Notiomystis cincta*, a New Zealand HONEYEATER.

STOMACH: a mammalian organ of which the equivalent in birds is the proventriculus and ventriculus (gizzard) considered together (see ALIMENTARY SYSTEM).

STONECHAT: substantive name of some *Saxicola* spp.; used without qualification, in Britain, for *S. torquata* (see CHAT (1); THRUSH).

See photos SEXUAL DIMORPHISM.

STONE-CURLEW: usual or alternative substantive name for species of Burhinidae; applied without qualification, in Britain, to *Burhinus oedicnemus* (see THICKKNEE).

STOOPING: term used of a bird-of-prey descending steeply on its quarry from a greater height in the air (see FALCONRY) or of any bird making a real or threatening attack in like manner ('dive-bombing').

STORING OF FOOD: see FOOD STORING.

STORK: substantive name for most of the 17 species in the Ciconiidae (Ciconiiformes, suborder Ciconiae).

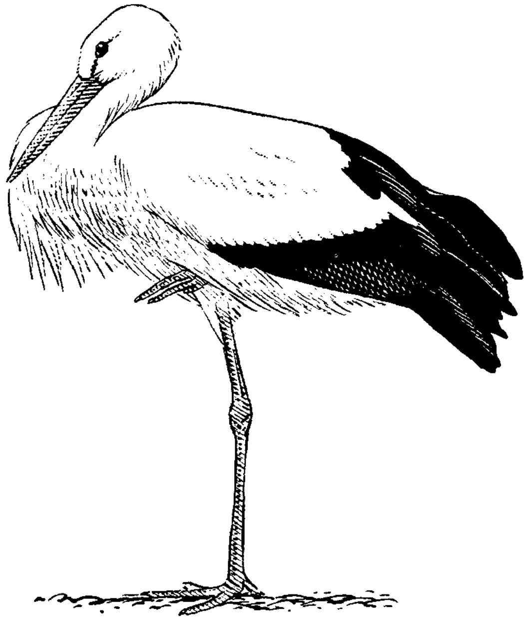
Characteristics. Storks are large birds (up to 100 cm long and standing from 60 to 120 cm tall) with long bills, necks, and legs and with webbing at the base of the toes. They have long, broad wings, short tails and elongate undertail coverts, and fly with a slow flapping or soaring flight, often at great heights. Twelve species have essentially all black and white plumages; the other 5 are the all-white Jabiru *Jabiru mycteria*, the all-black African Openbill Stork *Anastomus lamelligerus*, and 3 largely grey and white species, the Marabou Stork *Leptoptilos crumeniferus* and the closely related Lesser and Greater Adjutant Storks *L. javanicus* and *L. dubius*. Males of all species tend to be slightly larger than females and, except for sexual dimorphism in the eye colour of the Saddlebill Stork *Ephippiorhynchos senegalensis* and Black-necked Stork *E. asiaticus*, the sexes are similar in appearance. Although superficially resembling large herons, and often occurring in the same habitats, storks differ chiefly in being heavier bodied and having the head more extensively bare while most species fly with neck extended.

The storks are most appropriately divisible along morphological and behavioural lines into 3 distinct groups. The tribe Mycteriini is composed of 4 species of wood storks *Mycteria*, and 2 species of openbill storks, *Anastomus*. The wood storks are quite similar in appearance, behaviour and ecology, all species having unfeathered heads as adults, heavy, slightly decurved bills, and varying amounts of pink, yellow, or salmon-coloured feathers during the breeding season. The openbill storks have mostly feathered heads and a long specialized bill with a conspicuous gap between the central portion of the upper and lower mandibles. The tribe Ciconiini consists of 5 species of 'typical' storks, *Ciconia*, characterized by a relatively thin and straight bill, a ruff of feathers on the lower neck, and a mostly feathered head. The third tribe is the Leptoptilini, composed of 3 rather diverse genera, which exhibit ties along behavioural lines. The Black-necked Stork and Saddlebill Stork are tall, slim-bodied species with feathered heads and similar iridescent black and white plumage patterns, including strikingly marked white wings with black linings. Both have long and slightly recurved bills, while the Saddlebill has a broad fleshy lappet, yellow in colour, at the base of the upper mandible. The remaining 4 species in the tribe have bare or sparingly feathered heads and necks, and massive bills, slightly recurved in the Jabiru and Lesser Adjutant Stork. The Marabou Stork and Greater Adjutant Stork possess inflatable, pendent throat pouches, which are suggested to have a role in courtship displays.

Habitat. Storks generally are characteristic of mixed woodland and savanna regions, that include various amounts of wetland, although the Black Stork *C. nigra* occurs in extensive forests in parts of its range and the Abdim's Stork *C. abdimii* is found in drier regions than the other species. Most storks nest in trees and feed in shallow water, although there are notable exceptions. Black Storks may nest on cliffs, Abdim's Storks on rocky islands and village huts, the Maguari Stork *C. maguari* may nest on the ground in dense marsh, and the White Stork *C. ciconia* is famous for nesting on rooftops and other elevated, man-made structures. Some storks also feed in non-aquatic sites, notably Abdim's Stork, the Woolly-necked Stork *C. episcopus* and White Stork, which feed in varying degrees in dry fields, and the Marabou Stork and the 2 adjutant storks, which are attracted to carrion and human rubbish dumps. Tree-nesting species often locate their nests and roosts either near the tops of tall trees or in woody vegetation on islands or over standing water.

Distribution. Storks are primarily an Old World family, the greatest number of species occurring in tropical and subtropical regions of Africa and south-eastern Asia. In the tribe Mycteriini, the American Wood Stork *Mycteria americana* occurs from the southern United States to Argentina, the Yellow-billed Stork *M. ibis* is widespread in Africa south of the Sahara, and the Milky Stork *M. cinerea* and Painted Stork *M. leucocephala* are in south-eastern Asia, the former occurring between Indochina and Java, and the latter more widely distributed between India and China. The Asian Openbill Stork *Anastomus oscitans* is found from India to Indochina, and the African Openbill Stork occurs throughout most of tropical Africa and Madagascar. Of the typical storks, the Black Stork breeds across Eurasia and in southern Africa; the small Abdim's Stork in central Africa north of the Sahara and in the south-western Arabian Peninsula; the Woolly-necked Stork is widespread in much of tropical Africa and in south-eastern Asia as far east as the Philippines; the Maguari Stork occurs east of the Andes in South America, and the White Stork breeds across Europe and temperate Asia, formerly east to Japan (the far eastern birds may be specifically distinct) and in north-western Africa, with a small isolated population nesting in South Africa. The 6 species in the Leptoptilini are all tropical species, with the Black-necked Stork breeding from India to the Indochina region, and disjunctly in New Guinea and northern Australia, while the Saddlebill Stork occurs throughout tropical Africa. The monotypic Jabiru occurs in the New World tropics between southern Mexico and northern Argentina, the 2 adjutant storks are in tropical south-eastern Asia, and the Marabou Stork is widespread in tropical Africa.

Population. Quantitative information on numbers of birds and population trends are only known in portions of the ranges of 3 species. White Storks have shown the greatest decline or been extirpated as breeders mainly in north and west Europe, China and Japan. Populations in eastern Europe have shown more varied trends, including slow declines, areas of stability and some local increases, but overall numbers have also declined in this region. International censuses in Europe in 1934 and 1958 revealed an approximately 50% total decline in breeding White Storks. Black Storks have also declined or been locally extirpated in western Europe, but have increased in numbers in some east European countries, mainly since the 1930s. American Wood Storks numbered approximately 30,000 breeding pairs in the United States during the 1930s, but had declined to 10,000 pairs by 1960, and 5,000 pairs in 1978. One large nesting colony of Wood Storks in southern Mexico has been roughly stable since the early 1970s, with between 5,000 and 8,000 pairs annually. No regional numbers are available for other species, but no species is thought to be seriously threatened, although the decline of the White Stork and Black Stork, in portions of their range, and of the disjunct United States population of Wood Storks, is likely to continue, due to habitat loss.



White Stork *Ciconia ciconia*. (*R.G.*).

Movements. Only the White Stork, Black Stork, and Abdim's Stork are truly migratory. White and Black Storks migrate from their Eurasian breeding grounds to spend the winters in eastern and southern Africa and southern Asia. Neither species makes long flights over large bodies of water, so many thousands of birds circumvent the Mediterranean Sea by crossing at the Straits of Gibraltar and the Bosphorus. Abdim's Stork is a transequatorial migrant in Africa, where it breeds north of the Equator and migrates into the Southern Hemisphere during the northern dry season.

The movements of other species of storks are dispersals rather than true migration. Species or populations respond to the seasonal nature of rainfall characteristic of tropical and subtropical regions by moving to locations where surface water conditions favour optimum feeding. Where seasonal rainfall patterns are regular between years, the movements of storks may also be regular, and appear similar to true migration, but these same species may also perform more irregular movements in response to less regular rainfall or drought conditions. For example, American Wood Storks that breed in Mexico and southern Florida abandon their nesting grounds and disperse northward at the time when heavy summer rains cause disruption of local feeding conditions. The magnitude of the dispersal, both in terms of numbers of birds and distance travelled, generally varies in direct relationship to the amount and extent and timing of rains on the nesting grounds. Likewise in Africa, Marabou Storks abandon portions of their range during periods of heavy rainfall, when certain live prey becomes less available.

Food. Availability of food may be the single most important factor that regulates the movements of most storks and the timing and success of nesting. In Florida, up to one-half of the total Wood Stork population may not nest in years when water conditions do not provide adequate food. White Storks in Europe produce fewer young per nesting pair in cooler and wetter years, when food resources are apparently adversely affected.

Most storks obtain food by slowly walking through suitable habitat until visual contact is made with a prey item, which is quickly captured with the tip of the bill and swallowed with the aid of a backward toss of the head. Typical storks *Ciconia*, with the exception of Abdim's Stork, hunt at ponds, marshes, river edges and wet and dry fields, and capture such diverse food items as fish, insects, frogs, snakes, mice and lizards. The somewhat more specialized Abdim's Stork preys upon insects captured at upland sites but, like the White Stork, especially on locust swarms. The Black-necked and Saddlebill Storks and Jabiru usually hunt for food in shallow water, and feed more exclusively on fish and some frogs. The *Leptoptilos* storks are carrion feeders, although the Lesser Adjutant is less so, and all 3 species may capture frogs or fish when nesting.

The species most specialized in food preference and feeding techniques, notably the 4 wood storks and the 2 openbill storks, are the most colonial in nesting habits and may congregate in large numbers at feeding sites. American Wood Storks may fly up to 110 km between colony and feeding site, although shorter distances are much more usual. Wood Storks wade through shallow water where fish are concentrated, holding their partially open bills vertically submerged. When a small or medium-sized fish strikes the bill, the stork instantly snaps shut upon it. When groping for fish in this manner the stork may stir the bottom with one foot, which increases movement by the fish and apparently improves the chance that one will strike the bill. Openbill storks feed to a large extent on freshwater molluscs, which they capture by probing along the bottom of ponds and streams and are able to open with their specialized bill.

Behaviour. Wood storks, openbill storks, the 2 adjutant storks and the Marabou Stork are colonial nesters, and may feed either individually or in groups depending upon distribution of food. The *Ciconia* storks are solitary nesters, except for Abdim's Stork which often forms nesting colonies, and the White Stork and Maguari Stork which occasionally occupy sites where several active nests are within sight of one another. The Black-necked and Saddlebill Stork and Jabiru are solitary nesters. Non-colonial nesters may maintain pair-bonds through several years, while colonial species apparently do not; probably related are the more elaborate pair-bond displays among colonial species. Typically the male arrives first at the beginning of each breeding season. In colonial species the male rigorously defends the site against intrusion from adjacent males, but eventually accepts the approach of the more passive and persistent female. The common nest-site greeting display among all species is an up-down ceremony, where both sexes raise and lower their heads, sometimes with the bill reaching a vertical position, and often accompanied by vocalizations or bill-clattering.

Voice. Adult storks are generally silent except for calls given during nest-site displays. These are most often given during the up-down display, and include whistles by the *Ciconia* storks, hissing by the wood storks, nasal honking by openbills, and squeals and low groaning calls by the *Leptoptilos* storks. Nestling American Wood Storks utter a loud, repetitive bleating call, especially in response to approach by an adult, which produces a chorus audible at long distances.

Breeding. Storks that breed in tropical and subtropical regions are either dry season or wet season nesters, depending upon the effect that rainfall and high or low water levels have upon food resources. Thus Asian Openbill and Abdim's Storks nest in wet seasons when molluscs and insects, respectively, are more available or abundant. The American Wood Stork and Marabou Stork are dry season nesters when fish and other foods are concentrated in drying pools, and scavenging is best. Both sexes share in nest building, incubation and feeding young. Old nests may be reused, especially by solitary nesting species. Egg-laying and hatching are asynchronous, incubation beginning with the first or second egg. Most species lay 3–5 eggs, and incubation lasts 28–36 days. Adults feed chicks several times daily by regurgitating food on to the floor of the nest. Often one or more young fail to survive to fledging, usually due to inadequate food. The nestling period ranges from approximately 50 days in the smaller species to over 100 days in the Marabou and other large species. First breeding by young storks often occurs from between 3 and 5 years of age, although White Storks may occasionally begin nesting at 2 years.

See photos MECHANICAL SOUNDS; MOBBING. J.C.O.

Cramp, S. & Simmonds, K.E.L. (eds.). 1977. The Birds of the Western Palearctic, vol. 1. Oxford.

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Kahl, M.P. 1966. A contribution to the ecology and reproductive biology of the Marabou Stork (*Leptoptilos crumeniferus*) in East Africa. J. Zool. 148: 289–311.

Kahl, M.P. 1971. Social behavior and taxonomic relationship of the storks. Living Bird 10: 151–170.

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STORK, HAMMER-HEADED: see HAMERKOP.

STORK, SHOE-BILLED or WHALE-HEADED: see SHOEBILL.

STORM-PETREL: substantive name of species of Hydrobatidae (Procellariiformes); in the plural, general term for the family (see PETREL).

STRATEGY: in a biological or evolutionary sense, a behaviour or complex of behaviour patterns which confers or might be supposed to confer a selective advantage on the individual employing it. In analyses of the survival value of a behavioural or any other trait it is often useful to compare the observed trait with hypothetical alternatives. One can then ask why natural selection has favoured one alternative rather than another. The 'alternatives' in such an analysis are sometimes referred to as strategies. For example two alternative reproductive strategies for a male bird might be to defend a territory and advertise for mates, or to attempt to 'parasitize' other territorial males by stealing matings when females approach.

STREAMCREEPER: *Lochmias nematura* (see OVENBIRD (1)).

STREAMERTAIL: *Trochilus polytmus*, a Jamaican HUMMINGBIRD notable for the extraordinary elongation of the 4th pair of tail-feathers in the male.

STRIATED: streaked.

STRIGES; STRIGIDAE: see below.

STRIGIFORMES: an order, alternatively 'Striges', comprising 2 families, Tytonidae and Strigidae (see OWL).

STRIGOPINAE: see PARROT.

STRUCTURAL COLOURS: see COLOUR.

STRUTHIONES; STRUTHIONIDAE: see below.

STRUTHIONIFORMES: an order, alternatively 'Struthiones', of 'ratite' birds, comprising 4 suborders: Struthiones, Rheae, Casuarii, Apteryges, and 6 families: Struthionidae (OSTRICH), Aepyornithidae (extinct) (ELEPHANT-BIRD), Rheidae (RHEA), Dromaiidae (EMU), Casuariidae (CASSOWARY), Dinornithidae (extinct) (including Anomalopteryginae, Dinornithinae) (MOA), Apterygidae (KIWI). Flightless, cursorial birds, including the largest living birds (African Ostrich *Struthio camelus*). As the flight-muscles are reduced, the breast-bone has no keel—hence the old name Ratitae, from *ratis* (raft), in distinction from other birds collectively known as Carinatae, from *carina* (keel). There are no ordinary flight-feathers, but differences in this respect between families are great. Anatomical structure (e.g. bony palate) and morphology are usually considered primitive, but opinions differ on which of the characteristics are really old and which are secondary adaptations to cursorial life. The relationship between the suborders has been much discussed. Current opinion favours the theory of phylogenetic affinity. Recent distribution is mainly in southern continents, often in relict areas, such as Madagascar (Aepyornis, extinct), New Guinea (CASSOWARY), Australia (CASSOWARY, EMU), New Zealand (KIWI and extinct MOA).

STRUTTING GROUND: special term in North America for the social display ground of the Sage Grouse *Centrocercus urophasianus* (see GROUSE; LEK).

STUMP-TAIL: in the plural, alternative general term for the crombecs *Sylvietta* spp. (see WARBLER (1)).

STUPEFYING BAITS: see PESTS, BIRDS AS; TRAPPING.

STURNIDAE: a family of the PASSERIFORMES, suborder Oscines; see STARLING.

STYMPHALIAN BIRDS: see FABULOUS BIRDS.

SUB-ADULT: an imprecise, but often useful, term for a bird which is not in fully adult plumage.

SUBCLASS: see under CLASS; TAXON.

SUBCUTANEOUS FAT: see ENERGETICS; MIGRATION.

SUBFAMILY: see under FAMILY; NOMENCLATURE; TAXON.

SUBGENUS: see under GENUS; NOMENCLATURE; TAXON.

SUBMERGENCE: see SWIMMING AND DIVING.

SUBORDER: see under ORDER; TAXON.

SUBOSCINE: term applied collectively to the suborders of the Passeriformes other than the Oscines (see PASSERIFORMES).

SUBSONG: see VOCALIZATION (Song development); BEHAVIOUR, DEVELOPMENT OF (subsong).

SUBSPECIES: a population of which the members can be morphologically distinguished, if sometimes only on average, from the members of other populations of the species to which all belong; the term 'race', or 'geographical race', is used synonymously and is in some ways a truer representation of the concept. In Mayr's (1959) words, subspecies are 'geographically defined aggregates of local populations which differ taxonomically from other such subdivisions of a species'.

Subspecies are designated trinominally, a third term being added to the specific binomen; the subspecific form corresponding with the original description of the species is treated as the 'nominotypical subspecies', the third term of the trinomen being a repetition of the second. An early notion that the nominotypical subspecies was 'the species'—other races representing, as it were, departures from the orthodox—was based on a misconception; the original choice of a particular population as the basis of the specific name was of course purely fortuitous. The nominotypical subspecies has in reality no greater importance than others, and it is 'typical' only in a nomenclatural sense.

Ornithology passed through a phase, earlier in the present century, when there was a tendency—not yet completely defunct—to treat the subspecies as the natural unit, losing sight of the fact that the species is the only taxon that can be defined in objective terms (see SPECIES). As Mayr has said: 'Four features of geographic variation make it difficult to delimit a subspecies objectively: (1) the tendency of different characters to show independent trends of geographic variation; (2) the independent re-occurrence of similar or taxonomically indistinguishable populations in widely separated areas (polytopic subspecies); (3) the occurrence of micro-geographic races within formally recognized subspecies; and (4) the arbitrariness of the degree of distinction selected by different authors as justifying subspecific separation of slightly differentiated local populations.'

The subspecies is therefore 'merely a practical device for the taxonomist', and many that have been described have since proved to be no more than samples arbitrarily taken from a population continuum showing clinal variation (see CLINE). Attempts have been made by taxonomists to give an appearance of objectivity to such subspecies by applying an arbitrary rule that 75% (some say 50%) of specimens must be identifiable. On the other hand, a geographically isolated population, whether or not it has been recognized as subspecifically distinct (or as including more than one subspecies), may be an incipient species and thus of potential importance as an evolutionary unit (see SPECIATION; also RING-SPECIES).

Mayr, E. 1959. Trends in avian systematics. Ibis 101: 293–302.
Mayr, E. 1982. Of what use are subspecies? Auk 99: 593–595. (See also discussions on the same topic by other authors, *ibid*: 596–615).

SUBSTANTIVE NAME: see NAME, SUBSTANTIVE.

SUGARBIRD: (1): substantive name of the 2 species (*cafer* and *gurneyi*) of *Promerops*, at present placed in the Promeropidae (Passeriformes, suborder Oscines) representing the only family of birds peculiar to South Africa. The evolutionary history of *Promerops* has been much debated, with a recent study (Sibley and Ahlquist 1974) suggesting that the sugarbirds are related to the starlings (Sturnidae) and not to the Australasian honeyeaters (Meliphagidae) as was thought formerly.

Characteristics. Sugarbird males are larger than females and total length exceeds 23 cm. They are readily distinguished from sunbirds (Nectariniidae), by being larger, by having a generally dull brownish plumage, long decurved beak and elongate tail feathers. The tail in males is normally considerably longer than in females, and can attain a length of 30 cm in the Cape Sugarbird *Promerops cafer*. Gurney's Sugarbird *P. gurneyi* is shorter tailed and redder on the chest and crown than *P. cafer*.

Habitat and distribution. Both species live in close association with *Protea* vegetation. They are found usually where proteas are in bloom, mainly along mountain slopes. The Cape Sugarbird is common in the southern and south-western Cape Province of South Africa. Gurney's Sugarbird, which replaces *P. cafer* in eastern Cape Province, occurs in Natal, the eastern and north-eastern Transvaal, and as far north as the eastern highlands of Zimbabwe. No long distance movements are known, or suspected, but populations undertake regular, altitudinal migration, up and down mountains, in association with seasonal variation in the flowering phenology of proteas. Dense concentrations of birds are found locally at stands of flowering proteas during the non-breeding season.

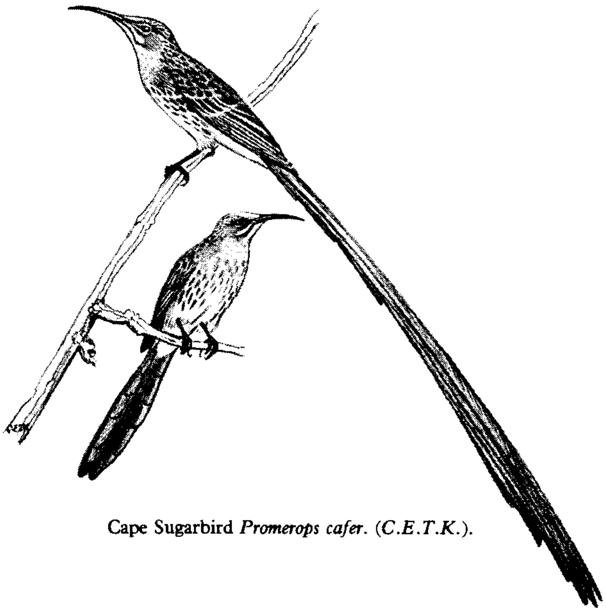
Food. Sugarbirds are adapted (e.g. tongue structure) for feeding on nectar, especially of proteas, and it is likely that they are important POLLINATORS of many species in the genus *Protea*. They also take insects and spiders, usually by probing in protea inflorescences, especially during the breeding season when the females require extra supplies of protein for the formation of eggs and for feeding young.

Voice. The song of Gurney's Sugarbird consists of 3 or 4 ascending notes, the last repeated several times, whereas *P. cafer* sings a series of jangling metallic 'gratings' and churrings. The alarm call is somewhat like the squeak of a rusty gate.

Behaviour. Both species are territorial and monogamous when breeding. The males of *P. cafer* perform a very conspicuous display flight in which the tail is held over the back of the bird while the wings are clapped vigorously. The fifth primary has a wide bulge, which is functionally concerned with this display.

Breeding. In the winter-rainfall region of South Africa the breeding season of *P. cafer* extends from February to August, with a peak in April–June when certain *Protea* spp. are flowering in the lowlands. During this period, the weather tends to be cool and wet and sugarbirds choose relatively sheltered microhabitats in selecting sites for their open, cup-shaped nests which are normally placed 90–160 cm above the ground in dense protea bushes (Burger *et al* 1976). Only the female builds, depositing grass and small dead twigs, and then pressing and moulding them with her body into the required shape. The nest lining invariably consists of a thick layer of protea seed pappi or fluff. The usual clutch is 2, and the eggs vary from light buff to reddish-brown, covered with blotches of dark purple or fine brown spots and lines. Only the female incubates, and the eggs hatch on the 17th day after incubation began.

The young are at first sparsely covered with long, thin, grey down. The female frequently covers them during the day, as well as by night, for the first 6 days. Both parents feed the young, but the female does the bigger share; some nectar is brought, but chiefly insects and spiders. Faeces are removed to a particular bush at the boundary of the territory. The young leave the nest after 18–20 days, but receive parental attention for about 3 weeks more. The attitude of the parents to the young then becomes



Cape Sugarbird *Promerops cafer*. (*C.E.T.K.*).

aggressive; but it sometimes happens that the female has started to incubate the second clutch while the young of the first brood are still dependent. Sugarbirds are normally double-brooded, and male and female remain paired for the whole of the breeding season. W.R.S.

Broekhuysen, G.J. 1959. The biology of the Cape Sugarbird *Promerops cafer* (L.). Ostrich supp. no. 3: 180–221.

Burger, A.E., Siegfried, W.R. & Frost, P.G.H. 1976. Nest-site selection in the Cape sugarbird. Zoologica Africana 11: 127–158.

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Skead, C.J. 1967. The Sunbirds of Southern Africa, also the Sugarbirds, the White-eyes, and the Spotted Creeper. Cape Town.

SUGARBIRD (2): used, especially by aviculturists, as substantive name for species of Thraupinae in the genera *Dacnis*, *Chlorophanes* and *Cyanerpes* (see HONEYCREEPER) and for *Coereba flaveola* (see BANANAQUIT).

SULIDAE: see under PELECANIFORMES; GANNET.

SUNANGEL: substantive name of *Heliangelus* spp. (see HUMMINGBIRD).

SUN BATHING: see COMFORT BEHAVIOUR.

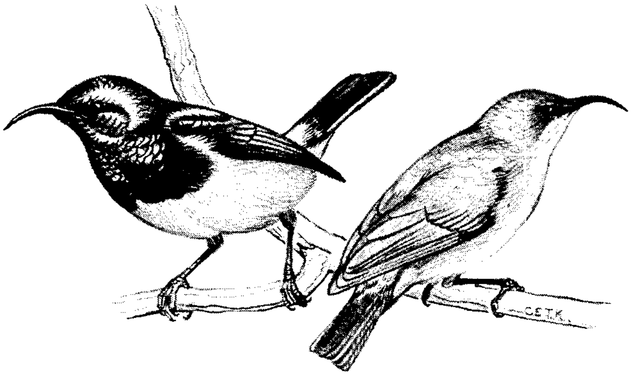
SUNBEAM: substantive name of *Aglaeactis* spp. (for family see HUMMINGBIRD).

SUNBIRD: substantive name of most species of Nectariniidae (Passeriformes, suborder Oscines); in the plural, general term for the family. A few species in south-east Asia are called 'spider-hunters'. For well over a hundred years, the name sunbird has been applied to this family of brightly plumaged little birds of the Old World tropics and adjacent parts of the Middle East and the Indian subcontinent. The family was the subject of a beautifully illustrated monograph by Shelley in 1876–1880. The African species were revised by P.L. Sclater and the whole family by Delacour in 1944. Delacour's revision reduced the number of full species to 106 and the genera to only 5; *Cinnyris* was lumped with *Nectarinia*. In the latest authoritative classification of the family, A.L. Rand (1967) followed Delacour's generic groupings, but resurrected *Hypogramma* and referred *Neodrepanis* (the false sunbirds, see ASITY) to the Philepittidae.

Characteristics. Except for the spider-hunters (*Arachnothera*), sunbirds are a well-characterized, uniform group of passerine birds. They are small (*c.* 16 cm) to very small (*c.* 8 cm) passerine birds, most of which weigh less than 20 g and have long, thin, curved bills. Fine serrations are present on the bills of most genera, probably to enhance capture and holding of the hard-bodied insects; the nostrils are oval, placed in a groove and covered with an operculum; the tongue is tubular in its anterior two-thirds and split near the end; rictal bristles are absent. The tarsus is strong and scutellate; the toes are short and stout with sharp nails. The rounded wing has 10 primaries. The tail is square, rounded or graduated; the 2 central rectrices are narrow and lengthened in males of some species. The plumages of males are usually bright, iridescent and sometimes velvety, but plumages of females are usually dull without metallic lustre. In a few species, both sexes are dull plumaged. The structural basis of iridescence in sunbird feathers still awaits study.

Generic limits and species groupings are based on differences in bill morphology, tail length and shape, and texture and patterns of male plumage. For example, those species placed in *Anthreptes* have shorter, less curved bills than those placed in *Nectarinia*. The presence or absence of coloured pectoral tufts seems to have little value as a taxonomic criterion. Delacour emphasized female rather than male plumage characters. Spider-hunters are quite distinct from other sunbirds; they lack bright plumage colours and have larger and stronger, decurved bills. Their nests are cup-shaped, not hanging domed structures, and they sew leafy nest material together with cobwebs. Both male and female spider-hunters incubate, unlike any other sunbird.

Sunbirds have long been allied with FLOWERPECKERS (Dicaeidae) which they strongly resemble in morphology, habits and nest structure. Conversely, sunbirds are not closely related to other Old World nectar-feeding birds like the Australian honeyeaters (Meliphagidae) or white-eyes (Zosteropidae). The sugarbirds (*Promerops*) of South Africa, false sunbirds (*Neodrepanis*) of Madagascar, and Fire-tailed Myzornis *Myzornis pyrrhoura* of the Himalayas are all convergent forms derived from other passerine families. C.G. Sibley's biochemical data suggest that sunbirds may be related to ploceine weavers.



Variable Sunbird *Nectarinia venusta*, male (left) and female. (*C.E.T.K.*).

Habitat. Sunbirds inhabit most habitats including primeval and second growth lowland forest, clearings, parklands, thorn scrub, gardens and the moorlands on the highest mountains in Africa. In general, and particularly in Africa, the brilliant species are found in the more open habitats, while the plain-coloured species inhabit shady, heavy forest. Some species are canopy dwellers, others live primarily in the lower strata of forests. The habits of many African species are described in detail by Bannerman (1948) and Skead (1967).

Distribution. Currently 116 species of sunbirds are recognized. Most occur in Africa and its islands, including Madagascar, but other species are distributed through the Middle East, India, Sri Lanka and Burma to Malaysia, the East Indies, New Guinea and Australia. One species related to the African forms is found in Israel and Palestine; 4 species occur in Arabia, and one of the many Indian species is found in Baluchistan. The genus *Aethopyga* is confined to India and south-east Asia while members of the genus *Arachnothera* are found primarily in Malaysia. A few sunbirds coexist with small, sunbird-like honeyeaters (*Myzomela*, Meliphagidae) in New Guinea and the Bismarck Archipelago. The largest species in the Ethiopian region is the Sao Thomé Giant Sunbird *Nectarinia thomensis*, restricted to the island of Sao Thomé in the Gulf of Guinea; males measure 22 cm in length and with their strongly graduated tails resemble little WOODHOOPOES (Phoeniculidae). Other large species are found in the mountains of East Africa, where more than 25 species are found in a limited geographical region. Three medium sized *Nectarinia* species of West Africa are also renowned for their spectacular colours, the Superb Sunbird *N. superbus*, the Splendid Sunbird *N. coccinigaster*, and Madame Verreaux's Sunbird *N. johannae*.

Movements. The Pygmy Long-tailed Sunbird *Anthreptes platura* moves south from the Sudanese arid belt to the Uelle district of Zaire in December to breed. Its 3½ month stay in Zaire is timed to the flush of flowering by savanna trees and bushes. Regular altitudinal movements in relation to flower availability also occur in East Africa in such species as the Golden-winged Sunbird *N. reichenowi* and the Red-chested Sunbird *N. erythrocerca*.

Food. Sunbirds feed on insects and nectar, the relative importance of which varies among the different species. Small, short-billed species search actively for insects in the foliage and crevices and feed opportunistically at a wide variety of flowers, including many small, insect-pollinated flowers with minute nectar volumes. Large, long-billed species are more dependent on the nectar in long corollas of large, conspicuous, red or orange flowers, which in turn may depend on the sunbirds for pollination. Short-billed sunbirds often pierce the base of long flowers with otherwise inaccessible nectar. Typical sunbird flowers in Africa include species of *Erythrina*, *Spathodia*, *Symphonia*, *Loranthus*, *Aloe*, *Leonotis*, *Kniphofia*, *Strelitzia*, *Lobelia*, *Protea*, *Tecomaria*, *Halleria*, *Burchellia* and *Schotia*. Flower choice is affected by details of fit between a species' bill and floral corollas, which determine the potential rate of nectar uptake. Sunbirds normally perch while feeding at such flowers; they rarely hover like hummingbirds.

Behaviour. Non-breeding sunbirds often defend feeding territories centred on favoured flowers; these are defended against sunbirds of all species. Territory size appears defined by an individual's or pair's energy requirements. Such aggressive activity is determined in some cases by economic considerations based on the intensity of competition for nectar (Gill and Wolf 1979). The effectiveness of territorial defence depends on the dominance relations of different sized species.

Although many sunbirds may aggregate at suitable flowers, they rarely if ever form cohesive flocks. Some species, especially *Anthreptes*, may join mixed species parties. Many species are highly nomadic and wander great distances in search of nectar; it is not unusual to hear individuals flying high overhead from one horizon to another.

Voice. Sunbirds have sharp metallic voices. Many species have loud, high-pitched, fast-paced, tinkling songs. Accompanying Skead's monograph on South African sunbirds is a record of their vocalizations. Vocal dialects have been described for the Splendid Sunbird by Grimes (1974).

Breeding. Breeding seasons relate to rainfall patterns and especially to peaks of flower and insect availability. Subordinate species in East Africa may breed opportunistically when possible in the absence of dominants that would usurp energy supplies. Some species may breed at almost any time of the year. Pairs are often double-brooded and may raise as many as 5 broods in succession. The asynchronous prolonged nature of breeding often produces, in local populations, a mixture of individuals of many different ages and stages of moult. In contrast to the promiscuous mating systems of hummingbirds, sunbirds typically form monogamous pair bonds; no examples even of polygamy have been documented. Male sunbirds feed the young, but do not help with incubation or nest building. The male often accompanies the female on trips to gather nesting material, but this is interpreted as defence against cuckoldry, since the male merely consorts but does not help (Wolf and Wolf 1976). The males defend flowers from which their mates obtain nectar; breeding male sunbirds have a reputation for being extremely pugnacious. The courtship displays of some species are described by Skead. Vent pecking following copulation is common.

All sunbirds build a covered or oval nest which is suspended from a bough or leaf of a tree, less often from a bush. It is usually an elaborate structure decorated or held together by cobwebs, and often has a porch-like projection above the lateral entrance. In many nests the outside has a ragged appearance and in some, a tail of loose building material is suspended. The eggs are normally 2 in number, more rarely 3; they are spotted or blotched, or streaked longitudinally on a ground which is usually white or pale bluish-white. A close association between several species of nesting sunbirds and aculeate Hymenoptera has been noted. Incubation lasts 13–15 days in South African sunbirds; the nestling period lasts from 14–19 days. Several of the African species are parasitized by cuckoos.

Moult. Males of some sunbird species moult into a dull-coloured plumage resembling that of females after breeding. These off-season plumages have been called eclipse plumages and compared to the dull post-breeding plumages of ducks. The details of plumage sequences in sunbirds still require study; the presence of eclipse plumages varies among closely related species and even among populations of the same species. Presumably, the costs of moult are off-set by advantages of camouflage and social interactions in some situations but not others.

F.B.G.

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Delacour, J. 1944. A revision of the family Nectariniidae (Sunbirds). Zoologica 29: 17–38.

Gill, F.B. & Wolf, L.L. 1979. Nectar loss by Golden-winged Sunbirds to competitors. Auk: 96: 448–461.

Grimes, Ll.G. 1974. Dialects and geographical variation in the song of the Splendid Sunbird *Nectarinia coccinigaster*. Ibis 116: 314–329.

Rand, A.L. 1967. Family Nectariniidae. *In* Paynter, R.A. Jr. (ed.) Checklist of Birds of the World, vol. 12. Worcester, Mass.

Shelley, G.E. 1876–80. A Monograph of the Nectariniidae or Family of Sunbirds. London.

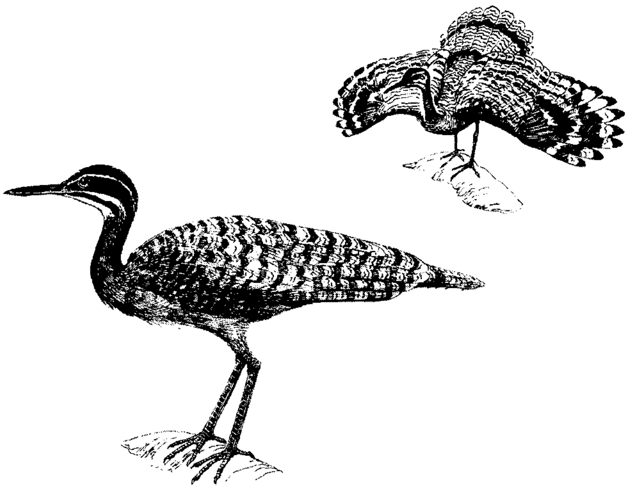
Skead, C.J. 1967. The Sunbirds of Southern Africa, also the Sugarbirds, the White-eyes and the Spotted Creeper. Cape Town.

Wolf, L.L. & Wolf, J.S. 1976. Mating system and reproductive biology of Malachite Sunbirds. Condor 78: 27–39.

SUNBIRD, FALSE: name sometimes applied to *Neodrepanis* spp. (see ASITY).

SUNBITTERN: *Eurypyga helias*, sole member of the family Eurypygidae (Gruiformes, suborder Eurypygae).

Characteristics and distribution. It is found in the forested regions of America from southern Mexico to Bolivia and central Brazil and is represented by three races. About 46 cm long, this graceful, stout-bodied, long-necked, long-legged, largely ambulatory bird is most intricately barred, spotted, and mottled. The sexes are alike. The head is almost black, with a narrow white superciliary stripe and a broader white stripe along the lower edge of each cheek. The neck, shoulders, and breast are brown. The throat, abdomen, and under tail coverts are white and pale buff. The remaining plumage is largely grey and olive in general tone, with prominent black bars and white spots; and the long tail is crossed by two broad black bands. Only when the Sunbittern spreads its wings does it reveal its brightest colour, a large round shield of deep orange-chestnut set in an area of pale orange-buff in the middle of each wing, like a sun darkly glowing in a sunset-tinted sky. The upper mandible of the long, straight bill is largely black and the lower is orange. The eyes are deep red, and the long, naked legs are bright orange.



Sunbittern *Eurypyga helias*. (*C.J.F.C.*).

Habitat. Singly or in pairs, Sunbitterns forage along watercourses that traverse the forests, up to an altitude of 1,000 m (rarely 1,800 m in northern Venezuela). With slow, sedate steps, they walk along the muddy shores of sluggish streams and over the exposed rocks in rushing mountain torrents, where they fly across the deeper pools but wade through shallow water. They also frequent swampy areas in woodland.

Food. Their food, which consists largely of insects, spiders, small crustacea, minnows and the like, is caught beneath shallow water or gathered from exposed mud and rocks, with heronlike jabs.

Voices. Generally silent, the Sunbittern is reported to utter soft, long-drawn whistles, low trills, plaintive pipings, and a loud, ringing *ko wáy*.

Behaviour. From the nature of their habitat, it seems that Sunbitterns must pass most of their lives in the shade, but they are said to seek sunny openings in the forest, where they sometimes display. Widely spreading their wings with the richly coloured upper surface tilted forward, they fan out the raised tail to fill the gap between them, thereby forming a semicircle of plumage, in the midst of which the head stands.

Breeding. Although there are reports of Sunbitterns breeding on the ground, usually the nest is built in a tree or bush. One beside a Costa Rican mountain stream was precariously saddled upon a 5 cm branch about 6 m above the ground. The dark, roughly globular structure, about 30 cm in diameter, was composed of decaying leaves and stems, some green moss, and apparently also mud. In the top of the bulky mass was a shallow depression lined with green leaves, on which 2 eggs rested, apparently the usual number. The nearly oval eggs are buffy or clay-coloured, with darker spots and blotches. The most complete available account of the nesting of this bird is that of a pair who bred in the Gardens of the Zoological Society of London more than a century ago. Both sexes built the nest of vegetable materials and mud, and they alternately incubated an egg which hatched after 27 days. The newly hatched young was thickly covered with short down and resembled the chicks of plovers (Charadriidae) and snipe (Scolopacidae). Fed by both parents with food carried in the bill, it remained in the nest until, at the age of 21 days, its wing feathers had expanded and it could fly to the ground. It is remarkable that, although the young Sunbittern resembled a precocial chick, it was attended like an altricial nestling; but it is not known whether the behaviour of this captive pair was typical. A.F.S.

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SUN COMPASS: see ORIENTATION.

SUNGEM: *Heliactin cornuta* (for family see HUMMINGBIRD).

SUNGREBE: see FINFOOT.

SUNNING: behaviour by which a bird deliberately positions itself in the sun, often adopting a special posture. The synonym 'sun-bathing' is also widely used but the term 'bathing' is better restricted to true bathing in water; see COMFORT BEHAVIOUR. There are two types of sunning: (1) sun-basking and (2) sun-exposure, each being basically a reaction to the sun as a precisely identified source of heat.

Sun-basking. Unlike sun-exposure (see below), this is mainly a form of thermoregulatory behaviour together with other forms of heat-basking such as SMOKE-BATHING, the sunning bird absorbing heat from the sun and hence reducing the metabolic expenditure needed to maintain its optimum body temperature—especially in cool or cold conditions. Often overlooked by ornithologists, particularly in the smaller species, such simple and casual sunning is widespread among birds. It may occur during loafing and preening spells at any time of the year (in temperate areas, especially in spring, autumn, and winter) and at any time of the day (in tropical areas, especially early and late—particularly if the nights are cold). Use is often made of sheltered 'sun-traps', that also provide background reflected heat, or of other sunny places out of the wind. During the heat of the day, however, the birds often seek cool shade if possible unless they deliberately perform sun-exposure behaviour. It seems likely that sun-basking is the more primitive type of sunning from which sun-exposure behaviour developed; though quite distinct in its basic function, sun-basking could share other functions with sun-exposure.

Sun-exposure. At times, birds deliberately position themselves in the full heat of the sun when heat absorption is evidently not the main purpose of the behaviour. Passerines and other landbirds especially often frequent favourite 'hot-spots', typically on the bare ground and usually near cover into which they retreat if they become overheated or danger threatens; the temperature at such sunning sites can be many degrees higher than the air temperature. This form of sunning is widespread and is the one most often seen. In temperate areas, it occurs mainly when the sun is high in the hemisphere and mainly during those hours of the day when the sun is also high in the sky and at its hottest. Early and late in the day, and on cooler days with fitful sun, the birds may show low-intensity sun-exposure or a combination of sun-basking and sun-exposure behaviour, or fluctuate between the two. The basic function of sun-exposure would seem to lie in the realm of feather maintenance (see COMFORT BEHAVIOUR), especially with the effects of the sun's heat on the feathers—principally the wings and perhaps also the tail, the areas that sunning birds display most to the sun. The maintenance of the good condition of the remiges in particular could well be a major function of sun-exposure behaviour in birds generally. In griffon vultures *Gyps*, for example, it has been demonstrated experimentally that sun-exposure rapidly restores the flight-feathers to their original shape after they have become deformed by the stresses of flight, and this could well apply to other birds too, especially large species that soar or flap for long periods. Like sun-basking, sun-exposure helps to dry the plumage at times. It has also been suggested that sunning increases the flow of preen-oil and causes ectoparasites to become more active or to disperse from those areas of the plumage that are inaccessible or difficult to reach with the bill; both the preening directed to feathers near the neck and wings, and the frequent head-scratching that accompanies or follows the sunning, could well be components in a functional chain of feather-maintenance activities, though it is possible that such behaviour is merely an incidental response to irritation caused by the sun on the skin or by the displacement of feathers. It has been further suggested that the effect of the sun's non-thermal rays (particularly in the ultra-violet range) on the plumage or skin is beneficial, either directly in some way or indirectly by acting upon the organic lipids (preen-oil, etc.) for the synthesis of Vitamin-D or other purposes. Finally, attempts have been made to establish a functional correlation between sunning and moulting; although sunning birds are sometimes in moult, and the beneficial effects of sun-exposure could well be of relevance to that state, the correlation may well be merely seasonally coincidental, as in the case of ANTING and moulting, while speculation that sunning and anting are complementary 'comfort-motivated' activities that soothe the skin during feather replacement seems particularly ill-founded.

Yellow-crowned Night Heron *Nycticorax violaceus* female sunning on rocky shore, Galapagos. (*Photo: N. van Swelm*).

Sunning postures. When sun-basking, the bird may orientate itself at any angle to but often facing the sun. Though it may show no special behaviour otherwise, it often fluffs the feathers of head and body—at times, while trying to reduce heat loss by keeping the wings and legs covered by the plumage; or it will squat or sit down with feathers slightly erected and both wings drooped close to its sides so that the back is exposed, this simple 'wings-down' sunning posture being found in many birds, both passerine and non-passerine. Some species that sun-bask, e.g. the Greater Roadrunner *Geococcyx californianus* and certain grebes (Podicipedidae), have associated areas of black-based feathers or black-pigmented skin that facilitate the absorption of the solar energy when exposed. During the early morning hours, and intermittently during the day in cool clear weather, the roadrunner (a desert bird subject to low night temperatures) sun-basks with slightly drooped wings held away from the body and the mid-dorsal feathers erected, its back orientated perpendicularly to the sun; it does not sun itself when the ambient temperature is in or above its zone of thermoneutrality—unlike species that show deliberate sun-exposure behaviour. The grebes that sun-bask do so on the water, back to the sun, with the closed wings lifted and the feathers of the lower back and flanks erected.

The wings-down and other simple sunning postures are also shown at times by birds that are sun-exposing. Most sun-exposure postures are more elaborate however, typically involving the extension of one or both wings (exposing their dorsal or ventral surfaces), the spreading of the tail, and the erection of the head, neck, and body feathers, often exposing the

Blackbird *Turdus merula* female sunning. (*Photo: R.J. Chandler*).

oil-gland; they may be accompanied by gaping and panting or gular-fluttering. The postures of most passerines are of two distinct types: a 'lateral' one, in which the sunning bird squats or sits down, usually on the ground, and leans to one side away from the sun with the flank exposed or with the 'sun-wing' lowered and partly unfolded and the fanned tail brought round to the same side; and a 'spread-eagled' one—most often adopted when the sun is near or at its zenith—in which it squats or lies flat with both wings right open and extended outwards and the tail fanned. In a few species, including the Dunnock *Prunella modularis* and presumably other accentors (Prunellidae), the spread-eagle posture is replaced by a 'raised-wing' one, the bird leaning over with the sun-wing partly open and lifted more or less vertically. A fuller raised-wing posture is used by pigeons (Columbidae) both for sunning and rain-bathing (see COMFORT BEHAVIOUR). A number of large non-passerines—including pelicans (Pelecanidae), cormorants (Phalacrocoracidae), darters (Anhingidae), storks (Ciconiidae), herons (Ardeidae), New World vultures (Cathartidae), and the hawks and allies (Accipitridae, including the Old World vultures *Gyps*, etc.)—adopt more elaborate 'spread-wing' postures for sunning (of both types) and other purposes, including wing-drying: a shield-like 'delta-wing' position, with wings half open and primary tips crossed under the tail, and a 'full-spread' one, with wings stretched open at right angles to the body. When sun-exposing thus, the bird typically faces the sun so that the undersurfaces of the wings are exhibited. Among tropical seabirds, frigatebirds *Fregata* also adopt full-spread sun-exposure postures facing the sun with the wings twisted 'inside-out', boobies *Sula* a delta-wing one with back turned to the sun so that the uppersurfaces of the wings are shown, and noddies *Anous* a lateral one side-on to the sun.

Birds engaging in sun-exposure behaviour often stare at the sun. They clearly suffer from heat stress at times and some features of their postures—feather ruffling, exposure of the oil-gland, gaping, panting—are obviously, in part at least, superimposed thermoregulatory components facilitating the loss of excess heat. Finally, birds suffering from extreme heat stress when they cannot get out of the sun use sunning-like spread-wings postures at times both for heat-dumping and to shield the young. K.E.L.S.

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(For further references see ANTING; COMFORT BEHAVIOUR; SMOKE-BATHING).

SUPERCILIARY: term applied to a marking, in some plumage patterns, above the eye.

SUPERFAMILY: see under FAMILY; NOMENCLATURE; TAXON.

SUPERORDER: see under CLASS; TAXON.

SUPERSPECIES: a grouping of species, of lesser rank than a subgenus and having no nomenclatural status; the term was introduced by E. Mayr and defined as a 'monophyletic group of very closely related and largely or entirely allopatric species'. It is implied that the included species are geographical representatives of a common stock, but have at least probably attained true reproductive isolation and are not merely subspecies of a single polytypic species. 'Artenkreis' is a partly equivalent term. A 'species group' (in one sense of the term) differs in that the included species may be less closely related and often sympatric (see SPECIES GROUP (2)).

SUPPLEMENTARY PLUMAGE; see PLUMAGE.

SUPRAOCCIPITAL: a paired bone of the SKULL.

SUPRASPECIFIC: general term applied to taxa higher than the species (see TAXON).

SURANGULAR: a paired bone of the lower jaw (see SKULL).

SURFBIRD: *Aphriza virgata* (see SANDPIPER).

SUTHORA: former generic name sometimes used, in the plural, as a general term for the Paradoxornithinae (see PARROTBILL).

SWALLOW: substantive name of most species of Hirundinidae (Passeriformes, suborder Oscines). The long-tailed species are often termed swallows and their shorter-tailed relatives called martins but the division is inconsistent and taxonomically unsound. In many aspects of morphology, habits, and their insect diet taken on the wing, they are convergent with the swifts (Apodidae).

Characteristics. Swallows are usually rather small, typically weighing 20 g and measuring *c.* 15 cm (plus tail streamers) but ranging overall from 12–23 cm. The family is characterized by having more or less complete bronchial rings. Half-rings are found amongst other Oscine families and anomalously in one hirundine genus, the river martins *Pseudochelidon*. The plumage is commonly dark blue or green and glossy above, paler below and sometimes streaked. In several species there is a conspicuous pale rump. The first year plumage may be brownish and readily distinguishable from the adults (e.g. Tree Swallow *Tachycineta bicolor*). The bill is short and compressed, with a wide gape. The compact streamlined body, long narrow wings and the tail, usually forked and often bearing streamers, confer highly efficient flying, gliding and turning capabilities. The outermost of 9 primaries is much reduced. Serrations on the outer primaries are present in 2 rather dissimilar genera, *Psalidoprocne* and *Stelgidopteryx*, the rough-winged swallows. The tarsi are short and with the feet are sometimes feathered (e.g. House Martin *Delichon urbica*). The feet are not powerful but strong claws characterize burrowing and cliff-dwelling species. The sexes are usually similar, in some cases distinguishable by the length of the tail streamers (longer in males) or other features, but often only in the hand during breeding by brood-patch size. There is a single post-nuptial moult: for North Temperate species this is suspended and mainly or wholly occurs in winter quarters. There are 74 recognized species, currently split into 17 genera. The largest genus is *Hirundo* containing the Common or Barn Swallow *Hirundo rustica*, one of the most widely distributed of all bird species. Intergeneric hybridization is comparatively frequent (e.g. Common Swallow × House Martin) and serves to emphasize the taxonomic uniformity of the family.

Habitat. Swallows are usually found in open country often near fresh-water. Riversides, lakes, marshes, cliffs, savanna and forest edge are typical habitats, whereas closed-canopy forest, barren lands and marine environments tend to be avoided. Extremes of latitude and oceanic islands have few or no swallows although altitudes in excess of 3,000 m are exploited by feeding hirundines in more favourable environments. In the breeding season segregation by habitat often follows from nest-site specialization. Thus in areas relatively free from the influence of man, the House Martin, for example, selects rocky cliffs for nest building whereas the Sand Martin or Bank Swallow *Riparia riparia* excavates its nests in sandy banks. But the widespread habit of swallows nesting on buildings or within excavations in association with man often provides a variety of nest sites in one place, and sympatry is then common. Hybridization occurs most frequently under these conditions (e.g. Common Swallow × Cave Swallow *Petrochelidon pyrrhonota*).

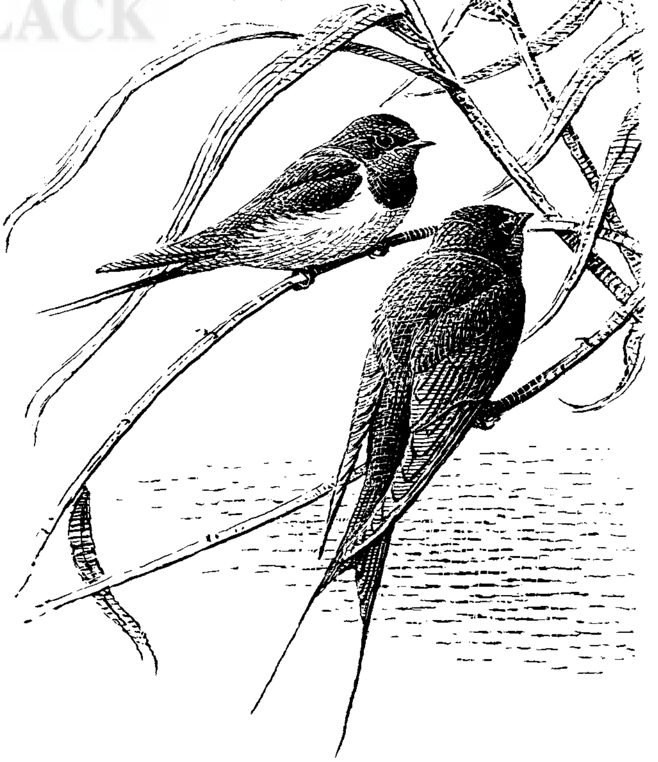
Distribution. The genus *Hirundo* is truly cosmopolitan, being found in all the zoogeographical regions of the world except Antarctica. *Petrochelidon* and *Riparia* are also widely distributed but others are restricted to the Old World (e.g. *Delichon*, *Psalidoprocne*) or to the New World (e.g. *Progne*, *Tachycineta*). The White-eyed River Martin *Pseudochelidon sirintarae* is a recent addition to the world avifaunal list being discovered in 1968 wintering in Thailand. Elsewhere the distinctive hirundine genus of *Pseudochelidon* occurs only in central Africa. The Afrotropical region holds the most varied fauna, supporting nearly 50% of hirundine species at some stage of their annual cycle.

Movements. Conspicuous migratory behaviour characterizes temperate representatives, whereas tropical species are more often sedentary. The Common Swallow is a widely recognized harbinger of the North Temperate summer, albeit, with a caveat: Aristotle, 'One swallow does not make a spring' (elsewhere 'summer'), related to the unpredictability of spring weather (Aristotle, Nicomachean Ethics, Book 1). Northbound movements of swallows are nevertheless closely linked to the northward shift of warm weather itself encouraging the emergence of insect food. Occasionally, unseasonal weather causes widespread mortality in early spring and late autumn amongst early arrivals and late departures. In winter quarters, which are either in tropical regions or exploiting the Southern Hemisphere summer (conversely Southern Hemisphere breeders move northwards to the tropics) catastrophic mortality can occur (e.g. amongst Common Swallows and House Martins). The migratory patterns of the Common Swallow are amongst the best known of all birds. Populations from the Western Palearctic mostly move south of the Equator in winter and discrete breeding populations show a greater or lesser attachment to specific wintering sites. Although some tropical species are believed to be sedentary (e.g. some African *Psalidoprocne* species) many migrate in response to the rains.

Food. Swallows specialize on day-flying insects taken while in sustained flight but will take grit and occasionally food from the ground and elsewhere. Wind-drifted spiders (Araneae) and lepidopteran larvae suspended from leaves do appear in the diet but prey are otherwise winged and mainly Diptera, Hymenoptera, Hemiptera and Coleoptera. Diptera tend to predominate at high latitudes whereas Hymenoptera are most frequent in tropical environments: a trend probably related to differences in insect availability. Fruit is sometimes taken by one species, the Tree Swallow of North America. There is evidence of insect size and taxon specialization for both tropical and temperate species. The height, proximity to both vegetation and nest sites and the manner of feeding correspond to the distribution of preferred prey: specialists on small items for example tend to feed higher, less vigorously and further from the nest. Amongst European hirundines at least, those with stouter bills take larger insect prey. Colonial breeding species often form feeding flocks but even solitary breeders will feed communally outside the breeding season.

Physiology. Swallows share with swifts a striking energetic economy in flight. During sustained flight the House Martin, for example, expends less than half the energy of other passerines under comparable circumstances: flight costs are often reduced by frequent gliding. Torpidity has been reported for the White-backed Swallow *Cheramoeca leucosternum* and evidently characterizes the massed huddling groups which occur under exceptionally severe conditions (e.g. Common Swallow, House Martin). The degree of hypothermia is generally slight however (30–35°C) and cannot be compared with the nightjars, hummingbirds or swifts (see TORPIDITY); in the wild it commonly precedes death in both adults and mature nestlings, even though recovery is possible if food and warmth are restored. Heat stress, mainly sustained in tropical or sub-tropical environments, may lead to leg exposure during flight to encourage heat dissipation. Diurnal migration, allowing periodic feeding, leads to comparatively undramatic fat deposition, compared

Swallow *Hirundo rustica*. (*D.W.*).



with nocturnal migrants, prior to the birds' conspicuous migratory departures.

Behaviour. Monogamy is typical and, although polygamy has been recorded, it is rare. Male Sand Martins and perhaps other species pursue a mixed reproductive strategy; holding a single female and competing for supplementary matings with other females. Kin altruism is widely reported for Common Swallows and House Martins, evidenced by young birds from the first brood feeding the second brood. Hirundines are commonly gregarious when feeding, collecting nest material, breeding, roosting and to a lesser extent on migration: gatherings in excess of a million birds have been reported away from breeding areas. Whether the function of aggregations is mainly protection from predators, enhances foraging efficiency or serves some other primary purpose is not established. Solitary breeding species hold conventional territories around the nest-site but may share feeding areas. In colonial species the territory comprises the nest interior, exit hole and approach route alone with no exclusive feeding areas. Dense flocks can form to mob aerial or, less commonly, ground predators. When roosting away from the nest site, emergent vegetation, buildings, vacant nests, telegraph wires and trees are favoured. Although all species are diurnal, some may stay aloft at night in the manner of SWIFTS (Rheinwald 1975).

Voice. Song is often poorly developed but may be a more or less melodious chirping or twittering, uttered in flight or from a perch or nest. Alarm calls are usually given at the approach of predators or when the nest is threatened and are typically brief and emphatic.

Breeding. Three nest types can be distinguished: (i) 'natural' holes (with or without additional mud around exit), (ii) excavated burrows and (iii) mud nests. 'Natural' holes may be in trees, caves on cliffs or buildings, or be vacated woodpecker or kingfisher excavations. Burrows are in soft ground, ancestrally in river banks and the like but now frequently in sand quarries. Mud constructions range from a simple bracket cup to an enclosed chamber with entrance passage. They are placed on trees, cliffs and typically nowadays on buildings, invariably sheltered from rain. The thixotropic properties of mud (i.e. liquifies under pressure) are exploited by swallows which agitate the moist material and thereby establish a secure bond between the numerous mud pellets used in nest construction. Evolutionary grouping on the basis of nest type has been proposed by Mayr and Bond (1943): natural holes characterizing the primitive, generally solitary, species, burrows being intermediate, while mud nests typify the most advanced, usually gregarious species. Patterns of nest dispersion range from generally solitary, through loosely colonial to massive dense coloniality. Loose coloniality, such as can often be found in Common Swallows, appears to result from limited nest sites. Sand Martins however will form dense colonies, at times with more than 1,000 pairs, even if suitable sites are abundant. The degree of coloniality in hirundines appears to be linked to the type and predictability of the food supply; mainly colonial species exploit unpredictable insect supplies.

Clutch sizes range from 1–8 eggs with 4–5 most common in temperate regions and 3 in the tropics. Single, double and occasionally triple broods are attempted. Incubation, lasting 12–16 days, is frequently by the female alone. Generally in social species both male and female incubate with the latter taking the greatest share. The nidicolous young spend 15–30 days (and longer if severely undernourished) in the nest and lose weight in the latter stages. The recession involves at fledging a loss of 15–27% of the peak weight, itself greater than the adult weight, mainly brought about by desiccation of the integument. An allied feature is the nestling's fat store. Carcass analyses have revealed lipid indices (lipid/lean dry weight) of 0.4–1.0 compared with 0.1–0.5 for a typical passerine nestling at the same stage: this is established as an insurance against food scarcity and to sustain fledglings while they learn to forage. Parental feeding continues for several days after fledglings leave the nest.

See photos AGGRESSION; ECTOPARASITE; FEEDING HABITS; FLIGHT; PARENTAL CARE. D.M.B.

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SWALLOW-SHRIKE: see WOOD-SWALLOW.

SWALLOWTAIL: *Eupetomena macroura* (for family see HUMMINGBIRD).

SWALLOW-TANAGER: *Tersina viridis*, a bird of uncertain systematic position, now placed in the tanager family (Thraupidae; Passeriformes, suborder Oscines).

Characteristics, habitat and distribution. The Swallow-tanager, a bird about 15 cm long, bears some resemblance to the tanagers (Thraupinae) but—in addition to having a very peculiar palate—differs in being longer-winged and short-legged, as well as in having a wide flattened bill slightly hooked at the tip; in its nesting habits, also, it stands apart from the tanagers. The male is mainly a brilliant turquoise blue, with a black face and throat, and black bars on the flanks; the female is green above and yellowish below with green barring. The Swallow-tanager is found in northern parts of South America up to Panama, and in Trinidad. The birds are migratory, at least in parts of the range; they breed in the mountains, where they prefer wooded country with clearings, and spend the non-breeding season in the humid lowlands.

Food. The Swallow-tanager is both an insect-eater and a fruit-eater. Insects are captured on the wing, a method of feeding which gives the bird its name; fruit is taken from a perched position. The method of eating fruit is peculiar: the bird holds the whole fruit in the widely opened bill and turns it about until all the pulp is scraped off. The seed is not swallowed, as it is by many frugivorous birds, but is dropped after the flesh has been eaten off it. Relatively large masses of fruit are swallowed and held in a distensible throat-sack.

Behaviour and voice. The Swallow-tanager's calls are varied but unmusical: the song of the male is poorly developed. During the breeding season territories are held.

Breeding. The nest is built at the end of a horizontal burrow in a bank or in an artificial hole in a wall or similar structure. Holes in earth banks, the natural site, may be excavated by the birds themselves or taken over from other species. The nest is a cup-shaped structure made of a variety of materials such as rootlets, grasses, and vegetable fibres. The eggs, usually 3 in number, are glossy white. Incubation is by the female alone; but the male takes a part, smaller than that of the female, in feeding the young. Outside the breeding season Swallow-tanagers are highly social, forming flocks that—unlike those of most other tropical passerine birds—never associate with other species. D.W.S. (1)

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SWALLOW-WING: *Chelidoptera tenebrosa* (see PUFFBIRD).

SWALLOW, WOOD-: see WOOD-SWALLOW.

SWAMPHEN: substantive name used in Australia for *Porphyrio* spp. (see RAIL).

SWAN: substantive name of *Coscoroba coscoroba* and *Cygnus* spp., all in the tribe Anserini (with the 'true geese') of the subfamily Anserinae of the Anatidae (see under DUCK). 'Swan' is of common gender, but 'cob' and 'pen' are sometimes used as special terms for male and female swans and 'cygnet' for the young. See photo FEEDING HABITS.

SWIFT: substantive name (varied to 'SWIFTLET' in some cases) for the species of Apodidae and Hemiprocnidae (Apodiformes, suborder Apodi); in the plural, general term for the suborder. The swifts form a very well defined group of birds with purely superficial resemblances to swallows (Hirundinidae). Swifts are usually united in one order (Apodiformes) with the hummingbirds (Trochilidae), an often debated relationship on which the dust has yet to settle. Both swifts and hummingbirds have an extremely short, thick humerus, a short ulna with short secondary feathers, and a long carpus with 10 primaries; the wing is narrow, with a shallow camber, adapted for high-speed flight. However, while swifts have long wings and are primarily adapted for sailing through the air, hummingbirds have relatively much shorter wings and are specially adapted for hovering; further, in breeding and feeding habits, in coloration, and in form of bill, the two groups are extremely different. Swifts are usually regarded as constituting a suborder, of which the Hemiprocnidae (crested swifts) include only 1 genus of 4 species, and the Apodidae (true swifts) include all the rest.

Characteristics. The Apodidae is best considered as consisting of 3 subfamilies—the Cypseloidinae, Chaeturinae and Apodinae. The Cypseloidinae and Chaeturinae have an anisodactyl foot (3 toes forward and 1 behind); the Cypseloidinae are diastataxic and have soft rectrices and rather weak feet while the Chaeturinae are eutaxic (see WING) and most (not *Collocalia*) have stiffened tail feathers with spiny tips that, along with their strong feet, help the bird support itself against vertical surfaces. The Apodinae, which also lack the stiffened rectrices and spiny tips, are eutaxic, have a reduced number of toe phalanges, and possess a unique form of grasping foot in which toes 1 (hallux) and 2 oppose toes 3 and 4 (as in heterodactyly; see LEG). However in these swifts the grasping motion is lateral inward, not front to back as in most birds, a motion which is highly adapted to holding on to the soft plant materials and feathers which they glue together to make their nests. When not grasping (and in museum specimens), the toes of the Apodinae lie together giving rise to the often repeated misconception that swifts have all 4 toes pointed forward (Pamprodactyly).

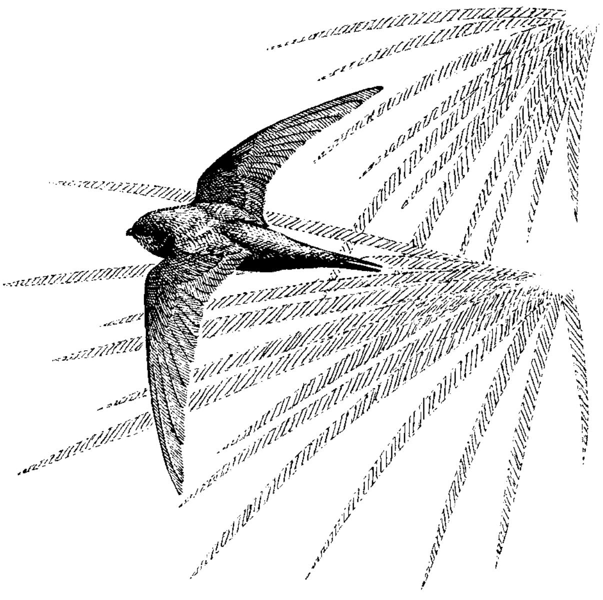
Distribution and characteristics. In all there are some 82 species in 18 genera, spread through Eurasia, Africa, North and South America; none breed in Australasia except in the extreme north. The majority of species are tropical, but a few breed in northern parts of Europe, Asia and North America and overwinter in the tropics or in the southern hemisphere after a transequatorial migration.

Apodidae. The true swifts are the most aerial of all birds, feeding entirely in the air, drinking and bathing by descending to water, and regularly spending the night on the wing (see FLIGHT). They range in size from 10.5 to 25 cm in length with extremes represented by the diminutive Glossy Swiftlet *Collocalia esculenta* (7.5 g) and Pygmy Palm Swift *Tachornis furcata* (weight unknown), and the giant White-naped Swift *Streptoprocne semicollaris* (175 g) and Purple Needletail *Hirundapus celebensis* (180 g). All are predominantly sooty or brown in colour, with some patches of white or pale grey: some species have a marked iridescence which changes colour during feather wear. The legs are extremely short, the strong claws being adapted for clinging. They do not normally settle on the ground or vegetation, although some of them roost on vertical cliffs or more rarely on trees. Contrary to many accounts, swifts can take off from flat ground, although with difficulty.

Swifts are apparently unique in copulating in the air (although also in the nest), and spending the night on the wing. In northern regions they may travel hundreds of kilometres to avoid depressions, returning after these have passed.

Adult survival rates are high, frequently above 80% per year, and life expectancy is very good for such small birds. Swifts have few regular predators but small falcons at times take considerable numbers. All swifts are subject to a variety of endo- and ectoparasites including at least occasionally cestode tapeworms, cimicid bugs, and an array of feather mites (Acarina; Eustathiidae). Swifts commonly host feather lice (Mallophaga) with up to 2 species of *Dennyus* and 1 of *Eureum* being recorded from a host species; these genera of lice are confined to swifts. The most striking ectoparasite of the Common Swift *Apus apus* is the flightless hippoboscid louse-fly *Crataerina*, of which 12 may be found on a single young bird and over 20 on an adult. Although bloodsucking, *Crataerina* seldom causes the death of its host, to whose life cycle its own is beautifully adapted.

Food. Swifts gather all their arthropod food on the wing, usually well above ground; they occasionally glean from a water surface, tree foliage, and under eaves of buildings. Ballooning spiders are taken when available, but insects are the usual food items with the orders Diptera, Hymenoptera, Coleoptera and Homoptera predominating; day to day variability is great.



Palm Swift *Cypsiurus parvus*. (*N.A.*).

Behaviour and voice. The extreme mobility of swifts has hindered study of their social and display behaviour. Although some species appear to be solitary breeders, most are more nearly colonial and can be observed in closely packed, vocal flocks particularly early in the morning or at roosting time dashing past their nesting sites. The vocalizations of the Chaeturinae are a rapidly repeated series of sharp chips, while those of the Apodinae, particularly *Apus*, can best be described as a drawn out buzzy *scree* or scream. Mixed flocks of swifts of several species as well as other birds can be observed where food is abundant or locally concentrated. Resource partitioning seems more a matter of the size, rather than taxonomy, of the food items taken, and of the foraging area typically utilized by each swift species.

Breeding. Most swifts glue their nest-material together with saliva produced by seasonally enlarged salivary glands. The material in many cases is collected in the air. Clutch size varies from 1 in *Cypseloides* to 4–6 in *Aeronautes* and some *Chaetura* spp. The incubation period is rather long for the size of the bird, being 19–20 days in *Apus* and 22–23 in *Cypseloides*. The nestling period is also long, and is unusually variable (from 5–8 weeks, depending on the weather) in *Apus apus*. When feeding young, swifts return to the nest with a food bolus consisting of possibly several hundred food items glued together with saliva and carried in the distended sublingual region of the mouth. Feeding rates vary from one visit every 15–20 minutes to once every few hours or longer.

The Common Swift has several adaptations for an unusually variable food supply, since air-borne insects are plentiful in warm, dry and calm weather, but very scarce in cold, windy, and wet weather. The interval between the eggs, normally 2 days, is lengthened to 3 days if food is short. The parents normally relieve each other in turn on the eggs, but if food is short they leave the eggs unbrooded, these being unusually resistant to cooling. The young can likewise be left unbrooded, and can also withstand several days of starvation by utilizing their fat reserves and retarding their rate of development. Further, feathered young can, if starved, loose their temperature control and become temporarily poikilothermic, while the adults can clump together in a semi-torpid condition, although for how long is not known (see TORPIDITY).

Nest sites for the hole-nesting swifts may be in short supply; inter- and intraspecific competition appearing at times to be severe. Prolonged grasping-grappling fights for a nest site, sometimes lasting for several hours, have been reported for *Apus apus* during the pre-nesting period. Similar contests with other species, particularly Starlings *Sturnus vulgaris*, have been recorded; the Horus Swift *Apus horus* regularly evicts bee-eaters to obtain suitable nesting burrows. Once obtained, nest sites are faithfully reutilized for several years in succession, even in migratory species.

Cypseloidinae. The genera *Cypseloides* and *Streptoprocne* include 12 species only one of which is not confined to the neotropics; *C. niger*

Moustached Crested Swift *Hemiprocne mystacea*. (*N.A.*).

migrates and breeds as far north as Alaska. The mossy nest of these swifts contains little or no salivary glue and is placed on a damp rock surface or ledge close to water, frequently near or behind waterfalls but occasionally on sea cliffs or in caves.

Chaeturinae. The several genera in this group include some 23 species in Asia, Africa, and North and South America, the best known of which is the Chimney Swift *Chaetura pelagica* of eastern North America; under natural conditions nearly all nest inside hollow trees, but several now use chimneys, the bracket shaped nest of twigs being attached to the vertical inner surface. *Collocalia* includes an additional 20 small species of cave swiftlets in south-east Asia and the islands of the Pacific and Indian Oceans (see SWIFTLET).

Apodinae. The genus *Apus* comprises 10 Old World species, most of them in Africa, and includes the Common Swift (or 'Swift' unqualified in Britain) *A. apus*. They usually nest in holes in cliffs or buildings, one species *A. horus* in burrows, and several in old nests of hirundines.

Cypsiurus consists of 2 small African and Asian palm swifts with long forked tails; they build a small open nest on the inner side of a palm leaf, the egg being glued to the nest with saliva (in Africa), and the bird brooding vertically. Of the other 3 small genera, all in the New World, *Aeronautes* nests in holes in cliffs; *Panyptila*, with a long tail-fork, builds a hanging sleeve some 60 cm long under a branch or rock ledge, with a nest chamber near the top and entrance at the bottom; while *Tachornis* places a bag-shaped nest in palm foliage.

Hemiprocnidae. The crested swifts *Hemiprocne* spp. in this small separate family are found in south-eastern Asia and the western Pacific, from India to the Solomon Islands. They do not show such extreme specialization for an aerial habit as the true swifts, are capable of greater manoeuvre, perch freely on trees, and have patches of bright colour and crests. The tiny cup-shaped nest is just large enough to hold the single egg; it is attached to the side of a lateral branch of a tree, the branch taking the weight of the brooding bird which straddles the nest.

See photo CARRYING. (D.L.) C.T.C.

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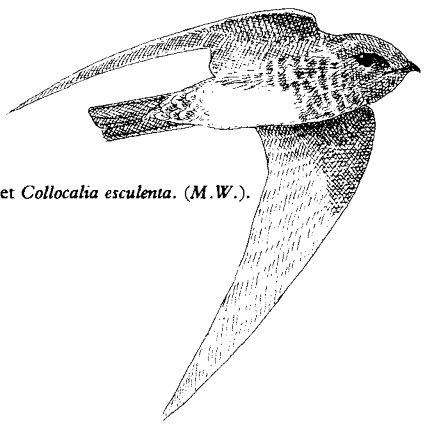
SWIFTLET: substantive name of a group of small swifts (Apodidae) formerly placed in a single genus *Collocalia*, but recently allocated to the tribe Collocaliini and subdivided into 3 genera: *Collocalia* (*sensu stricto*), *Aerodramus* and *Hydrochous* (Brooke 1970; Medway and Pye 1977).

Characteristics and distribution. The tribe contains some 15 species of Old World distribution ranging from islands of the western Indian Ocean (Seychelles) through southern continental Asia, the Philippines and the Indo-Australian Archipelago to northern Australia and the west and southwest Pacific. In body-length they range from *c.* 7.5–13 cm. Their plumage is usually dull blackish brown to glossy black, some species showing a limited area of white or dull grey on the belly and rump. The wings are long and pointed, adapted to aerial feeding, the tail is short and usually square-cut, rarely furcated. Morphological differences, in particular in the medium-sized uniform dull blackish-brown species, are unobtrusive, making identification in the field often impossible. Even in the hand, the differences are minute and for this reason the taxonomy of this group has for a long time been confused. The present classification is based on some minor morphological characters, but primarily on nest type (see EDIBLE NESTS) and the ability to echo-locate (see ECHOLOCATION).

The largest genus, *Aerodramus*, contains 12 species. The Three-toed Swiftlet *A. papuensis* is the only member of its family with 3 toes (all other swifts have 4) and may not be closely related to other *Aerodramus* species, but is provisonally allocated to this genus (see Somadikarta 1967). Three of the *Aerodramus* species are well known for their edible nests (see EDIBLE NESTS). The genus *Collocalia* contains only *esculenta* (Glossy Swiftlet) and *troglodytes* (Pygmy Swiftlet), while the genus *Hydrochous* contains only *gigas* (Giant Swiftlet). This largest of the swiftlets has a wing-length of 142–159 mm, body-weight 35–38 g, followed by the uniform blackish-brown *Aerodramus* species: *maximus* with wing 125–140 mm, weight 11.5–14 g; *vanikorensis* with wing 115–123 mm, weight 9–13.5 g; and *fuciphagus* with wing 110–118 mm, weight 8–9.5 g. The smallest are those of the genus *Collocalia*, with *troglodytes*, wing *c.* 90 mm, weight unknown, and *esculenta* with wing 95–100 mm, weight 7–7.2 g.

Behaviour and food. Swiftlets are mainly active by day, although some have rather acute vision in dim light. Thus the Giant Swiftlet, a species with relatively large eyes, is sometimes a crepuscular feeder, and the Indian Edible-nest Swiftlet *Aerodramus unicolor* has been recorded feeding by night with the assistance of artificial illumination. Feeding is strictly aerial as in the other swifts, although there is one observation of the Glossy Swiftlet climbing upside down along a ceiling of a house (constructed of dry palm leaves) searching for insects (Spennemann 1928). Caged swiftlets usually creep along the walls and hang on the ceiling upside down, and even die firmly attached in this position. Swiftlets of the various genera are ecological specialists. Some, like the Glossy Swiftlet, usually forage alone or in aggregations at low elevation in cultivated areas over open water but also over fig trees at times when winged figwasps (Hymenoptera, Agaonidae) are swarming. *Aerodramus* species forage more dispersed, often singly, above the tree canopy, often over virgin rainforest areas, and only aggregate near their breeding sites at the dusk inrush. The main prey items are Hymenoptera, which sometimes make up 99% of the food items, followed by Ephemeroptera (mayflies), Homoptera and Diptera, while other insect orders are rather poorly represented. The larger species, especially the Giant Swiftlet, specialize on Isoptera (flying termites) and Hymenoptera (Formicidae; flying ants). The food is given to the young in the form of foodballs, as in other swifts. In the Edible-nest Swiftlet *Aerodramus fuciphagus* foodballs average 0.57 g in weight and contain *c.* 500 prey items (range of 100–over 1,200); the heaviest foodballs contained either flying ants (Formicidae, including the hard-headed carpenter ants) or flying termites (Isoptera) (Langham 1980). It has been estimated that the *c.* 4,500,000 swiftlets



Glossy Swiftlet *Collocalia esculenta*. (*M.W.*).

breeding at Niah cave, Borneo, eat *c.* 5,000 kg of insects daily, comprising not less than 10^8 individuals (Harrisson 1974). Such a vast consumption of insects must have a significant ecological impact.

Voice. The usual call of the Glossy Swiftlet is a low chirp, infrequently uttered. Cave-breeding species which nest in complete darkness produce bursts of sharp clicks, the so-called rattle call, for orientation in the dark (see ECHOLOCATION). Giant Swiftlets aggregate at dusk or shortly after sunset near the breeding or roosting place (i.e. near waterfalls) in noisy flocks. The birds produce loud, rising and falling trilling flight-calls in chorus, reminiscent of the Swift *Apus apus* but higher in pitch (Becking 1971, and unpublished).

Breeding. Swiftlets nest gregariously, mainly in caves (both sea caves and inland in limestone outcrops) but also in old buildings in Chinese quarters (Edible-nest Swiftlet), while the Glossy Swiftlet occasionally also breeds in occupied houses, under bridges and in drainage tunnels etc. The Giant Swiftlet breeds on ledges under or near waterfalls, sometimes having to dive through a curtain of falling water to reach the nest (Becking 1971). Some species, especially the Black-nest Swiftlet *Aerodramus maximus* and Edible-nest Swiftlet, nest in pitch darkness deep inside caves, sometimes 400 m or more from the entrance, where they orientate by means of echolocation, a faculty which they have developed to a higher degree than any other bird species. The Giant Swiftlet and Glossy Swiftlet lack the ability to echolocate, and consequently breed in the open or near the entrance of caves, in dim light.

Breeding is the best known in the Edible-nest Swiftlet. This species has two peaks of maximal breeding activity, the first October–December, the second February–April. Nest-building takes at least a month (Franck 1926, Medway 1962) and incubation starts usually with the first egg. The 2 eggs are laid with *c.* 3-days interval and incubation lasts 23 ± 3 days. The fledging period is *c.* 43 ± 6 days, giving the rather protracted incubation and fledging period of *c.* 70 (65–75) days (Langham 1980). This period is estimated at over 90 days for the larger Black-nest Swiftlet at Niah, Borneo (Medway 1962). In a study of the Edible-nest Swiftlet in Malaya the overall breeding success was found to be *c.* 48% (Langham 1980). Eggs are eaten by a cave cricket (*Rhaphidophora oöphaga*), which sometimes also attacks young, and many young die by falling and then being eaten by cave snakes or in houses by shrews (*Suncus* spp.) and rats, but they seldom fail in the final exit flight, their first, which sometimes involves negotiating half a kilometre or more of dark tunnels.

See photo EDIBLE NESTS. J.H.B.

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SWIMMING AND DIVING: terms that cover the methods of aquatic locomotion, broadly comprising: (a) swimming on the surface; (b) diving from the surface and swimming under water; (c) plunging into the water from a height. At least 390 species, in 9 orders, habitually swim, while many others can do so. About two-fifths of the regular swimmers seek their food by diving, the remainder normally feeding on the surface, or upending in shallow water, or plunging from the air. The surface-feeders show comparatively minor adaptations to this mode of life, the most obvious being in the position and proportions of the hind limbs and in the webbed feet or lobes on the toes to increase their effective area (see LEG). Diving and plunging birds show more extensive modifications in structure and physiology. Effective diving requires the specific gravity of the bird to approach that of water (normally it is much less). This minimizes the energy used simply to remain submerged. Unlike many diving mammals, birds dive after inhalation, but in these birds this volume of air is somewhat less than that in other birds owing to the decreased pneumaticity of their bones and to a corresponding simplification of the air-sac system (see PNEUMATIZATION OF BONE and RESPIRATORY SYSTEM). Immediately before submerging, diving birds reduce their specific gravity by compressing their body plumage thus forcing out most of the air normally trapped within it. (For eye adaptations to diving, see VISION.)

Emperor Penguins *Aptenodytes forsteri* can descend to at least 265 m and remain submerged for over 18 min under natural conditions; and some diving birds can stay alive for as much as 15 min when forcibly held under. Several physiological adaptations make this possible. While under water important sources of oxygen are oxyhaemoglobin and oxymyoglobin stored in the muscles. The latter is particularly high in penguins, approaching the amounts in diving mammals. Diving birds can obtain energy from anaerobic, as well as the usual aerobic, breakdown of glycogen. In addition, the regulation of the circulation is so modified that in diving the flow of blood to the muscles and perhaps to other organs can be greatly reduced, the supply being reserved mainly for the central nervous system and heart. Heat loss from the limbs to the water may be reduced by cooling the blood entering the limbs. This is done in a network of blood vessels in which arterial blood to the limbs gives off heat to the cooler venous blood returning to the body.

Most diving birds use either the wings or the feet, but not both, for propulsion while under water. Wing-propelled diving birds are largely marine whereas foot-propelled ones predominate in fresh water. Among living birds, the penguins are supreme as wing-propelled divers, literally flying under water. Their flippers distal to the shoulder are relatively inflexible, lack normal flight feathers and have remarkably flattened bones. The leading edge is raised on the upstroke and lowered on the downstroke, thus acting as a hydrofoil producing thrust on both strokes. As in other birds with a powered upstroke, the supracoracoideus muscle, which raises the wing, is large. On the surface, penguins float low in the water. Their high density results from the reduced pneumaticity of the bones and the short body feathers, which trap relatively little air. A thick layer of subcutaneous fat compensates for the reduced insulating function of the feathers.

The divers or loons (Gaviidae) are perhaps the most specialized of living, foot-propelled diving birds. The feet are set far back and the shanks are bound to the sides of the body, which is thus considerably wider than deep and relatively stable when on the surface.The front toes are fully webbed and alone are used for steering as well as propulsion under water. The grebes (Podicipedidae) superficially resemble the divers, but differ greatly in the structure of their limbs and limb girdles. Their toes are lobed distally and joined by webs proximally. The independent derivation of diving birds from different groups of swimming birds is a recurrent theme in avian evolution. Striking examples are the early foot-propelled Hesperornithiformes and the wing-propelled Plotopteridae (Pelecaniformes) (see FOSSIL BIRDS).

Red-throated Diver *Gavia stellata* swimming on fresh water. (*Photo: H.E. Grenfell*).

The petrels (Procellariiformes) float high on the water and swim easily. A few, like the Sooty Shearwater *Puffinus griseus*, pursue their prey by diving, and are unusual in having both the wings and feet modified for use under water. The 4 diving petrels (Pelecanoididae) are small, wing-propelled divers which are remarkably similar to the small species of auks and occupy a corresponding niche in the Southern Hemisphere. These petrels are short-winged, with a whirring flight in the air. They may dive from the wing into the sea, continue to 'fly' under water, and emerge flying in the air.

Tropicbirds (Phaethontidae) feed by plunging into the sea from heights of 15 m or more, but are comparatively poor swimmers and divers. The young seem unable to dive. Brown Pelicans *Pelecanus occidentalis* feed by plunging from the wing, but other Pelecanidae feed by dipping their long bills and necks while floating high on the surface. Their legs are short and stout, not laterally compressed as in most swimming birds; the feet are large, and webbed between all 4 toes.

Gannets and boobies (Sulidae) feed by plunging, sometimes from over 30 m. As they are large birds, their momentum on striking the surface is considerable, and they show special adaptations to prevent damage on impact, notably strengthening of the skull, imperforate external nares and a remarkable system of subcutaneous air-sacs which are thought to be primarily shock-absorbing. They sometimes pursue fish under water, and may use wings as well as feet in swimming. Cormorants are largely foot-propelled. They ride low in the water and dive from the surface, often remaining under for more than a minute and at times reaching depths of about 10 m. Unlike that of most aquatic birds, the plumage of cormorants readily becomes sodden. The long, stiff tail is used as a rudder: in most other diving birds the tail seems to be unimportant. Darters, like cormorants, ride low in the water, and often only the head and neck remain visible; underwater they swim with the wings slightly expanded. Like cormorants, they too become sodden.

Screamers (Anhimidae), although marsh birds, only occasionally swim. All ducks, geese, and swans (Anatidae) swim, and possibly all can dive, although only about one-third of the 148 species habitually do so. Accomplished divers are found among many of the groups: the White-backed Duck *Thalassornis* (Dendrocygninae), steamer ducks *Tachyeres* (Tadorninae), Torrent Duck *Merganetta* (Anatinae), and all the Merginae and Oxyurinae. The Long-tailed Duck or Oldsquaw *Clangula hyemalis*, like the Great Northern Diver or Common Loon *Gavia immer*, is a deep-diving bird, apparently feeding down to 160 m in the Great Lakes of America. Most diving ducks are foot-propelled while under water, although eiders *Somateria* and scoters *Melanitta* dive with their wings partly opened but with the carpal joint flexed so that the primaries lie beneath the secondaries, making a smaller, stronger paddle or steering mechanism. Steamer ducks use their wings partially extended while under water.

Nearly all rails swim well, although only the gallinules *Gallinula* spp., *Porphyrio* spp., etc. and coots *Fulica* are primarily aquatic. The gallinules are swimmers, with the long toes typical of the family increased in swimming efficiency by narrow strips of skin extended laterally. They rarely dive when feeding but may do so if disturbed, when they sometimes flap the wings slowly in swimming under water. The coots, which have lobed toes, are habitual divers; they do not use their wings while submerged. Coots are less adept at diving than other bottom-feeders; in a given depth of water the duration of their dives is much less; food plants are brought to the surface rather than eaten at the bottom.

The 3 species of finfoot (Heliornithidae) are good swimmers with broadly-lobed toes. They swim very low in the water. Their ability as divers is in dispute. The jacanas (Jacanidae), normally using their extraordinarily long toes to walk on floating plants, are like the Moorhen *Gallinula chloropus* in their ability to swim and to dive in escaping danger.

Among the waders (Charadrii), the phalaropes are the only group strongly specialized for swimming. They have lobed, semi-palmate toes, flattened tarsi, and dense body plumage. They feed afloat, sitting high on the water, commonly turning rapidly about and picking up small invertebrates near the surface. Avocets and stilts (Recurvirostridae) and the Crab-plover *Dromas ardeola* also swim well and more frequently than other waders. The Black-winged Stilt *Himantopus himantopus* can dive well.

Skuas, gulls and terns all have fairly short legs and fully-webbed feet. The gulls swim very much more than the others. Some gulls, skuas and many terns plunge for food but none go deep or travel far under water.

The 22 species of auks are highly specialized divers, using their wings for underwater propulsion at relatively high speeds. Except for *Cepphus*, they tend to feed pelagically rather than at the bottom. Their short wings with very short inner secondaries are folded when used underwater, providing a smaller, stouter paddle than the spread wing during aerial flight. The feet are used primarily for steering underwater. The dense body plumage of auks is less obviously compressed prior to diving than is that, for example, of grebes.

Little Pied Cormorant *Phalacrocorax melanoleucos* diving for Minnow or Mosquito Fish *Gambusia affinis* in experimental tank. (*Photo: G.F. van Tets*).

The remaining orders contain only 2 families of regularly aquatic habit. In the Coraciiformes, the 87 species of kingfishers include a number of fish-eaters that feed by plunging either from a perch or while hovering over water. Other members of the family are non-aquatic woodland birds, feeding by pouncing on insects and other prey on the ground or by pursuing them in the air. Some bee-eaters also fish. The techniques and structure of the fish-eaters show only very minor adaptations, for the prey is taken with the bill at or close to the surface and prolonged immersion does not occur. Unlike most other plunging birds, they do not regularly swim; that is true also of the fish-eaters among the Acciptriformes and owls, which grasp their prey with their talons.

Among the Passeriformes, the 5 members of the family of DIPPERS are aquatic. They swim well, using their feet when on the surface and in walking on the bottom, but they rely on their wings for progression under water and to keep them submerged. Their plumage is very dense, like that of phalaropes, and they float high in the water as a result of the large amount of air trapped among the feathers. Some approach to similar habits is found in the little-known *Enicurus* spp. (Turdinae) and in *Cinclodes* spp. (Furnariidae) (see THRUSH; OVENBIRD (1)). Otherwise no members of the order are aquatic, although some frequent the vicinity of water and some tyrant-flycatchers (*Pitangus* spp. and *Lessonia rufa*) regularly take food from the surface. (H.J.B.) R.W.S.

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SWORDBILL: *Ensifera ensifera*, a large Andean HUMMINGBIRD with a remarkably long bill, as long as the head and body combined and far longer than that of any other hummingbird.

SYLPH: substantive name of *Aglaiocercus* spp. (for family see HUMMINGBIRD).

SYLVIIDAE; SYLVIINAE: family and subfamily of PASSERIFORMES, suborder Oscines; WARBLER (1).

SYMBIOSIS: association of two organisms, the result of which are beneficial to each. See under BROOD-PARASITISM; NESTING ASSOCIATION.

SYMPATHETIC NERVES: see NERVOUS SYSTEM.

SYMPATRIC: occurring in the same geographical area—in contrast to ALLOPATRIC.

SYMPHYSIS: union or junction of two bones (see SKELETON, POST-CRANIAL).

SYNALLAXINAE: see OVENBIRD (1).

SYNANTHROPIC: see under EUSYNANTHROPIC.

SYNAPOSEMATIC: see under APOSEMATIC.

SYNCHRONIC: existing at the same level of geological time—contrasted with ALLOCHRONIC.

SYNCHRONOUS HATCHING: see HATCHING.

SYNDACTYL; SYNDACTYLOUS: having two toes (III and IV) coalescent for part of their length. See LEG.

SYNECOLOGY: term for the ecology of communities—contrasted with AUTECOLOGY; see also ECOLOGY.

SYNONYM: see NOMENCLATURE.

SYNSACRUM: the long fused portion of the vertebral column to which the pelvic girdle is firmly attached (see SKELETON, POST-CRANIAL).

SYNTYPE: see TYPE SPECIMEN.

SYRINX: the organ of voice or song (plural 'syringes'). It differs from the mammalian larynx in both situation and structure; the larynx in birds lacks vocal cords and has little or no role in voice production. The syrinx is situated at or near the bifurcation of the windpipe (trachea) into 2 bronchi and typically comprises a resonating chamber (tympanum), vibrating membranes, and control structures of varying complexity, including cartilages and muscles. Syringes traditionally have been classified on the basis of location, as tracheal, bronchial or tracheo-bronchial, but studies in the mid-20th century showed these distinctions to be less clearcut than previously believed. Even the terms 'trachea' and 'bronchus' are difficult to apply consistently in the area where these passages meet. The division of the single passage into two often does not coincide with the transition from single ('tracheal') rings into paired ('bronchial') rings or semirings. It is common to apply the adjective 'tracheo-bronchial' to any syrinx that appears to contain components derived from both tracheal and bronchial tissues.

The syrinx in taxonomy. From the middle of the 19th century on, certain features of the syrinx figured prominently in bird taxonomy, especially within the order Passeriformes. Beddard, Garrod, Forbes and other late-19th century anatomists considered the number and position of insertion of the syringeal muscles to be taxonomically significant. More recently, work by Miskimen, Ames (1971), Warner and others has shown that the extent and type of variation must be determined before syringeal structure is used for taxonomic decisions.

In general, the gross characteristics of the syrinx are quite consistent within a family, but many details may be rather variable. The extent of fusion and the sculpturing of cartilaginous elements may be highly variable within a single species in one case, yet uniform across an entire family in another.

Myological characters have been central to the taxonomic use of the syrinx. The muscles are considered *extrinsic* if they originate off the syrinx (e.g. on the sternum) and insert on the syrinx (or on an otherwise unmodified part of the trachea near the syrinx). *Intrinsic* muscles originate and insert within the specialized area defined as the syrinx. (There is some circularity in this, for the muscles themselves also serve to define the syringeal region.) In all but a few groups (e.g. parrots) there are two pairs of extrinsic muscles: the Mm. sternotracheales, which connect the syrinx to the sternum or to the intercostal muscles, and the Mm. tracheolaterales, which originate on or near the larynx and lie on the lateral surfaces of the trachea, inserting in the syringeal region.

Intrinsic muscles vary greatly from one order to another and sometimes within an order. Where clearcut intrinsic muscles are lacking, their position, and probably their function, is often occupied by the Mm. tracheolaterales, suggesting that intrinsic muscles evolved through segmentation of the tracheolateral muscles. In the simplest condition of intrinsic muscles, found in many non-passerines and a few passerines, each intrinsic muscle is merely a specialized terminal segment of the tracheolateral muscle. Only a few groups have been found with more than one pair of intrinsic muscles: parrots and most passerines.

Types of syringes.

Tracheo-bronchial syringes. This type of syrinx is the most widespread and is so variable that a generalized description is impossible. The lowest rings of the trachea are often fused into a cylindrical tympanum, somewhat flared posteriorly, where it is movably connected with the adjacent 'bronchial bars' ('intermediary bars' of some authors). The medial surfaces of the bronchi usually are membranous and these 'internal tympaniform membranes' (ITM's) are the basic vibrating elements in the oscine syrinx and probably in most others. Work by W.B. Gross in the 1960s showed that in the chicken the external tympaniform membranes (ETM's) are the sound sources. The same may well prove true of pigeons and parrots, in which the syrinx contains large lateral membranes.

Other components frequently present are the *pessulus*, a bony bar lying at the junction of the ITM's, the *bronchidesmus*, a ligament connecting the bronchi to each other and usually to the oesophagus, and up to five pairs of intrinsic muscles, which function to control the tension of the membranes or to close the aperture of each bronchus, through movements of modified cartilages.

Tracheal syringes. In this group the presumed vibratory membranes lie among modified tracheal cartilages. Most syringes in this structural group contain modified bronchial elements and many have tracheo-bronchial muscles. ITM's usually are present but their vocal function remains uncertain. In the best known group, the New World antbird-ovenbird group (suborder Furnarii of the order Passeriformes), the lower trachea is dorsoventrally compressed and provided with membranous 'windows' (with or without narrow crossbands of cartilage), which most authors since Johannes Muller (1847) have believed to be vibratory.

Bronchial syringes. In this type of syrinx the vibratory membranes are located well posterior of the tracheo-bronchial junction and intrinsic muscles, if present, originate and insert on the bronchi. There is no fusion of tracheal elements into a tympanum. To date, this type of syrinx has been clearly identified only in certain cuckoos.

Syringeal operation. Much recent research has focused on the mechanisms of syringeal modulation and on the roles of the trachea, bronchi and air sacs in sound production. Most of the *in vivo* and *in vitro* work in the laboratory has utilized the chicken or readily obtainable songbirds as subjects. Even this limited sample has yet to produce consistent information on the complex interrelationships of the various components of the vocal system.

Greenewalt (1968) was the first to use modern electronic techniques to analyse the calls of a wide array of birds, from grebes to songbirds, in search of a unified theory of sound production. He concluded that the same basic mechanism could produce all of the sounds that he examined. He postulated that the basic vibratory membranes, the ITM's, are bulged inward by pressure of the interclavicular air sac. Thus stretched, the ITM's are set into vibration by the moving stream of exhalant air. Amplitude (volume) and pitch (frequency) are modulated by three interrelated mechanisms, singly or in combination: by altering the pressure of the air sac relative to that in the bronchi, by occluding the air passages with the external labia and by tension of the syringeal muscles, acting on the cartilages supporting the ITM's. Greenewalt suggested that when the ITM vibrates freely without touching the bronchial wall, 'whistled' song is produced, relatively free of harmonics. As the bulging ITM is pushed closer to the outer wall of the bronchus, harmonics appear and the output enters the harsher 'harmonic' domain.

A number of workers before Greenewalt had noted that certain birds are capable of producing two or more harmonically unrelated sounds, indicating the presence of as many independent oscillators. Thorpe (1961) suggested that there might be as many as four such sources. Greenewalt demonstrated that this 'two-voice' phenomenon is present in a great many birds over a wide taxonomic range. Evidently the right and left halves of the syrinx are acoustically and neurologically independent.

In a number of separate studies in the 1960s and 1970s, Brackenbury (1978) and the Gaunts (1977) have used advanced instrumentation to record synchronously in live birds the actions of syringeal muscles, changes in air pressure in various parts of the vocal system, and output sound characteristics.

These workers have demonstrated that the extrinsic muscles function to regulate the position of the syrinx in the neck and, in some species and situations, to control the tensions of vibrating membranes through relative movements or rotations of syringeal components.

The air pressure events are similar in the chicken and the Starling *Sturnus vulgaris*, but in the latter the external labium (EL), absent in the chicken, controls air flow more precisely than in the chicken. This increases loudness while conserving air. In both birds the pressure in the interclavicular air sac is high before and during calling and drops at the end of the call. Tracheal pressure in the chicken is elevated above atmospheric pressure but in the Starling, apparently due the action of the EL, it remains at atmospheric pressure. P.L.A.

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SYSTEMATICS: the aspect of biological work dealing with the systematic description of the forms of life, and also with their orderly arrangement (see CLASSIFICATION). The latter is the special concern of taxonomy, but as it permeates the whole that term is often used synonymously with systematics (see TAXONOMY). The handmaid of systematics is NOMENCLATURE.

Systematic work is a basic necessity for other kinds of ornithological endeavour, as it defines the subjects of study. It is itself grounded largely on morphology and geographical data, as the museum specimen is of necessity the main material in the descriptive or analytical phase, as well as being the permanent record. In the taxonomic or synthetic phase, however, ornithological systematists—although primarily using morphological criteria—have increasingly drawn upon the data of field studies to assist in elucidating problems of phylogenetic relationships; various laboratory tests are also being increasingly invoked (see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA). What has been called 'the new systematics' goes further, into a third phase in which the aim is to investigate the factors influencing the evolution of the different forms. The systematic biologist of today has thus to take account of ecological, ethological, physiological, and genetic data bearing on the problems that the results of earlier faunistic and morphological labours suggest.

In ornithology, systematic work in the old Linnean tradition has been pursued with notable assiduity—so much so that it has been claimed that birds are better known taxonomically than any other class of animals. This places a heavy responsibility on the ornithological systematist to make the fullest use of the opportunity for making still further contributions to general biological knowledge. To do this he must abjure conservatism in his concepts of taxonomy, the limitations of the typological approach, and the pedantry of regarding nomenclature as more than a means to an end. It has been well said by Stresemann that 'whoever wants to hold firm rules should give up taxonomy. Nature is too disorderly for such a man.'

The present tendency is, indeed, towards a much more fluid concept of 'population systematics'. In this study, as Mayr has pointed out, cognisance must be taken of three major phenomena: (1) the geographical isolate, possibly an incipient species (see SPECIATION); (2) the population continuum, subject to clinal variation (see CLINE); (3) the zone of secondary intergradation, due to isolates re-establishing contact (see HYBRIDIZATION, ZONE OF SECONDARY). An isolate may or may not have been formally recognized as a subspecies, or it may comprise more than one; a continuum, likewise, may or may not include forms that have been accorded subspecific rank (see SUBSPECIES).

See references under TAXONOMY.

T

TACHURI: substantive name of the 2 South American tyrant-flycatchers of the genus *Polystictus* (see FLYCATCHER (2)).

TACTILE SENSE: see TOUCH.

TADORNINI: see DUCK.

TAGS: see MARKING.

TAIGA: coniferous forest-land, typical of vast areas of the North Temperate Zone, lying south of the TUNDRA.

TAIL: in descriptive ornithology the conspicuous feather appendages, protruding from the fleshy tail proper which is organized around the shortened hindmost portion of the vertebral column. The plumage elements are the large tail quills (rectrices) and the rows of major and minor covert feathers (tectrices) that overlap the bases of the rectrices. The elongate tail of *Archaeopteryx* has undergone a dramatic transformation, culminating in the inconspicuous, stubby tail of recent birds. A particularly remarkable part of the transformation is the derivation of the bulb of the rectrices, the mechanism that provides the anatomical basis for the array of positions and movements of the tail during flight and its other specialized activities.

In the conversion of the avian tail to its present compact form, several important modifications have taken place: (1) truncation of the tail having the effect of concentrating the whole tail mass nearer to the centre of gravity of the trunk. This truncation involved consolidation of the terminal vertebral segments, producing the pygostyle, as well as incorporation of the proximal caudal vertebrae into the synsacrum; (2) liberation of most of the rectrices from direct attachment to the caudal vertebrae; (3) evolution of the paired rectricial bulbs into which the tail quills became implanted; and (4) development of a highly mobile joint between each rectricial bulb and its socket.

Generalized topography of the avian tail. The width of the avian fleshy tail is more than one-half that of the pelvis. Viewed from above, its caudal border, where the rectrices are inset, varies from semicircular to angulated. From the rear, the follicles of the right and left rows of rectrices intersect one another producing a tent-shaped configuration (Fig. 1). The lateral borders of the tail exhibit pronounced bulges marking the underlying rectricial bulbs. In most birds more or less distinct constrictions exist at the tail–trunk junction (e.g. *Gallus*); in others (e.g. *Anas*) the tail merges imperceptibly into the pelvic part of the trunk. In profile, the vent protrudes from the abdominal wall just inferior to the fleshy tail mass; the uropygial gland rests on the pygostyle (see SKELETON, POST-CRANIAL) and the two central rectrices (Fig. 1). *Rhea*, a so-called tail-less bird, possesses rudimentary tail muscles attached to the reduced free caudal vertebral column at the end of the rump.

Structure of the tail. The following descriptions are based on the pigeon *Columba livia*. Examples of charadriiform, anseriform, gruiform, accipitriform, falconiform, galliform, psittaciform, and passeriform birds have been compared. The tail structure of all of them is essentially the same as that of the pigeon; however, in smaller forms, the morphological details are less well defined.

The endoskeletal framework of the tail consists of a series of 6 free caudal vertebrae, articulating with one another, with the terminal pygostyle (coccyx) and with the last synsacral caudal vertebrae. The slightly moveable joints between the bodies of the free vertebrae are ligamentous, connected to one another by fibrous discs, contrasting with the synovial joints of the cervical and thoracic regions.

The intrinsic tail muscles are modified axial muscles originating from the synsacrum and proximal free caudal vertebrae and inserting into the more distal vertebrae, pygostyle, rectricial bulb, and rectrices. The extrinsic tail muscles arise from lateral pelvic elements (ala of ischium, shaft of pubis) and the femur, inserting into rectrices, fasciae and aponeuroses of the intrinsic muscles. Some of the extrinsic muscles participate in cloacal function and support of the body wall in the region of the vent. More of the tail musculature is concerned with depression than with elevation of the tail (see later: Movements of tail feathers). Actions of the muscles are inferred, based on anatomical evidence and observations made during manipulations of the tail of fresh specimens. The names themselves of the tail muscles provide some information on their attachments or actions.

The intrinsic muscles (Figs. 1–3) are the paired M. levator caudae, M. depressor caudae, M. lateralis caudae, M. adductor retricium, and M. bulbi rectricium. M. depr. caud. is somewhat unusual in that its superficial tendon decussates with its opposite counterpart on the lower surface of the rectricial bulbs, forming the expansive cruciate aponeurosis; its deep tendon inserts directly on the pygostyle. Contraction of both depressor caudae muscles causes the wings of the cruciate aponeurosis to draw down the lateral part of each bulb, enhancing tenting of the tail feathers, then rotates each bulb, depressing its rectrices and ventrally flexing the entire tail. Acting unilaterally M. caudofemoralis deviates the tail to its side with the assistance of the ipsilateral M. pubocaud. int. M. bulbi rectr. initiates spreading of the rectrices; M. lat. caudae carries out the rest of this action. The non-striated M. add. rectr. extends transversely from one rectrix to the next, paralleling the elastic interrectricial ligament; both of these structures adduct the rectrices, folding the outspread tail.

The paired extrinsic tail muscles (Fig. 1), M. pubocaudalis externus, M. pubocaudalis internus, and M. caudofemoralis act with M. depressor caudae in ventral flexion of the tail. Acting unilaterally, M. pubocaud. ext. and M. dep. caud., and the contralateral M. lev. caud. tilt the tail, i.e., rotate the entire tail around its longitudinal axis. An exaggeration of such rotation is exhibited during soaring by the Black Kite *Milvus migrans*. M. pubocaud. int. has a complex structure, its superior and inferior bellies being joined by a tendinous intersection. Not only does this muscle contribute to depression of the tail, but it affects the shape of the cloaca (see below).

Rectricial bulb (Fig. 2). The rectrices and their major coverts on each side are embedded in the Bulbus rectricium, a well-organized fibro-adipose body enveloped by its capsule of striated muscle. Only the central pair of rectrices that flank the pygostyle has any ligamentous

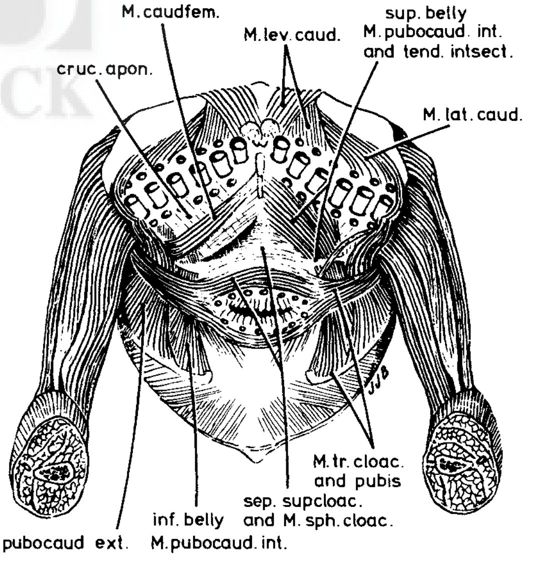

Fig. 1. Tail muscles of the pigeon *Columba livia*. Caudal view; tail somewhat elevated; vent drawn inferiorly; legs sectioned slightly distal to knee. Superior belly of M. pubocaudalis internus has been removed on left side to display the deeper lying structures. Note narrow M. levator cloacae (unlabeled) passing deep to M. sphincter cloacae on right side.

Abbreviations: cruc. apon. = cruciate aponeurosis; M. tr. cloac. = M. transversus cloacae; Sep. supcloac. = Septum supracloacale; Tend. intsect. = tendinous intersection.

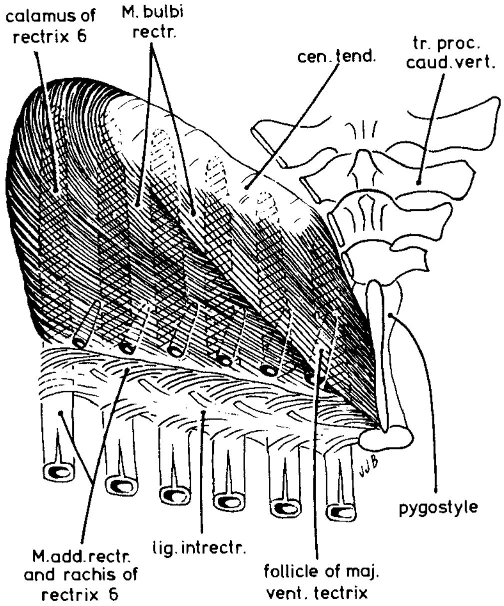

Fig. 2. Bulb of the rectrices (Bulbus rectricum) of the pigeon *Columba livia*. Right side, ventral aspect. Portions of transverse processes cut off; bulb drawn laterally away from pygostyle to demonstrate attachment of part of M. bulbi rectricum to pygostyle.

Abbreviations: caud. vert. = caudal vertebra; cen. tend. = central tendon; Lig. intrectr. = Ligamentum interrectriciale; tr. proc. = transverse process.

attachment to the tail skeleton. The bulb is dorsoventrally compressed, and viewed from above it is somewhat rhomboid. The socket of the bulb is located between the levator caudae and depressor caudae muscles which form its roof and floor. The medial wall of the socket is formed by the pygostyle and the dorsal processes of the adjacent vertebrae; its lateral wall is the inner surface of M. lat. caud. The bulb and its socket form an ellipsoid 'joint' in which rotatory movements bring about elevation and depression of the bulb and its implanted feathers.

Symmetrical movements of elevation and depression of the folded tail, involving dorsi- and ventriflexion of the tail vertebral column and rotation of the bulbs, takes place about a transverse axis projecting through the apices of the two bulbs. The oblique axis of rotation of the bulb is used for elevation–depression movements of the outspread tail. This axis projects in an infero-latero-cranial direction from the caudo-dorsal corner of the pygostyle, forming an angle of about 45° with the median plane of the body and about 20° with the dorsal (horizontal) plane. From the neutral position of the tail, more elevation of the tail feathers is possible than depression, since depression is limited by contact of the tail with the underlying rear of the trunk and the vent. On account of the obliquity of the axis, during downward rotation of the bulb the lateral rectrices descend farther than the more medial ones, increasing tenting of the tail. Movements of one bulb may be independent of the opposite bulb.

The interior of the bulb (Fig. 3) is compartmentalized, i.e. subdivided into fat-filled locules; the calami of the rectrices are suspended in the fibrous partitions separating the locules. The basal ends of the calami are embedded in a tough, deformable fibro–adipose mass, the basal pad, which binds the tips of the calami together as a unit, but is flexible enough to permit movements of the individual calami. Individual movements of the calami are also accompanied by displacement of locular fat and deformation of the walls of the bulb. Side-to-side movements of the rectrices during spreading and folding of the tail, as well as their elevation–depression movements take place within the bulb. The lateral rectrices are more mobile than the medial ones because of the fixation of the central rectrices to the pygostyle. Therefore, during depression, this extra mobility of the lateral rectrices yet further accentuates the tent-shaped lower surface of the tail. This is additional to that caused by the obliquity of the axis of rotation of the bulb and the action of the depressor caudae muscles. Conversely, elevation tends to flatten the lower tail surface. Part of M. bulbi rectricium anchors the bulb to the pygostyle (Fig. 2); this muscle also appears to help M. lat. caud. in spreading the rectrices, initiating abduction of the rectrices by drawing the tips of the calami together and, by means of its slips, inserting on the calami and the fibrous partitions within the bulb, stabilizes the rectrices.

Summarizing the foregoing, the avian tail demonstrates combinations of: (1) gross movements of the entire tail, i.e., depression, elevation, tilting and lateral deviation; (2) movements of each rectricial bulb in its socket, mainly producing elevation and depression of the tail feathers; and (3) movements of individual rectrices within the bulb as in spreading–folding and elevation–depression of the rectrices themselves.

Tail–cloacal interrelationships. Movements of the tail are not only associated with defaecation and copulation but influence these activities. In its neutral position the tail proper compresses (flattens) the adjacent cloaca, cloacal bursa (Fabricii) and duct. The muscles on the lower surface of the tail are separated from these organs by M. sphincter cloacae and Septum supracloacale; the latter is a transverse fibrous sheet connected laterally with the tendinous intersection of each M. pubocaud. int. (see Fig. 1). Elevation of the tail to its upright position brought about by the Mm. levatores caudae decompresses the cloaca, enlarging its dorso–ventral dimension. Simultaneous contraction of the Mm. pubocaudales internus and externus on each side draws these muscles away from the cloaca, lifting the lateral margins of the supracloacal septum and the sphincter muscle. Thus pressure on the sides of the cloaca is also relieved, increasing the lateral dimensions of the cavity of the cloaca.

Nerves and vessels of the tail. The blood supply of the tail, including its integument, is largely derived from intersegmental rami of the median caudal artery and to a lesser degree from the lateral caudal artery, a branch of A. iliaca interna. From these sources two prominent arteries pass to each rectricial bulb: A. dorsalis bulbi is an enlarged dorsal ramus of an intersegmental branch of the median caudal artery that serves the part of the bulb dorsal to the implanted calami of the rectrices. A. ventralis bulbi stems from the lateral caudal artery and enters the ventrolateral aspect of the bulb. Rami to the follicles of the rectrices and the major coverts from these arteries become hypertrophied during replacement of these feathers after their moult.

The intrinsic tail muscles and integument of the dorsum of the tail are innervated by the segmental caudal spinal nerves. The ventral rami of the caudal nerves communicate, forming the caudal plexus. Dorsal and ventral Nn. bulbi rectricum arise from the caudal plexus. Rami of these nerves are distributed to M. bulbi rectricium, the socket of the bulb, and to the perifollicular tissues. Presumably those to the socket and the follicles of the rectrices and major coverts are proprioceptive afferent

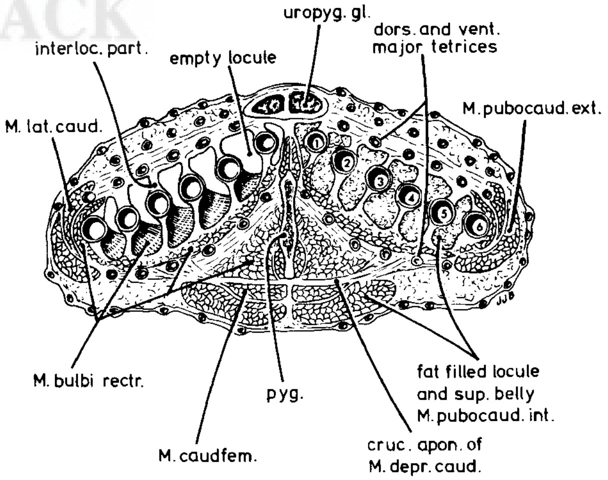

Fig. 3. Cross section of tail of the pigeon *Columba livia*. Level of section through the lamina of pygostyle; section approximately 3 mm thick. Rectrices are identified by numerals. Note deep parts of M. bulbi rectricum extending from follicles of rectrices to adjacent interlocular partitions. Note also attached to base and apex of pygostyle small attachments of M. levator caudae and M. depressor caudae (unlabeled).

Abbreviations: cruc. apon. = cruciate aponeurosis; interloc. part. = interlocular partition; pyg. = pygostyle; uropyg. gl. = uropygial gland.

nerve fibres, conveying impulses centrally about the position and movements of the bulb and the rectrices. The extrinsic muscles of the tail, the integument of the lateral and ventral aspect of the tail and the vent and surrounding region are innervated mainly by branches of the pudendal nerve plexus.

Shape of tail. Kiwis, cassowaries, emus, and rheas are practically tailless, no special tail feathers being recognizably differentiated from the general plumage covering the hinder parts; the Ostrich *Struthio camelus* is an exception among the 'ratite' birds in having something of a tail. In grebes the quills are rudimentary; and in many aquatic birds the tail is very short, e.g. in divers and in penguins.

Tails may be rather short and stumpy, of moderate or substantial length, or greatly elongated. Very long tails are found, for instance in the tropicbirds, in many true pheasants, in certain parrots, in the mousebirds (Coliidae), and in species of various passerine families—e.g. in tyrant flycatchers of the genus *Muscivora* in the New World, and in the Paradise Flycatcher *Terpsiphone paradisi* and the Paradise Whydah *Vidua paradisaea* in the Old World. (The Japanese have a breed of domestic fowl with a 'train' of enormous length, in which the feathers grow continuously without moult.) Elaborate tails are often much more highly developed in the male of a species.

The end of the tail, depending on the relative lengths of the paired rectrices, may be square or rounded, forked or wedge-shaped—examples are too well known to need citation. Very long tails are sometimes due to elongation of the central pair of rectrices, whether the others be graduated or of uniform length. In some fork-tailed species, however, it is the outer rectrices that are very long.

Modifications of rectrices. Various modifications occur in the shape of separate rectrices. Sometimes the distal part of the rachis carries no web but projects as a spine, e.g. in the spine-tails of the family Furnariidae and in the spine-tailed swifts (Chaeturinae). Some other birds are 'racket-tailed', notably the motmots; here the terminal part of the shaft in the 2 central rectrices carries a web on both sides, but there is a sub-terminal part that is bare, thus isolating the 'racket' (or 'raquet') from the main web. In the male Marvellous Spatuletail *Loddigesia mirabilis*, a hummingbird, it is the outer pair that carry raquets at the end of long wire-like shafts that cross over. Sometimes certain rectrices may be twisted in the vertical plane, e.g. the somewhat elongated central tail feathers of the Pomarine Skua *Stercorarius pomarinus*. In some birds-of-paradise the central tail feathers are elongated in wire-like or narrow ribbon-like form, often much twisted or curled.

In several different groups of birds that either climb or cling to vertical surfaces, such as tree-trunks or walls, the tail is used as a prop; and the rectrices tend to be stiffened in adaptation to this habit. Examples are the woodpeckers, spine-tailed swifts (Chaeturinae), woodcreepers, tree-creepers, and oxpeckers.

Ornamental tail plumes are by no means always modified rectrices. In the male Peacock *Pavo cristatus*, for instance, the gorgeous feathers of the train are greater upper tail coverts. The ornamental plumes of the male Ostrich have probably this same homology. In some species, the birds at rest may appear to have ornamental tail feathers but these in fact belong to the wings, as can be seen when the latter are unfolded. This is exemplified in the cranes; thus in *Grus grus* one of the most noticeable characters is what appears to be a large and loosely feathered tail, but the plumes are actually elongated secondary wing feathers. In the Pennant-winged Nightjar *Macrodipteryx vexillarius* it is an enormously elongated primary on each side that, in the breeding male, extends beyond the tail when the bird is at rest.

Movements of tail feathers (see above). In flight the tail forms part of the surface on which the air presses, and it can give some assistance to the wings in steering and braking (see FLIGHT). The tail tends to be broad in soaring species and short in rapid flyers. The tail, when of some length, may also be used in helping to balance a perched bird.

The tail in some birds is normally cocked up, as for instance in the Wren *Troglodytes troglodytes*, the Grey Gallito *Rhinocrypta lanceolata*, and the Rufous Scrub-bird *Atrichornis rufescens*. Among the stiff-tailed ducks (Oxyurini), e.g. in the North American Ruddy Duck *Oxyura jamaicensis*, the tail of the swimming bird may be either cocked up or extended horizontally. Other birds momentarily cock up the tail, e.g. on alighting—the familiar characteristic movement of the Blackbird *Turdus merula*. Many birds also raise the tail to a greater or lesser extent in the act of defaecation. The female's tail is usually, and that of the male sometimes, deflected laterally during copulation.

Grey Starling *Sturnus cineraceus* male at nest hole. Note support given by tail. (*Photo: Y. Shibnev*).

In many different kinds of birds there is a repeated or continual wagging, shaking, or flirting of the tail. These movements are often associated with bobbing or twitching of the whole body; indeed, the tail is in some instances not moved separately at all but merely serves to accentuate the movement of the body. The continual up and down movement of the tail in wagtails *Motacilla* spp. is familiar, and is performed while the bird is otherwise still. In the forest wagtails *Dendronanthus* spp. the tail has been described as being wagged from side to side; but here it is in fact the whole body that is continually swung, through a horizontal arc, on motionless legs. The function of such movements is not understood, but it has been remarked that the tendency seems to be especially common among birds that have their usual habitats in the neighbourhood of running water. Apart from the wagtails, one thinks at once of the 'teetering' of sandpipers of the genus *Actitis*, the similar movements of waterthrushes *Seiurus* spp. (Parulidae), and the bobbing dippers *Cinclus* spp.; and those furnariids of aquatic habits, *Cinclodes* spp., are not called 'shaketails' without reason. Yet examples among birds not particularly associated with water are not lacking; for instance, the African Pitta *Pitta angolensis*, a bird of thickets and dense woodland, constantly bobs its body and flirts its tail like a dipper.

If the tail is of any considerable size, whether it has ornamental plumes or not, it commonly plays a large part in display postures, particularly those of males in courtship performances; it is often erected, sometimes depressed, and generally spread fanwise in addition (see DISPLAY). It may also be quivered by females or young in solicitation or begging postures. For sounds made by the tail, e.g. the drumming of snipe *Gallinago* spp., see under MECHANICAL SOUNDS. A.L.T. and J.J.B.

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TAIL COVERTS: see TOPOGRAPHY.

TAIL STREAMER: a slender elongated tail feather.

TAKAHE: *Notornis mantelli* (for family see RAIL).

TALKING BIRDS: see under MIMICRY, VOCAL.

TALON: a claw (toe), especially of a bird-of-prey and mainly used in the plural.

TAMENESS: toleration by birds of the close presence of human beings, in some instances amounting to a positive tendency to seek such presence. A substantial degree of tameness is characteristic of certain species, and this is presumably genetic. Tameness may also be acquired by individuals or communities of a species in favourable circumstances; again, however, there seems to be a genetic element, in that some species become tame much more readily than others.

An innate lack of fear of man may be shown by birds inhabiting remote islands or other relatively inaccessible places. The tameness of birds on the Galápagos Islands has been remarked on by visitors from Charles Darwin onwards. In the case of large species breeding in such places, e.g. boobies (Sulidae) and penguins, a reaction to predators of any kind, if these do not normally intrude on the nesting grounds, may be absent from the birds' psychological make-up.

On the other hand, the many species of birds that have become adapted to using houses and gardens, finding their nesting sites and feeding opportunities in the vicinity of man, show various degrees of toleration of the presence of the human beings who also live there. Similarly, the birds will follow the gardener or agricultural worker to take the food-prey that he incidentally disturbs or uncovers—much in the way that the Cattle Egret *Bubulcus ibis*, for instance, accompanies grazing mammals, domesticated or wild. So also there may be a great attendance of gulls at a fishing harbour; and so on. It is clear that there is an advantage in the association with man; and where the latter is friendly in his attitude towards the birds, tameness may become normal behaviour.

Special interest attaches, however, to the differences between species in their natural tameness or capacity to acquire tameness. In Britain, where the Robin *Erithacus rubecula* is mainly a garden bird, the species is outstanding in its capacity for familiarity with man; as has been said, it is never the Dunnock *Prunella modularis* that perches on the gardener's spade. In truly wild habitats in northern Europe, the amazing tameness of the Rednecked Phalarope *Phalaropus lobatus* and the Purple Sandpiper *Calidris maritima* contrast with the extreme wariness of some other species of 'waders' (Charadrii) breeding on the same ground. Found from the Sahara to India, the House Bunting *Emberiza striolata* is a remarkably tame bird, feeding inside houses.

There are also some interesting geographical differences in this respect within a single species, and these are not easily explicable. Thus the Robin, so tame in Britain, is a shy woodland bird over much of Continental Europe, including countries in which it is subject to no persecution. Likewise, the Moorhen *Gallinula chloropus* readily becomes accustomed to man in the populous areas of Britain and some other parts of western Europe, but is elsewhere a notably timid bird. In North America, the Florida race of the Scrub Jay *Aphelocoma coerulescens* is described as bold and confiding, and the Great Basin race is furtive and shy.

As regards tameness acquired by individuals, it was pointed out by Edward Grey (1927) that birds became tame in relation to places rather than persons; he instanced the behaviour of the same individual ducks *Anas* spp. towards the same people at different points on his lake. The present writer has had eight Speckle-fronted Weavers *Sporopipes frontalis* come unhesitatingly on his hand, outstretched with crumbs, on the verandah of a house in Tanzania that he had never visited before but where the hostess regularly fed the birds.

It is better to discount as exceptional those cases in which a human being has taken more than usual pains to win the confidence of a wild bird or birds, thus establishing something like a personal relationship (cf. L. Howard 1956). Sometimes there may even be an abnormal factor in that the bird has become conditioned to accept a certain person as a substitute mate or parent (see IMPRINTING). One has also to allow for possible differences in temperament between individual birds of the same species. Residual tameness on the part of a bird that has been released from captivity is also outside the general picture considered here.

Further, it is necessary to distinguish boldness from tameness—the urge to continue sitting on eggs, or to remain with the young, or to seize prey, is for the time being stronger than the urge to flee. That there may be little real toleration in such cases is shown by the fact that in some species the passive role can give place to an attack on the human intruder; also by the fact that an incubating bird may desert its nest permanently if its capacity for sitting tight is strained to breaking point.

Of the acquisition of tameness by a local population of a species, habituated to human presence in places where no hostile action towards birds ever occurs, there can be no better example than the Woodpigeon *Columba palumbus*—so wild and wary in the countryside, so extremely tame in the public parks of London. It was noticed that during the Second World War, when steps to keep down these birds were taken, the degree of tameness became much less; but it has since become re-established.

There are some interesting points about the tameness or otherwise of young birds, including those reared in captivity. Interpretation is difficult, however, in the absence of controlled experiments. For the question of habituation see under LEARNING.

Wild birds, like various other animals, show little fear of vehicles, and can often be approached much more easily in a motor car than on foot. The shape of the vehicle apparently evokes no predator response.

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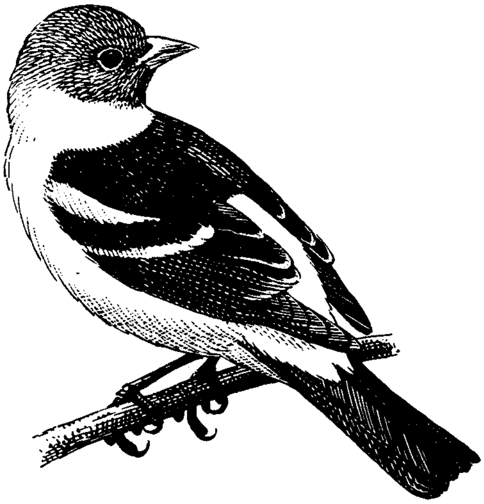
TANAGER: substantive name of species of Thraupinae and, in the plural, general term for the group—here treated as a subfamily of the Thraupidae (Passeriformes, suborder Oscines) but commonly given separate familial rank. The name comes from 'tangará' in the language of the Tupi Indians of Brazil. The tanagers are 9-primaried arboreal song-birds, confined to the Western Hemisphere (including the Antilles) and very largely to its tropical portion. Systematists now usually include in this subfamily certain genera of honeycreepers but for the present purpose it is convenient to give separate treatment to these small birds with bills and tongues highly modified for drawing nectar from flowers (see HONEYCREEPER, ORANGEQUIT). Another distinct genus, *Tersina*, which is here also included in the subfamily Thraupinae, is also given separate treatment (see SWALLOW-TANAGER). With these exclusions, the subfamily contains 54 genera and 215 species.

Characteristics. The tanagers, ranging in size from about 10 cm to (rarely) 28 cm in length, contribute more than any other family to the brilliant colour displayed by tropical American birds; although hummingbirds are more numerous in species and individuals, they are smaller and their bright metallic colours can be appreciated only in special conditions. For variety of colours and diversity of patterns, the 46 species of small tanagers of the genus *Tangara* (the largest genus) are outstanding even in this highly endowed family. One of the most gorgeous of these is the Paradise Tanager *T. chilensis*, the *siete colores* of South Americans. This 14-cm bird has the head largely golden-green. Its upper plumage is largely black, with a bright red lower back and red or yellow rump; the chin and throat are light purple; and the remaining under plumage is chiefly turquoise blue. The sexes are alike, or nearly so, as seems to be true throughout this brilliant genus, in which adults wear the same bright colours at all seasons.

The genus *Euphonia* also contains a number of small and colourful species, the 'euphonias'. Less varied in coloration than the aforementioned group, the males are mostly black, glossed with violet, blue, or green, on the upper parts and sometimes also on the throat; the forehead and more or less of the crown, and the underparts, are chiefly bright yellow. Female euphonias are usually greenish and yellowish, far duller than the males. *Ramphocelus* is a genus of larger and stouter tanagers, of which the males, but not the females, are richly coloured. The male Scarlet-rumped Tanager *Ramphocelus passerinii* of Central America is everywhere velvety black except the vivid rump, but the female is clad in shades of brown and olive. Both sexes of the widespread



Western Tanager *Piranga ludoviciana*. (*R.G.*).

Blue, or Blue-grey Tanager *Thraupis episcopus* have blue-grey body plumage with bright sky-blue wings and tails. Some races have a large white patch on each wing.

The male Summer Tanager *Piranga rubra* of southern United States is wholly red; the female, yellowish. The male of the Scarlet Tanager *P. olivacea*, which breeds in the United States and southern Canada, is brilliant scarlet with black wings and tail. It is of interest that this, the most migratory species in a generally nonmigratory family, is the only one known to undergo great seasonal changes in coloration; in the months of the northern winter, which the species spends in South America, the males are clad in greenish and yellow, much like the females. In the Western Tanager *P. ludoviciana*, which breeds on the Pacific side of temperate North America and migrates to Central America in winter, the annual changes of the males are less pronounced.

Among the less usual types of coloration in this extremely varied subfamily may be mentioned the Magpie-tanager *Cissopis leveriana*, widely distributed in South America, in which both sexes are largely white, with the whole head, upper back, and breast blue-black. The wings and the long, graduated tail of this exceptionally large tanager are black and white. Both sexes of the Orange-eared Tanager *Chlorochrysa calliparaea* of the eastern foothills of the Andes are largely brilliant metallic green, with a bright orange spot on the crown, a metallic orange patch on the rump, and a black gorget bordered with orange. By no means all tanagers are brightly coloured. The prevailing colour of the bush-tanagers of the genus *Chlorospingus* is olive-green, with white or blackish marks on the heads of some species. These plain little tanagers are found chiefly in the high mountains, where a few brilliant species also occur; but the subfamily is best represented at low and middle altitudes.

Habitat. Relatively few tanagers dwell in the dark depths of heavy forest. Many wander in mixed flocks through the upper levels of the forests and, like other treetop birds, they may forage and even nest in scattered trees and shrubbery of neighbouring clearings, plantations, and gardens. Many tanagers inhabit low, bushy growth; but only a few atypical members of the family, including the widespread Rose-breasted Thrush-tanager *Rhodinocichla rosea* and the Chat-tanager *Calyptophilus frugivorus* of Hispaniola, are primarily ground foragers.

Food. Tanagers as a whole are largely frugivorous, but probably all of them vary their diet with insects, which are sometimes captured on the wing, especially by the Summer Tanager. This species frequently tears open nests of small wasps to extract larvae and pupae. Grey-headed Tanagers *Eucometis penicillata* and some populations of *Habia* follow army ants (*Eciton*) in company with antbirds (Formicariidae), woodcreepers (Dendrocolaptidae), and many other small forest-dwellers, capturing the insects and spiders driven from concealment by the hunting ants rather than the ants themselves. The euphonias feed largely on the berries of mistletoes (Loranthaceae), the seeds of which pass through their alimentary tracts enclosed in a viscid envelope which attaches them to trees, so that these birds are important disseminators of the parasites. Tanagers are readily attracted to feeding trays where bananas and halved oranges are offered; over the years, 11 kinds have visited a single tray in southern Costa Rica.

Behaviour. Many species of tanagers remain mated throughout the year, but others travel in flocks in which pairs are not evident. In those that are constantly mated, the male sometimes feeds his partner, especially as the nesting season approaches. Nuptial feeding has been observed in species of *Tangara*, *Thraupis*, *Eucometis*, *Piranga*, *Euphonia*, and *Chlorophonia*.

Tanagers roost in trees and bushes, never in holes, as far as known; although euphonias snuggle into dense masses of moss, liverworts, or small orchids on epiphyte-laden boughs. Mated individuals rest near their partners rather than in contact with them. At times a number of pairs gather to roost in an attractive tree.

Voice. The tanagers as a whole are poorly endowed with song, and this is especially true of the most brilliant genus, *Tangara*, some of whose members are quite devoid of melody. A few species in other genera are known to have pleasing songs, among them the Scarlet Tanager, Grey-headed Tanager *Eucometis penicillata*, and the ant-tanagers of the genus *Habia*, which sing most persistently at dawn. Vocal mimicry has been reported for several species of euphonias. The poorly developed voices of many tanagers appear to be correlated with year-long pairing and weak territorial defence or absence of territoriality.

Breeding. Most tanagers build open, cup-shaped nests, high in trees, in low shrubs, rarely on the ground; no species (except the SWALLOW-TANAGER) is known to build habitually on or in the ground. The chief exceptions to this rule are the euphonias and chlorophonias, which construct covered nests with an opening in the side, embedded in moss on a trunk, in a cranny in a tree or post, or even in a tunnel in the ground. The Palm Tanager *Thraupis palmarum* builds its cup-shaped nest in a hole in a tree or other cranny. The versatile Blue Tanager may nest in an open shed, and sometimes it wrests a nest from some smaller bird and hatches its eggs and feeds its young along with those of the dispossessed builder. The nest is built by both sexes in numerous species of *Tangara*, *Thraupis*, *Eucometis*, *Euphonia*, and *Chlorophonia*; by the female alone in *Ramphocelus*, *Piranga*, and *Habia*.

Tanagers' eggs may be bright blue, blue-green, blue-grey, grey, cream, or white, and they are nearly always spotted, blotched, or scrawled with brown, lilac, or black. They are usually laid early in the morning, before or soon after sunrise, on consecutive days. The clutch consists of 2 or, more rarely, 3 eggs. Larger clutches, up to 4 or 5, are laid by the euphonias and chlorophonias, and by the migratory species of *Piranga* which breed beyond the tropics. The eggs are incubated by the female alone, who through the day takes a number of short sessions, often lasting from 20–30 min and rarely exceeding an hour. She keeps her eggs covered for about 60–80% of the daytime. Two female Blue Tanagers, attached to the same male, alternately incubated a double set of eggs. In another of the rare cases of bigamy recorded in this family, a male Red-crowned Ant-tanager *Habia rubica* had 2 mates and 2 nests simultaneously. Although there is no well-authenticated instance of incubation by a male tanager, he is actually attentive to his mate, sometimes bringing her food, or else, as in *Rhamphocelus*, presenting it to the eggs while she is absent, seeming thereby to anticipate the hatching of the nestlings. Recorded incubation periods of species with open nests range from 12–14 (rarely 15) days; but in the closed nests of euphonias they are often 16–18 days.

The nestlings hatch with tightly closed eyes and sparse (very sparse in *Euphonia*), loose down. The interior of the mouth is red. Brooded by the female only, they are fed by both parents, the chief known exceptions to this rule being certain nests of the Scarlet-rumped Tanager and the related Silver-beaked Tanager *Rhamphocelus carbo*, in which females are more numerous than males, with the result that some of the former rear their young without a mate's help. Food is brought to the nest in the parent's bill or mouth, except in the euphonias and chlorophonias, which regurgitate to the nestlings. Droppings are swallowed or carried away in the bill, and the nest is kept clean.

Juvenile or adult nest helpers have been found in a number of species. Immature Red-throated Ant-tanagers *Habia gutturalis* feed nestlings, probably their younger siblings, and they may even help to build. Likewise, first-brood young of the Golden-masked Tanager *Tangara larvata*, still in immature plumage, may help to feed a later brood of the same season. In this and several related species (e.g. Plain-coloured Tanager *T. inornata*, Speckled Tanager *T. guttata*, and Turquoise

Tanager *T. mexicana*) 3 to 5 individuals in adult plumage sometimes attend 1 or 2 young. At least 3 of a group of 7 apparently adult Dusky-faced Tanagers *Mitrospingus cassinii* fed 2 nestlings.

The nestling period varies in an interesting manner according to the form and site of the nest. It is shortest, 10 (rarely 8–9) to 13 days, in species that build low, open nests, including *Rhamphocelus*, *Eucometis*, and *Habia*. In the higher, open nests of *Tangara* and *Thraupis* it is longer, 14–20 days. In the covered, often high nests of *Euphonia* and *Chlorophonia* it is longest, 17–24 days. Tanagers scarcely ever give distraction displays when their nests or young are, or appear to be, in danger; but such displays have been witnessed in the ant-tanagers *Habia* spp. Euphonias and chlorophonias may take more than a year to acquire adult plumage, and the males sometimes breed in transitional attire. Many species of tanagers have more than one brood. A.F.S.

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TANAGER, SWALLOW: see SWALLOW-TANAGER.

TAPACULO: substantive name of some species of Rhinocryptidae (Passeriformes, suborder Deutero-Oscines, infraorder Furnarii); in the plural, general term for the family. This group of less than 30 species is considered to be related to the antbirds (Formicariidae).

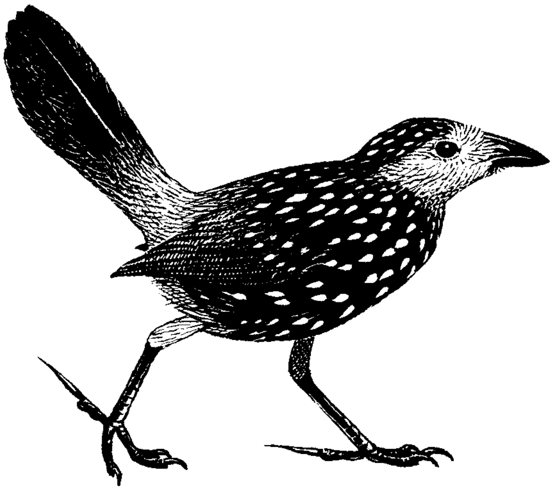
Characteristics, habitat and distribution. Tapaculos are ground-dwelling birds of South and Central America, from about the size of a wren *Troglodytes* sp. to that of a thrush *Turdus* sp. (12–25 cm in length). One of the special morphological characteristics of the tapaculos is a large movable flap (operculum) which covers the nostril completely and gave rise to the name currently used for the family (previously called Pteroptochidae). Another structural characteristic is that the back edge of the sternum (metasternum) has 4 notches.

The legs are long, indicating that locomotion is almost solely by them. Some species have strikingly large and strong feet that serve well for scratching on the ground. They move more by running than by hopping. They fly very little; their wings are short and rounded. Many species (*Scytalopus*) have a short tail, others have a strikingly long one (*Merulaxis*, *Psilorhampus*). The tail is always soft and therefore not very helpful to steering in flight. One of the special characteristics of the tapaculos is that they cock up their tails when they get excited, which is particularly impressive with the long-tailed species; in this respect they resemble the wrens (Troglodytidae), to which they have other similarities. It is this characteristic that has given them the name 'tapaculo', from the Spanish.

The tapaculos are usually dark, some species (certain *Scytalopus* spp.) being almost uniformly black; these birds spend their life hidden in dark thickets. Other species like the Barrancolino *Teledromas fuscus*, which live in the dry bush pampas, have a light colouring like that of larks, in keeping with the light-coloured surroundings in which they live. In this they resemble certain ovenbirds (Furnariidae), with which they share this habitat. Males and females are often coloured alike (e.g. *Liosceles thoracicus*), but sometimes not (e.g. *Merulaxis* spp.).

Food. The food consists mostly of insects, including larvae, and spiders; in some cases stomach contents have been found to include fibres and seeds.

Voice. It is as easy to hear the tapaculos as it is difficult to see them. Their song consists of more or less continuous monotonous calls. These are rather rough, as with *Scytalopus* spp., or melodious (e.g. the turcos *Pteroptochos* spp.); certain species produce a strikingly pure scale, going up or down (*Merulaxis ater*). The females also sing. Frequently the voice, like that of a ventriloquist, is hard to localize. They have sharp monosyllabic call-notes for attracting and warning.



Ocellated Tapaculo *Acropternis orthonyx*. (*P.J.K.B.*).

Breeding. The tapaculos build their nests on the ground, sometimes in burrows which they dig (e.g. *Scelorchilus* spp.), or in hollow trees (*Pteroptochos* spp.). There are some species (*Eugralla paradoxa*) that build a ball-shaped nest, with a side opening, in thickets about 1 m from the ground. For building material, the birds use moss, twigs, and so on. The 2–4 eggs are relatively large and uniformly white, although they get quite dirty at times and then appear to be spotted. Both parents share in incubation and raising the young.

Systematic characteristics. There are 12 genera with 28 species from Costa Rica to Patagonia. Half of the genera are monotypic. Chile, with 8 species, has particularly many tapaculos. On the western coast of South America they occur from sea level to an altitude of 4,000 m.

The Huet-huet *Pteroptochos tarnii* has the upper parts and foreneck very dark brown; crown, rump, and belly dark rust-coloured, partly with black bars. It is about 23 cm long and lives like a rail in the heavy underbrush of the forests of Chile and western Argentina, where it is well known because of its loud call; it sounds like *wed-wed-wed*, hence Huet-huet. They have other striking calls also. The nest is in a burrow as much as 50 cm deep, or in a hollow tree-trunk as much as several metres above the ground. Egg measurements are 37 × 29 mm.

The Grey Gallito *Rhinocrypta lanceolata* has a crested head, rust-coloured with white shaft-stripes; the upper parts are greyish olive, the under parts grey, the middle of the belly is white, and the flanks are chestnut. The length is about 20 cm. It is a common inhabitant of some dry grassy and bush-covered plains of Argentina, where it runs about rapidly with crest erect and tail cocked above the back, resembling a tiny domestic fowl (hence its name). It utters chirping calls and builds a large covered nest in thorny thickets.

The male of the White-breasted Babbler *Scytalopus indigoticus* is coloured like a Dipper *Cinclus cinclus*, but is much smaller (length about 10 cm). The female is more dully coloured. The birds live completely hidden in the thickest brush of eastern Brazil, where they move about like mice without making a sound. The song resembles that of the antshrikes *Thamnophilus* spp., consisting of a series of scratchy syllables, gradually gaining in speed. The nest is built on the ground. H.S.

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TARGET TISSUE: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

TARSAL: name of the bones of the 'ankle' (intertarsal joint), the proximal row in birds being fused in the tibiotarsus and the distal row in the tarsometatarsus (see SKELETON, POST-CRANIAL; and LEG).

TARSOMETATARSUS: the bone of the part of the leg commonly spoken of as the 'tarsus', in birds formed by a fusion of tarsal and metatarsal elements (see SKELETON, POST-CRANIAL; and LEG).

TARSUS: see above.

TASTE: the sensory receptors for taste are located in taste buds and the buds consist of a well-defined group of cells in the oral epithelium often associated with the excretory openings of the salivary glands. At the base of the taste bud there is a nerve plexus which gives rise to the fine fibres entering the bud. The shape of the taste buds and the nature of the cells within the bud differ in different bird species. The taste buds consist of a discrete group of modified epithelial cells ovoid in shape with long spindle-shaped receptor cells in the centre in some species (e.g. Mallard *Anas platyrhynchos*) whereas in other species (e.g. Chicken *Gallus*) the receptor cells are conical in shape. The base and sides of the receptor cells are protected by follicular cells which are continuous with the germinal layer of the epithelium. At the top of the bud there is an outer pore which connects the bud to the surface of the mouth. In comparison with mammals, birds have relatively few taste buds (Man, 9,000; Rabbit, 17,000; Hamster, 723; Rat, 1,265; Chicken, 340; Parrot Psittacidae, 350; Mallard, 375) and in many species (e.g. Chicken and Mallard) the majority of taste buds are not in the tongue but in the palate and oral mucosa of the sides of the lower jaw. The taste buds relay gustatory information to the brain in both the glossopharyngeal and facial nerves. Taste buds in the tongue and pharynx are innervated by the lingual and laryngo–lingual branches of the glossopharyngeal nerve and those in the more anterior parts of the mouth by the facial nerve.

Taste sensitivity of birds has been investigated using a number of different techniques. The nature and concentration of chemical solutions the taste receptors are able to detect can be assessed by recording the electrical activity in the nerves which serve the taste buds. Kadono *et al* (1966) showed in the chicken the following response thresholds: sodium chloride 0.025 Molar (m), sucrose 0.125 m, quinine hydrochloride 0.01 m. Responses have been obtained with 0.1 m acetic acid, 0.05 m citric acid and 0.01 m hydrochloric acid. Another electrophysiological method of measuring taste sensitivity is to record the gross electrical activity of the brain surface, the electroencephalogram (Gentle 1975). This provides a measure of sensitivity which is intermediate between the receptor threshold and behavioural measures and may provide a measure of perceived sensitivity. Using this technique, a clear response was obtained with 0.05 m acetic acid, half the concentration which gave a clear response using recordings from the lingual nerves.

Behavioural techniques have also been used to measure taste sensitivity. Mariotti and Fiore (1980) used an operant conditioning technique and have shown discrimination thresholds of 0.034 m sodium chloride solution and as little as 0.005 m for potassium hydrogen carbonate. Oral behaviour has been used successfully (Vince 1977) to measure taste sensitivity in the embryo of the domestic fowl. The number of beak claps shown by the embryo following oral stimulation was used to measure the response to hydrochloric acid, fructose, sodium chloride and quinine hydrochloride at least 2 days prior to hatching.

The preference or aversion shown by birds to a variety of chemical solutions has been investigated using behavioural technique. In some experiments the birds were offered a choice between the test solution and water whereas in other experiments, following a period of water deprivation, they were given either water or the test solution. In both of these experiments it is the amount of fluid drunk which gives a measure of preference. In many species of birds (e.g. Great Tit *Parus major*, House Finches *Carpodacus mexicanus*, pigeon *Columba*, chicken) salt solutions tend to be selected indifferently at low concentrations and rejected at higher concentrations. Some individual chickens have been observed to show a preference for 0.1 m sodium chloride over water and a marked preference for this solution is seen in the pigeon and bantam (Duncan 1962). Herring Gulls *Larus argentatus* have been observed to drink sea water (sea water approximately 0.5 m sodium chloride). Many birds will tolerate a wide range of acidity in their drinking water and Bobwhite Quail *Colinus virginianus* show a preference for sour stimuli. Domestic fowl chicks will tolerate strong mineral acids of pH 2 but in general chickens and pigeons show a pattern of indifference to low concentrations and aversion to higher concentrations. Pigeons show a significant rejection of hydrochloric acid at 0.0075 m and acetic acid at 0.01 m which are comparable in value to 0.005 m acetic acid solution that only just tastes sour to humans. Quail *Coturnix*, Great Tits, chicken and pigeon all reject substances which taste bitter to man, e.g. quinine hydrochloride, sucrose octoacetate. The chicken will reject quinine hydrochloride at a concentration of 0.001 m. The response of birds to sweet solutions is complex. Preferences for some concentrations of sugar solutions are shown by Bobwhite Quail, Great Tit, pigeon, chicken, parrots, Budgerigars *Melopsittacus undulatus* and Broad-tailed Hummingbirds *Selasphorus platycercus*. With regard to hummingbirds it is interesting to note that the nectar of most flowers in Arizona is composed of sucrose, glucose and/or fructose. Indifference to sucrose has been reported in many species including the Herring Gull, Starling *Sturnus vulgaris*, goose *Anser*, Siskin *Carduelis spinus* and Laughing Gull *Larus atricilla* (Kare 1965).

The diet of birds provides a complex mixture of gustatory stimuli which react together. Chickens reject a 10% glucose solution in preference to water (39% preference) as well as a 0.3 m solution of acetic acid (24% preference) whereas a mixture of these solutions results in an intermediate preference value (35.6%). The addition of sodium chloride may make a sucrose stimulus more discriminable to Red-winged Blackbirds *Agelaius phoeniceus*.

The preference or aversion birds show to a gustatory stimulus can be altered by their nutritional state. Short periods of water deprivation (as little as 6 h) significantly reduces the aversion shown by chickens to quinine hydrochloride solutions (Gentle 1976). Work by Hughes and Wood-Gush (1971) showed that chickens fed on a calcium-deficient diet developed a specific appetite for calcium which could occur using gustatory cues. Changes in taste preference for sucrose have been shown to occur in chickens fed a low-energy diet (Kare and Maller 1967). Chickens fed on an energy-sufficient diet show no preference for 10% sucrose solutions but, when fed a diet low in energy, rapidly show a preference for this sucrose solution.

The importance of the sense of taste to different avian species is difficult to assess and much more experimental work is needed on a wider variety of species. The distribution of taste buds in the mouth of the Mallard is directly related to the food pathway in the mouth and would allow the bird to monitor constantly the palatability of the food (Berkhoudt 1977). Birds rapidly learn to avoid unpalatable substances in laboratory experiments, e.g. unpalatable insects (Brower 1969). It has been proposed that taste plays a important role in the development of the system that controls food intake in domestic chicks (Hogan 1977). During the first few days after hatching the chick learns to associate ingestive consequences with the events that precede them and chains of associations are built up until gustatory cues present during ingestion become secondary reinforcers. M.J.G.

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Mariotti, G. & Fiore, L. 1980. Operant conditioning studies of taste discrimination in the pigeon (*Columba livia*). Physiol. Behav. 24: 163–168.

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TATTLER: substantive name of *Heteroscelus* spp. (see SANDPIPER).

TAUTONYMY: the application of one and the same name to a genus and to an included species (see NAME, SCIENTIFIC; NOMINOTYPICAL).

TAXA: plural of TAXON.

TAXIDERMY: the preparation and preserving of stuffed specimens of vertebrate animals.

TAXIS: movement directly towards or away from a source of stimulation; or 'locomotory behaviour involving a steering reaction' (compare KINESIS (2); and see FIXED ACTION PATTERN).

TAXON: general term (plural 'taxa') for any category used in classification, or any particular example of such a category (see CLASSIFICATION; NOMENCLATURE). The fundamental taxon is the species, which represents a real biological entity; this category can be defined generally in objective terms (see SPECIES), even although there is sometimes practical difficulty in applying the definition. All other taxa are either subdivisions of the species or groupings of species—concepts that cannot be defined except in terms involving subjective judgments. In many cases a subspecies may represent an objective reality, e.g. a distinctive form constituting an isolated population (possibly a species in the making—see SPECIATION); but the category in general cannot be defined in such terms. All supraspecific categories are theoretical, representing human ideas of degrees of evolutionary relationship among different species; that these ideas can sometimes be held with substantial confidence does not alter the principle.

The categories used by Linnaeus were 'classis', 'ordo', 'genus', 'species', and 'varietas'. Of these, class and species remain much as they were; order and genus are in practice applied more narrowly, and instances are thus more numerous; while varietas was rather a different concept from the subspecies or geographical race of modern taxonomists. Between order and genus the family has been added, and this taxon has acquired particular importance.

The primary taxa are thus now class, order, family, genus, species, and subspecies. The convention is that every species must be placed in a genus, family, order, and class, even if it be unique at any or all of these levels. A species may or may not be divisible into subspecific forms, i.e. it may be monotypic or polytypic.

Between these primary levels, when it is considered that relationships can be expressed in a more elaborate hierarchical system, secondary categories may be interpolated at will. Thus one may have subclass and superorder, suborder and superfamily, subfamily and tribe, subgenus and superspecies. These are, however, used only as required; it would be pedantic to name, say, a subfamily that would be the only one in its family.

The International Code of Zoological Nomenclature does not deal with any taxa higher than the superfamily (owing to a lack of general agreement); and it does not recognize, for nomenclatural purposes, any categories below the genus except subgenus, species, and subspecies. Only generic and specific names have operative significance in the nomenclature of species, with subspecific names in addition where subspecies are recognized and it is desired to refer to one separately by using a trinomen (see NOMENCLATURE).

For separate categories see CLASS; FAMILY; GENUS; ORDER; SPECIES; SUBSPECIES; also SUPERSPECIES.

TAXON CYCLE: a cyclical evolutionary sequence of expanding and contracting range, associated with diversification and specialization, postulated to account for patterns in the distribution and ecology of species. The concept has been used in analysis of the West Indian avifauna, but has been seriously called into question (Pregill and Olson 1981).

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Wilson, E.O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. Amer. Nat. 95: 169–193.

TAXONOMY: orderly arrangement—the science of classification; the term is often used synonymously with 'systematics', of which study taxonomy, with nomenclature as its tool, certainly forms a large part (see CLASSIFICATION; NOMENCLATURE; SYSTEMATICS). The three phases of systematic work, defined in the article thereon, have been called 'alpha, beta, and gamma taxonomy'.

Discrimination. The taxonomist's first problem is one of discrimination; he must separate and define the forms under study, and then determine the status of each. At this stage he is concerned primarily with the question of species; he has to assign the available material to particular species, and determine the distinctness of each of these in accordance with the objective definition of that category (see SPECIES). Sometimes this may be done on morphological grounds alone, where differences are substantial and clear-cut. Very often it will be possible only with the aid of adequate data on distribution and reproductive isolation. Where such data are lacking, the decision may have to be empirical—and therefore provisional. Even if there is apparent reproductive isolation, there may be no evidence as to whether it is purely geographical (with potentiality of full interbreeding) or constitutional (see SPECIATION).

Secondarily he is concerned with differences between and within populations of a species. There may be a number of allopatric forms sufficiently distinct to be regarded as subspecies (see SUBSPECIES); or a continuous geographical grading of characters (see CLINE); or a collection of sympatric 'morphs' or phases (see POLYMORPHISM); or, again, no more than the individual variation that is never absent. In all this, of course, account has to be taken of differences that are related solely to sex, age, or season.

Phylogeny. The taxonomist's second problem is that of classification, based on his estimate of probable phyletic relationships. For this purpose he requires different criteria; whereas for discrimination it is both convenient and proper to use readily visible characters, provided that they are not too variable, it now becomes necessary to consider what characters are fundamental rather than superficial. This question becomes increasingly important the higher the taxonomic category that is being considered—what shared characters can be regarded as primitive and so probably derived from a common ancestor? Here one must remember that a character is not necessarily primitive merely because it appears to be simple.

Much earlier work on these lines went astray through lack of appreciation of the effects of adaptive convergence; it is now realized that this may produce most striking similarities between species that are only distantly related (see CONVERGENCE). Sometimes the adaptation to a similar mode of life may lead to resemblance in a whole 'constellation of characters', which if reckoned separately might appear to establish a very strong case for relationship. There is the further point that some differences between species, without being fundamental, may not be directly (or at least obviously) adaptive; they may be by-products of the gene pattern, linked constitutionally with characters having adaptive value for natural selection (see GENETICS; NATURAL SELECTION).

Taxonomic characters. Towards the solution of these problems, the taxonomist has an increasing variety of criteria. General characters of external morphology remain predominant, as they are the most readily described and the most convenient to preserve for record in the museum specimen. In dealing with the more distant relationships, involving the higher taxonomic categories, greater recourse will be had to internal anatomy, and here osteological characters are particularly convenient. Research may, however, have to extend as far as cytological and embryological characters, or invoke laboratory tests for physiological differences such as in the chemical composition of the tissues (see DNA AND PROTEINS AS SOURCES OF TAXONOMIC DATA).

The trend, however, is not all towards the laboratory. Increasing taxonomic use is made of characters of the living bird observed in the field. Knowledge of geographical range is in any event essential. Among the ecological factors, parasites may be particularly helpful, in that their own phylogeny may be parallel to that of their hosts (see ECTOPARASITE). In the ethological sphere, behaviour related to sex (song, display) is of special importance owing to the part that it plays in the crucial matter of reproductive isolation. A.L.T.

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TAYLOR-BIRD: substantive name of *Orthotomus* spp. (see WARBLER (1)).

TCHAGRA: substantive name of *Tchagra* spp. (see SHRIKE).

TEAL: substantive name (unchanged in plural) of various small species of duck, properly of some in the genus *Anas* (used without qualification in Britain for *A. crecca*) but also applied to others (see DUCK).

TECTRIX: (plural 'tectrices') a covert, i.e. one of the feathers fulfilling the function of upper or lower wing coverts or tail coverts (see TAIL; WING).

TEETH: (plural of 'tooth'), not found in recent birds, even as embryonic rudiments. Teeth of reptilian type were, however, characteristic of earlier forms (see ARCHAEOPTERYX; FOSSIL BIRDS). In the modern bird the place of teeth is taken by the cutting edges (tomia) of the horny mandibles; and in some groups there are also ridges or papillae, which may even be partly calcified (see BILL). For another structure, in no sense truly dental, see EGG-TOOTH.

TELEMETRY: see RADIO TRACKING AND BIOTELEMETRY.

TELEOPTILE: term applied to plumage subsequent to (and especially that immediately following) the 'neossoptile' or natal down plumage, if any (see PLUMAGE).

TEMPERATURE, BODY: see GROWTH; HEAT REGULATION; TORPIDITY; also INCUBATION; MEGAPODE.

TENDON: see under MUSCULATURE.

TERN: substantive name of most species of the family Sternidae (Charadriiformes, suborder Lari); in the plural, general term for the family. The group is treated as a tribe of the Larinae (see GULL) by some authors including Moynihan (1959). The other substantive name used is 'noddy' for one genus. Some terns, like the Caspian Tern *Hydroprogne caspia*, the biggest representative, and Gull-billed Tern *Gelochelidon nilotica*, are conspicuously gull-like. Skimmers (Family Rynchopidae) are also close relatives, bearing most resemblance to one monotypic genus, the Large-billed Tern *Phaetusa simplex*.

General and systematic characteristics. Terns and noddies comprise 42 medium-sized species (20–56 cm). The sexes are alike throughout. Most (22 species) belong to the 'black-capped' *Sterna* group which, with long pointed wings, deeply forked tail, light build, and graceful, buoyant flight has earned the common name 'sea swallows'. The best known Palearctic representatives are the Common Tern *S. hirundo* and Arctic Tern *S. paradisaea*. With the exception of 3 'brown-winged' species, the typical plumage is white below, grey mantle and upper wings, with a black crown in breeding dress. Out of the breeding season, obvious changes are the whitening of the forehead, and darkening of bill and leg colour where yellow-red in the breeding season. The black cap is smooth in *Sterna* spp., but partly erectile in the *Thalasseus* group ('crested terns', 7 species), represented in Europe by the Sandwich Tern *S. sandvicensis*. The generic separation of *Thalasseus* from *Sterna* is by no means widely recognized, but is finding increasing favour on various behavioural grounds. The classic foraging technique of *Sterna* spp. and their close allies is plunge-diving head first into water from a height to seize small fish in the slender, tapering bill. Immersion is brief, with no propulsion underwater other than initial impact. Accomplished hovering in some species facilitates hunting. The feet are webbed, with the hallux vestigial. 'Marsh terns' (*Chlidonias*, 4 spp.) of which the Black Tern *C. niger* is the most familiar, and noddies (3 *Anous* spp., 1 *Procelsterna*), are distinguished from *Sterna* spp. by behaviour and morphology, both showing varying degrees of darker plumage. With all dark-brown bodies and whitish caps, the *Anous* spp. are virtually the 'negative' colour scheme of the *Sterna*/*Thalasseus* group, while their tails are wedge-shaped. Sometimes called White Noddy, the singular White (or Fairy) Tern *Gygis alba* has pure white plumage all over. Strikingly aberrant is the Inca Tern *Larosterna inca* of South America with slate-blue plumage, yellow fleshy wattles at the gape, and a white 'handlebar' moustachial plume near each eye.

Habitat and distribution. Terns and noddies enjoy world-wide distribution, from the Arctic to the Antarctic. Some, like the Little Tern *S. albifrons*, Roseate Tern *S. dougallii*, Caspian and Gull-billed Terns are, indeed, among the most cosmopolitan of all seabirds. Marsh terns, as implied, are (with the exception of the Black Tern in winter) largely independent of the sea, inhabiting freshwater marshes, lakes, and rivers right into the heart of continental land masses. Terns of the black-capped *Sterna*/*Thalasseus* group, embracing all except the highest latitudes, are essentially inshore species, favouring coastal waters, estuaries, rivers, and large inland water bodies. By contrast, the brown-winged *Sterna* spp. forage offshore in tropical and subtropical waters; among them, the Sooty Tern *S. fuscata* is the most pelagic of all terns, exploiting rich upwellings and narrow fronts often hundreds of kilometres offshore, even in the breeding season. Although also tropical and subtropical maritime terns, the noddies do not generally range so far offshore.

Populations. Total numbers vary enormously from species to species. Environmental pressures have reduced some to dangerously low levels, especially locally. According to the annual RSPB Tern Survey, Britain and Ireland supported about 2,000 pairs of Little Terns, while the total European population of Roseate Terns is only 550 pairs. Again, the Damara Tern *S. balaenarum*, endemic to southern Africa, has been reduced to 3,000 birds. By contrast, widely distributed pelagic species can number tens of millions, even locally, e.g. the Christmas Island (Pacific) population alone of Sooty Terns has been estimated at 14 million birds.

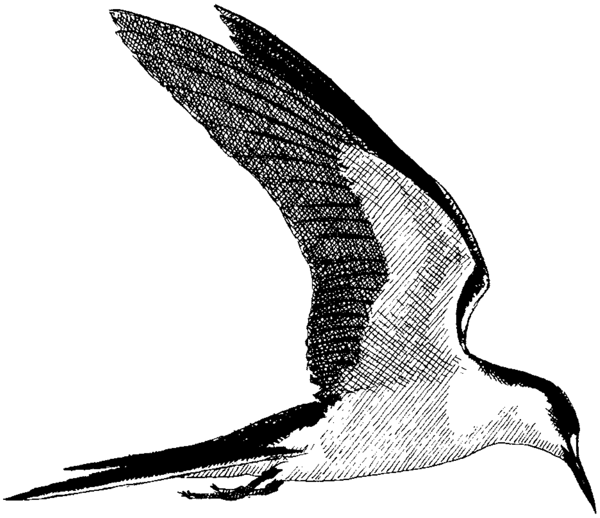
Movements. Most terns are migratory to varying degrees. The Arctic Tern is the most wide-ranging migrant known: those breeding north of the Arctic circle up to 82°N and wintering in Antarctic waters must cover a minimum of 12,800 km each way, while the round trip for some, deviating to exploit latitudinal wind belts, must entail 35,000 km. *Sterna*, *Thalasseus*, and *Chlidonias* species breeding in temperate latitudes migrate to the tropics outside the breeding season, seeking the coasts of Africa, Central and South America, India, or Australasia, depending on the longitudinal breeding range of the population. The vast majority migrate by sea though overland movements are undertaken by marsh terns, and even some marine terns. Prior to the southward migration, a post-fledging dispersal of juveniles and their parents from the natal colony has been shown for Sandwich, Common and Arctic Terns in the Northern Hemisphere, perhaps in response to local competition for food, or to exploit traditional post-breeding feeding grounds. Lateral migration is known for species confined to tropical and subtropical regions; juvenile Sooty Terns from the Dry Tortugas, Florida, cross the Atlantic to the Gulf of Guinea, and Seychelles juveniles likewise disperse east as far as Australasia. Moult of terns is typically arrested during migration; primaries are often moulted in 'periodic stepwise' fashion, which allows rapid replacement without impairing flying ability.

Food. The diet of marine terns is mainly fish, squid and crustaceans, the latter especially in polar regions, occasionally supplemented by pelagic molluscs and worms. Gull-billed Terns also feed on small terrestrial vertebrates, and insects hawked in the air, or plucked on the wing from the water surface; marsh terns likewise take insects, also small fish, frogs, tadpoles and leeches. Tropical terns are strongly, sometimes wholly, dependent on the actions of predatory fish, tuna especially, which send shoals of prey fleeing to the surface to be caught by dipping, or even in the air. Here noddies often use their feet for pattering, storm petrel style, and Common Noddies *Anous stolidus* are known to settle on the water surface and dabble. Most terns are diurnal feeders, though night feeding has been recorded in the tropics (Sooty Terns and even Palearctic terns), especially in moonlight. Birds far offshore may roost briefly on the water, but sustained flight for long periods is apparently feasible too. Prey for young are brought back crosswise in the bill by most terns, but regurgitated by noddies and 'brown-winged' terns.

Behaviour. Terns are highly gregarious, assembling to feed, roost, breed, and boldly mob predators at the colony. Essentially monogamous, pair bonds tend to persist from year to year. Breeding may begin as early as 2 years old, but commonly not till 3 or 4 in Palearctic sea terns, later in tropical terns if the Sooty Tern (4–9 years, average 6) is typical. Longevity is considerable, with up to 30 years or more recorded. Colonial breeding is normal, nesting densities varying with species and habitat. Colonies can number tens of thousands and inter-nest distance can be a mere bodylength in *Thalasseus* spp. Nesting territories serve the ground phase of courtship and pair formation, courtship feeding, copulation, nesting, and concealment and location of young. Nest-site fidelity between years is high in some species, though *Thalasseus* spp. are prone to shift the colony site altogether. Early courtship involves an elaborate climbing and gliding aerial display, ground courtship often a circling parade of partners.

Voice. Terns are highly vocal, noisy birds. The repertoire is based on harsh, clipped and drawn-out cries, or softer mewing and 'gurring' notes, serving territorial advertisement, aggression, and contact, among others. Fledged young generally have high-pitched, whistling begging notes.

Breeding. Usually seasonal, and annual, though some tropical terns breed at sub-annual intervals, with nesting usually continuous in the population as a whole. In a few cases, however, sub-annual synchronous breeding occurs, notably in Bridled Terns *Sterna anaethetus* and the highly adaptable Sooty Tern, which exhibits breeding intervals varying from 6, through 9–10 to 12 months, depending on local conditions. The nesting area is usually a flat, open piece of ground, often an island, sandy



Sooty Tern *Sterna fuscata*. (*B.P.*).

headland, shingle bed, or marsh, remote from disturbance. Noddies, however, nest on trees, bushes, and cliffs while Inca Terns, and sometimes Roseate Terns, are burrow-nesters. Noddies and marsh terns build a reasonable platform of vegetation; ground-nesting terns at best only a thinly-lined scrape, while the White (Fairy) Tern lays its single egg on the bare branch or leaf of a tree or on coral boulders and cliffs, the chick having well-developed claws for anchorage. Both sexes of terns share nesting duties from the outset. The normal clutch of usually cryptic blotched-olive eggs varies from 1 in tropical to 2–3 in higher latitudes, and incubation lasts 3–4 weeks. Downy at hatching, chicks are semi-precocial in ground nesters, occasionally crèching when older in *Thalasseus* and some *Sterna* spp. The fledging period varies from 1–2 months, but parental care (feeding) continues, sometimes for several months, and on into the winter quarters, while the young learn self maintenance.

See photos CONSERVATION; NEST; PARENTAL CARE; PERCHING. E.K.D.

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TERNLET: name sometimes applied to the smaller noddies *Anous* spp. (see TERN).

TERRITORY: a defended area. The area occupied by an individual, a pair or a group of birds is referred to as a HOME RANGE. When this area is defended against other individuals, usually of the same species, it is called a territory. Territories are occupied in a wide variety of contexts whenever scarce resources, such as space, food or mates, are economically defendable.

Some territories provide all the resources that a bird needs; for example Tawny Owls *Strix aluco* occupy a fixed territory for the whole of their adult lives. Other territories may simply consist of a nest site (e.g. some seabirds) or a food supply (nectar-feeding birds). Many territories are fixed in space but they may also be mobile as when some birds, such as warblers, just defend the bushes in which they are foraging at the time.

The three main types of benefit from territorial defence are food, mates and predator avoidance.

Feeding territories. There have been few precise quantitative studies of the costs and benefits of the defence of a food supply. Many species have smaller territories where their food supply is more dense. Hummingbirds and sunbirds feed on nectar and although the size of their territories varies by several hundredfold, each contains approximately the same number of flowers. It can be calculated that the nectar production from this number of flowers is just sufficient to support an individual's daily energy requirements.

Many species vary their defence strategies depending on the food supply. When food levels become very high, intruder pressure increases and an owner may give up defence of the territory. At the opposite extreme, the food level may become so low that, even with territoriality, a bird is unable to meet its energy requirements and so it abandons the territory. Therefore, there is an upper and a lower threshold for economical defence.

Mating territories. In some species males defend territories to which females are attracted for mating. The territories may contain vital resources which the females require, such as food or nest sites. If the resources are patchy in distribution, then some males may be able to defend better-quality territories than others, and therefore achieve greater reproductive success (see POLYGAMY).

For example male Orange-rumped Honeyguides *Indicator xanthonotus* defend bees' nests. Females visit the bees' nests to feed on the wax and the males copulate with them on the territory. Males with the best food supplies get the most copulations. Similarly, male hummingbirds that defend the best nectar supplies attract the most females. Males of these species in effect trade food for sex.

In other species males defend potential nest sites. Polygyny may occur if the differences among male territories are so great that females do better by pairing with an already mated male on a good-quality territory rather than with a bachelor male on a poor one. In the Red-winged Blackbird *Agelaius phoeniceus* certain types of vegetation provide safer nest sites from predators, and hence result in greater fledging success. Males whose territories contain the most of this suitable vegetation attract the most females. In the Lark Bunting *Calamospiza melanocorys*, one of the major factors responsible for nestling mortality is exposure to the heat of the sun. Males defending territories with the most amount of shade may attract two mates while those with exposed territories fail to attract any females.

Not all mating territories contain resources. In some cases the males aggregate at traditional, communal display areas, or leks, where they defend patches of ground and compete for dominance status. The territories on a LEK may just be tiny bare areas no more than a metre across, but they are vigorously defended against other males. Females only visit the leks in order to mate. After copulating they leave to lay their eggs elsewhere. In all the leks that have been studied, almost all of the copulations are performed by a few males, usually those who are defending the central territories. For example, in a study of the White-bearded Manakin *Manacus manacus* where there were 10 males on a lek, over 70% of the copulations were performed by one male. Similarly, in a study of the Sage Grouse *Centrocercus urophasianus*, on a lek of 14 males, over 80% of the copulations were achieved by the 3 central males.

The most successful males on a lek are usually the older males. Young birds remain on peripheral territories and move into more central locations as vacancies arise. In the Ruff *Philomachus pugnax* there appear to be at least two different strategies on the lek. Resident males, which have dark head tufts and usually dark ruffs as well, defend territories, while satellite males, which have white tufts and ruffs, adopt the sneaky strategy of attempting to steal copulations while the residents are busy chasing off intruders.

It is likely that, with more detailed observations of individuals in marked populations, many more examples will be discovered where males employ various strategies to compete for food or mates. In some sparrows *Zonotrichia*, as well as the conspicuous territory holders, there appears to be an 'underworld' of roaming individuals.

So far, it has proved difficult to measure the reproductive success of males who employ different strategies. For example, even if territory owners in the centre of a lek enjoy the greatest mating success in any one season, this does not necessarily mean that over a whole lifetime they are the most successful. Non-territorial males may copulate less each season but live for longer because they do not incur the high costs of territory defence.

Territories and predation. By defending a territory and thereby spacing out a nest site from those of neighbours, predation may be reduced. Nests of the Great Tit *Parus major* that are spaced furthest from their nearest neighbours suffer least predation by Weasels *Mustela nivalis*. Gull nests in large territories are less likely to be plundered by predatory crows or cannibalized by other conspecifics. The reason that closely-spaced nests suffer greater predation is that whenever predators are successful in finding a nest, they intensify their search in the immediate vicinity.

When adults actively defend their nest sites, then the opposite situation may occur; pairs with small territories in dense colonies may suffer least predation because closely packed adults form a more effective means of defence (e.g. Guillemots *Uria aalge*).

Interspecific territoriality. Birds usually defend their territories only against members of the same species; this makes sense because other species usually exploit different resources and defence against them would entail costs for little resulting benefit. However, sometimes it pays to defend against other species. For example, two species that nest in similar places may defend mutually exclusive territories, perhaps because a predator could be searching for the nests of both species at the same time (e.g. Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *A. schoenobaenus* in some habitats).

Interspecific territoriality may also occur where several species are exploiting the same food supply. In winter, Pied Wagtails *Motacilla alba* not only evict conspecifics from their feeding territories but also other insectivores including Grey Wagtails *Motacilla cinerea* and Meadow Pipits *Anthus pratensis*. Sometimes nectar-feeding birds may even evict bumblebees from their patches of flowers.

Group territoriality. Sometimes a territory is defended by a group, especially in those species where young from previous broods remain on the territory for several years (see CO-OPERATIVE BREEDING). Group territorial behaviour may occur where adult survival is high and suitable habitat is fully occupied, so that it pays the young to stay longer on their natal territory. The young may help to defend the territory as a 'payment' for the right to remain. In other species, unrelated birds may share a territory. For example, winter 'pairs' have been reported in Blackbirds *Turdus merula* and Pied Wagtails. These pairs are not concerned with breeding: they probably form simply because economical defence of a territory is only possible if the defence is shared between two birds.

Mechanisms of territorial defence. There is a three-tier system of defence in song birds. Song may act as a long-range signal that deters potential trespassers; visual displays are used to repel actual trespassers and then, if an intruder persists, it is chased and attacked. Experiments have investigated the role of DISPLAYS in territorial defence. Male Red-winged Blackbirds have a patch of bright red and yellow feathers on their wings which they display to intruders. If these feathers are painted black, the owners become much less successful at maintaining their territories. In another experiment, some males were prevented from singing by an operation which involved cutting the nerves to the vocal cords. These muted birds were less successful at keeping out intruders than were controls.

If male Great Tits are removed temporarily from their territories and replaced simply with a loudspeaker that broadcasts their song, then intruders are still kept at bay. Therefore song alone can act as a signal to tell other birds that a territory is occupied (see VOCALIZATION).

Territories and populations. In many species, when territory owners are removed experimentally or die naturally, their places are rapidly taken over by new birds. This suggests that potential settlers can be prevented from gaining a territory. In the Great Tit, the replacements come from poorer quality territories. In the Red Grouse *Lagopus lagopus scoticus* replacements come from flocks of non-territorial birds which would not have been able to breed and would almost certainly have died in the absence of a territory.

These observations show that territorial behaviour can limit population density. This does not mean that the limitation of populations is a selective advantage of territoriality. Such reasoning would imply natural selection at the level of the population and there are strong theoretical reasons for supposing that this does not normally occur. What it does mean is that the limitation of population density can come about as a consequence of territorial behaviour, which has itself evolved for some individual advantage. For example, the number of Tawny Owls in Wytham Wood near Oxford has remained constant for many years. This is because each pair requires a certain area of woodland in which to hunt. As a consequence, there is only enough room for a certain number of territories in the wood. The best-quality owls win territories and the chance to breed, while the rest are excluded and probably die. N.B.D.

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TERTIARY: or 'tertial', a term preferably treated as obsolete; at one time applied to the few innermost secondary remiges, especially in cases where these are differentiated in shape and colour from the other flight feathers borne on the ulna. The term has also been applied to feathers borne on the humerus in cases where they are developed to function as additional remiges instead of merely as coverts (see PLUMAGE; WING).

TESTIS: plural 'testes'; the male gonad on each side (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

TESTOSTERONE: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; and AGGRESSION.

TETRAKA: *Phyllastrephus madagascariensis*, a BULBUL endemic to Madagascar.

TETRAONINAE: see under GALLIFORMES; GROUSE.

TETRAPOD: a technical term literally equivalent to the ordinary word 'quadruped' but used in a special sense to embrace all the classes of four-limbed, essentially terrestrial, vertebrate animals—thus including birds.

THALAMI: parts of the forebrain (see NERVOUS SYSTEM).

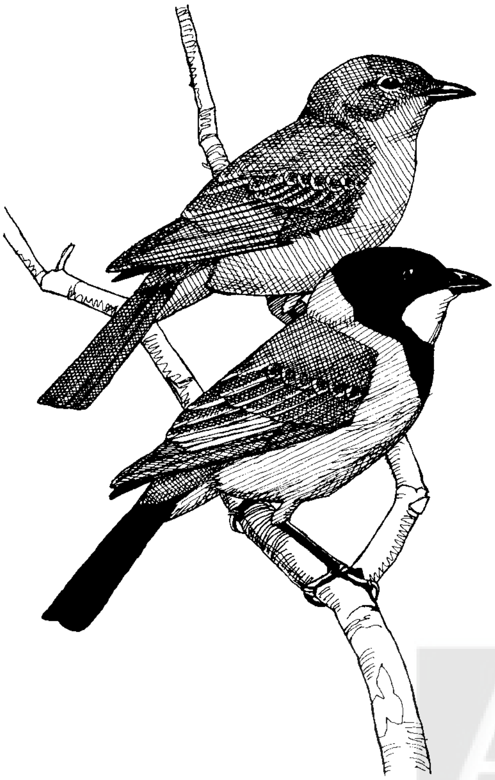
THECA: a sheath-like covering, as in such particular instances as PODOTHECA, RHAMPHOTHECA, and RHINOTHECA.

THERMOREGULATION: see ENERGETICS; HEAT REGULATION; RESPIRATORY SYSTEM; TORPIDITY.

THICKHEAD: substantive name, alternatively 'whistler', of species of the family Pachycephalidae (Passeriformes, suborder Oscines); in the plural, general term for the family. In Australia other substantive names used for several species are 'thrush', 'shrike-thrush', 'shrike-tit', and 'bellbird'. Mayr (1967) divides the group into 4 polytypic genera (*Pachycephala* with 26 species, *Pitohui* with 7 species, *Colluricincla* with 5 species, and *Falcunculus* with 3 species which are sometimes considered conspecific), and 5 monotypic genera (*Eulacestoma*, *Hylocitrea*, *Oreoica*, *Pachycare* and *Rhagologus*). The Australian robins in *Eopsaltria* are now included in the Muscicapidae, and the genera *Coracornis* and *Myiolestes* have been absorbed into *Pachycephalus* and *Colluricincla* respectively. A comparison of their egg-white proteins suggests that it is probable that most, if not all, members of the family are part of the Australian endemic complex (Sibley 1976).

Characteristics. Thickheads range in length from 12.5 cm (Golden-faced Pachycare *Pachycare flavogrisea*) to 28.0 cm (Rusty Pitohui *Pitohui ferrugineus*). All have robust bodies, thick and rounded heads, and imposing strong bills that are thick and laterally compressed in many species, and have a shrike-like hook at the tip; hence the name shrike-thrush for some species. Rictal bristles are few or absent in the Mottled Whistler *Rhagologus leucostigma*, the Wattled Shrike-tit *Eulacestoma nigropectus* and in *Falcunculus* species, but are most pronounced in the Black Pitohui *Pitohui nigrescens* which is the most shrike-like of the genus. Thickheads are relatively inactive, slow moving and tame.

The plumage colours of the majority of thickheads are dull rufous browns and greys, with some green, white and black. In contrast, the Golden Whistler *Pachycephala pectoralis*, the shrike-tits (*Falcunculus*



Golden Whistler *Pachycephala pectoralis,* female and male (below). (*N.W.C.*).

species) and the Golden-faced Pachycare all have bright yellow underparts. The Golden Whistler has the greatest geographical variation of any bird (at least 73 races have been described), the colours of the females ranging from dull rufous brown to the bright yellow of males. Conspicuous crests are found in the Crested Bellbird *Oreoica gutturalis,* Crested Pitohui *Pitohui cristatus* and the shrike-tits. The shrike-tits (*Falcunculus* species) and the Wattled Shrike-tit have wedge-shaped bills, and the latter has pink wattles at the base of its bill. The whistler on the Lesser Sunda islands, *Pachycephala nudigula,* has naked areas of skin about the throat but this and the other adornments previously listed are unusual in the family.

The sexes of several whistlers are distinguishable, females being either plain greyish or less boldly marked and coloured than the male. In the Mottled Whistler the female is much more heavily patterned than the male. In other genera the sexes cannot be easily distinguished in the field. Juveniles are deep rufous, streaked, or spotted, or else similar to the female.

Habitat, distribution and movements. Thickheads are found in a wide variety of habitats ranging from mangrove and rain-forest to much drier woodlands and riverine forests. The Brown-breasted Shrike-thrush *Colluricincla woodwardii* is found only on sandstone ranges where there are cliffs and gorges. Although they are concentrated in New Guinea and Australia, some species have a much wider distribution and the family ranges from south-east India through Malaysia, Borneo, and Sulawesi, northwards to the Philippines and eastwards to Fiji, Tonga, Samoa and other islands. Ringing studies in Malaya have shown whistlers to be resident there and this is likely to be true for most species. However, some are nomadic and the Rufous Whistler *Pachycephala rufiventris* is migratory in south-east Australia.

Food. The majority of thickheads feed on insects that are gleaned methodically either from the foliage or the branches, trunks and bark of trees or else from the ground. The Wattled Shrike-tit and the *Falcunculus* species, however, use their massive bills to strip and plough into bark for insects. The White-breasted Whistler *Pachycephala lanioides* often feeds on small crabs taken from mangrove swamps, and the Grey Shrike-thrush *Colluricincla harmonica* sometimes eats eggs, small birds, and invertebrates. In contrast, fruit is the sole diet of the Mottled Whistler and of *Hylocitrea bonensis,* and some fruit is taken by some pitohuis.

Behaviour. Whistlers, shrike-thrushes and other Australian members of the family are strongly territorial when breeding but solitary outside the breeding season. Shrike-tits and the Crested Bellbird often form parties that are thought to be families. In contrast, several pitohuis in New Guinea are always found in small parties of 3–6 individuals. They respond to playback of their calls and are often found in mixed parties containing other species of similar size and colour to the pitohuis. It has been suggested that these social groups have played a role in the evolution of similar plumage and in some cases similar voice patterns (Diamond and Raga 1978). Before its eggs hatch, the Crested Bellbird paralyses hairy caterpillars, known as bush-worms, by squeezing them. They are then put around the nest rim.

Voice. Many species of whistler are renowned for their explosions of song. Their calls are higher pitched and the sequence of notes longer than those of shrike-thrushes but these also have strong, mellow, and beautiful calls. The Crested Bellbird is ventriloquial and makes one of the most unusual and lovely sounds of inland Australia. The songs of the pitohuis are similar in quality to shrike-thrushes and at least two have a loud and striking simultaneous duet (Diamond and Raga 1978).

Breeding. Whistlers and shrike-thrushes build cup-shaped nests placed in forks of trees, in cavities or hollows. The terrestrial species use caves or cracks in rocks as nest sites. The nest of the Australian shrike-tits has a much deeper cup than the others, is decorated with moss and lichen and is placed among thin upright branchlets that are snipped off above the nest by the male. Materials used in nest construction are strips of bark, grass, rootlets, moss and other similar materials. Nests are placed at a variety of heights: 1–5 m by whistlers, up to 10 m for some shrike-thrushes, and as high as 10–20 m by Australian shrike-tits. Clutch sizes vary as follows: Bellbird, 3–4; whistlers and shrike-thrushes, 2–3, sometimes 4 or 5; and pitohuis, 1–2. The eggs have a ground colour of either cream or pearly white, sometimes tinged with pink, and are spotted with shades of browns and greys.

No incubation or nestling periods are apparently available but it is known that in most species both sexes incubate and tend the young. One exception is the White-breasted Whistler, of which the female alone takes responsibility. In New Guinea the Grey Shrike-thrush *Colluricincla harmonica* has raised 3 broods in the same nest, 2 in the spring and one 6 months later. Distraction display by both sexes of the Gilbert Whistler *Pachycephala inornata* and Buff-breasted Whistler *Pachycephala rufogularis* has been observed when ground predators have approached young.

H.J. de S.D. and L.G.G.

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THICKKNEE: name collectively used for members of the family Burhinidae (Charadriiformes, suborder Charadrii) based upon the characteristic thickening at the tibiotarsal joint (not the knee joint as the name implies). Other names for members of this family include 'Stone-curlew', 'Stone-plover', 'Norfolk Plover', 'dikkop' (Afrikaans origin), 'willaroo' and 'goggle-eye'.

The 9 species of thickknees are divided into 2 genera, *Burhinus* and *Esacus.* The latter has 2 species of which the Beach Curlew *E. magnirostris* is sometimes classified as *Orthorhampus magnirostris.* Also the 2 species of *Esacus* are sometimes classified as 2 subspecies of *E. magnirostris.*

Characteristics. The species in the genus *Burhinus* most closely resemble plovers (Charadriidae) being about the size of a Lapwing *Vanellus vanellus* (35.5 cm), except the larger Double-striped Thickknee *B. bistriatus* (51 cm), and having a short, stout bill. The 2 *Esacus* species are larger (up to 52 cm) with relatively long and massive bills, slightly upturned in the Great Stone-curlew *E. recurvirostris.* Thickknees have the nostrils as long slits perforated from side to side. The head is large and broad with abnormally large, staring yellow eyes, an adaptation to a predominantly nocturnal existence. The bare legs are long, yellowish or greenish, and the tarsus is reticulated all round. There is an obvious thickening at the tibiotarsal joint. There is no hind toe and the 3 toes are partially webbed, the middle one having the inner side of its nail dilated. The wings are long and pointed in some species, short and rounded in others. The plumage tends to be cryptic, blending well with the surroundings. In colour this is brown, grey-brown, or buff, barred, streaked and mottled, with a conspicuous wing and tail pattern in some species. The side of the head has broad stripes, especially noticeable in *Esacus*, *B. bistriatus* and the Peruvian Thickknee *B. superciliaris*. These species are also more uniform above with little or no streaking on the breast. The sexes are alike and the juvenile plumage resembles the adult but is usually paler. The downy young have extremely cryptic plumage, the chicks usually 'freezing' when danger threatens and relying on the mottled down pattern with dark stripes to escape detection.

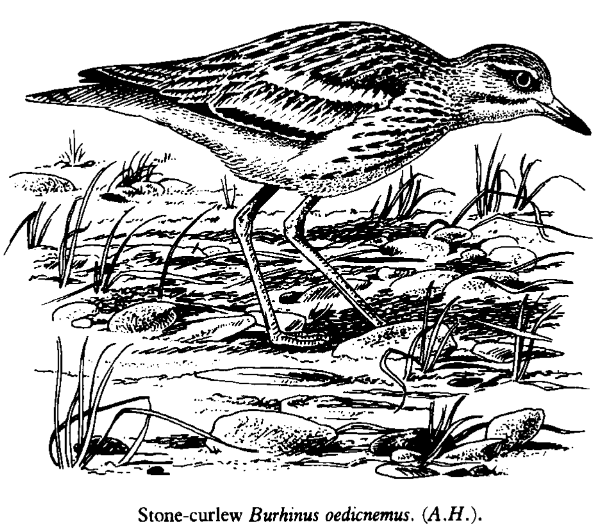
Habitat. Thickknees are mainly birds of dry, open, sandy or stony habitats. In the case of the Spotted Thickknee *B. capensis* and *B. superciliaris* scattered bushes are included in the habitat, and the Bush Curlew *B. magnirostris* is found in both sparse woodland and open country. Four species show an affinity with water: the Senegal Thickknee *B. senegalensis*, mainly along sandy river beds, the Water Dikkop *B. vermiculatus* and *Esacus recurvirostris* along river beds and the coastline, and *Esacus magnirostris*, exclusively coastal.

In Britain and some other west European countries the previous habitat of the Stone-curlew *B. oedicnemus* has undergone radical changes this century due to the ploughing of much of the stony downland and heathland to make way for forestry and agriculture.

Distribution. Thickknees are widely distributed in the Old World, with 2 species in the Neotropical Region. *B. oedicnemus* is the only representative in Europe, the breeding range extending from south-east England to North Africa eastwards to central Asia, India and Burma. In Africa there are 3 other breeding species apart from *B. oedicnemus*: *B. vermiculatus*, extending from tropical to southern Africa, *B. senegalensis* found in east Africa from Egypt to Kenya and Uganda and in West Africa to Gambia and Senegal, and *B. capensis* distributed throughout Africa south of the Sahara except in the southwest. In Asia *E. recurvirostris* is found on the Indian subcontinent and Burma and *E. magnirostris* inhabits the coasts from the Andaman Islands to the Solomon Islands, extending south to the coasts and offshore islands of north Australia. Also widely distributed in Australia is *B. magnirostris*. The 2 Neotropical species are *B. bistriatus* of Central America, including Hispaniola, and South America to north Brazil, and *B. superciliaris* found from Ecuador to southern Peru.

Populations. For most species there is very little information about populations. *B. oedicnemus* in Europe is known to have declined considerably since the mid-19th century and the species is now extinct in The Netherlands, West Germany and possibly East Germany. The decline is thought to be mainly due to an increase in cultivation and afforestation. *B. magnirostris* in Australia is also reported as becoming much scarcer in parts of its range.

Movements. Most species of thickknee are sedentary or show only local movements. The exception is *B. oedicnemus*, which is a summer visitor in the northern part of its range, although elsewhere it is considered resident. Relatively few *B. oedicnemus* have been ringed but recoveries from Britain show movement in a south–south-west direction through France in the autumn (where many are killed) to Iberia, where some certainly winter, with one interesting recovery in Sierra Leone, West Africa. There is a large influx of this species in north tropical Africa during the winter but the origins of the birds are unknown.



Stone-curlew *Burhinus oedicnemus*. (*A.H.*).

Food. Thickknees are probably opportunist feeders taking whatever they come across during their mainly nocturnal foraging. Prey is seen or heard up to several metres away and is usually approached rapidly. When close to the prey the thickknee takes on a heron-like stalking posture and stabs swiftly. Although no detailed studies of food have been made, the list of prey items recorded is long and varied; insects, especially Orthoptera and Coleoptera, worms, molluscs, crustaceans (mainly taken by *Esacus* sp.), amphibians, small reptiles, small mammals, birds' eggs and young and occasionally seeds and other vegetation. Most information on food has come from stomach analyses, but pellets of indigestible remains also contain useful information and a sample for *B. oedicnemus* from eastern England yielded 320 prey individuals belonging to at least 53 species of insect; mainly Dermaptera, Coleoptera (especially Carabidae, Staphylinidae and Curculionidae) and Hymenoptera.

Behaviour. Generally speaking, thickknees are most active from dusk to dawn and spend most of the day under the shelter of a bush, where they can be extremely difficult to detect. Sometimes they live in close association with man, *B. capensis* frequenting large lawns in city parks in some South African urban areas and *B. senegalensis* sometimes nesting on house roofs in Egypt.

Although thickknees are good fliers, they are often reluctant to fly, preferring to run, crouching low over the ground. Unless they are taken by surprise they will hide behind a bush or other cover, or flatten on the ground with outstretched head and neck until the danger has passed.

Most thickknees are gregarious in nature, forming flocks outside the breeding season, with autumn concentrations of up to several hundred birds at traditional sites. Even during the breeding season birds will meet for communal feeding and display activity. Display, involving much calling, is most intense during the early part of the breeding season although at least in *B. oedicnemus* unpaired birds and non-breeding pairs display and call much more than breeding pairs later in the season. Courtship displays and antagonistic displays between rival males make use of the bold black and white wing and tail patterns and the neck is stretched, bowed or arched in different postures.

Both sexes incubate the eggs and care for the young, the off-duty bird usually acting as a sentinel during incubation or the collecting of food for the young after hatching. Both parents react aggressively towards predators such as crow or fox and will also drive intruding sheep or cattle away from the nest.

Voice. Thickknees are generally quiet by day, unless disturbed, but may be extremely noisy at night, especially under moonlit conditions. The vocabulary is poorly understood owing to the largely nocturnal habits. The most common calls are variations of ***kur-leee***, ***ker-looo***, ***tuuee tuuee***, and various shrill whistles and excited, rapid piping and croaking calls.

Breeding. The nest is usually a shallow scrape made by the birds in open ground, often lined with small pebbles or shells. *B. vermiculatus* sometimes lays its eggs on the dried droppings of large mammals such as elephants. This species has another peculiar habit in some localities of nesting among breeding crocodiles. Two eggs are normally laid (only one in *E. magnirostris*), white to buff in ground colour and blotched with irregularly shaped brown markings, making them fairly difficult to see against a stony background. The incubating bird can be extremely difficult to pick out but both sexes incubate and change-overs occur regularly. Hatching takes place after 25–27 days' incubation and the parents carry away the egg-shells and eat them. The chicks are active within a day of hatching; they are covered with thick down and have large, strong legs. The parents take turns to guard the chicks and collect food and they may be moved considerable distances from the nest site. In *B. oedicnemus* the fledging period is approximately 6 weeks. There are records for *B. oedicnemus* of breeding at one year old but other studies suggest that first breeding may be more usual at 2 or even 3 years of age.

R.A.M.

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THIGH: see LEG; SKELETON, POST-CRANIAL.

THINOCORI; THINOCORIDAE: see under CHARADRIIFORMES; SEEDSNIPE.

THORACIC: pertaining to the thorax, or the region of the thorax.

THORAX: the 'chest', being the part of the body between the neck and the abdomen, and containing the heart and lungs (see HEART; RESPIRATORY SYSTEM).

THORNBILL: substantive name, alternately 'thornbill-warbler', of species in some genera (especially *Acanthiza*) of Acanthizidae (see WARBLER, AUSTRALIAN); also used as substantive name of *Chalcostigma* and *Ramphomicron* spp. (for family see HUMMINGBIRD).

THORNBIRD: substantive name of *Phacellodomus* spp. (see OVENBIRD (1)).

THORNTAIL: substantive name of *Popelairia* spp. (for family see HUMMINGBIRD).

THRASHER: substantive name for the genera *Toxostoma* and *Margarops*, and for *Oreoscoptes montanus*, *Ramphocinclus brachyurus*, and (formerly) *Mimodes graysoni* (see MOCKING-THRUSH).

THRAUPIDAE; THRAUPINAE: family and subfamily of PASSERIFORMES, suborder Oscines; TANAGER.

THREAT: see AGGRESSION.

THRESKIORNITHIDAE: see CICONIIFORMES; IBIS; SPOONBILL.

THROAT: see RESPIRATORY SYSTEM; TOPOGRAPHY.

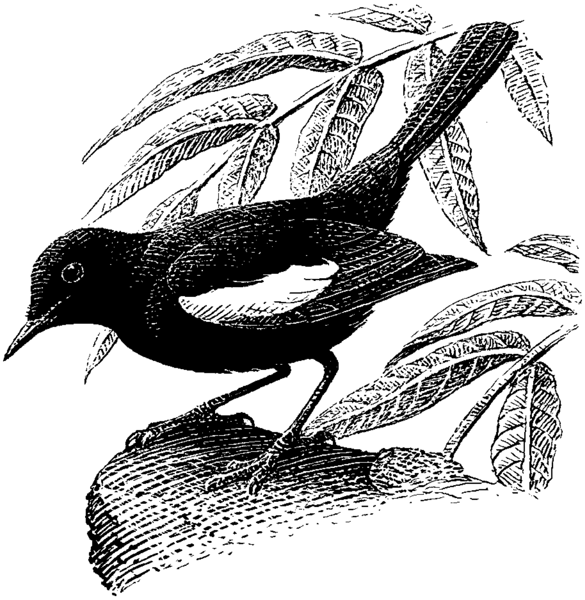
THROSTLE: archaic or poetic form of 'thrush'—cf. German 'Drossel' (see THRUSH).

THRUSH: substantive name of many typical species of the subfamily Turdinae of the Turdidae (Passeriformes, suborder Oscines); in the plural, general term for the subfamily. Many of the smaller species are known as 'chats', and others have special names. The name also appears in the compound 'water-thrush' for *Seiurus* spp. (see WARBLER (2)), and as a substantive name (sometimes 'shrike-thrush') of *Colluricincla* spp. (see THICKHEAD)—and see following entries.

Characteristics. Thrushes in general are slender-billed song-birds of medium size (12–26 cm) with 10 primaries and with a booted tarsus in most cases, the feet being ACUTIPLANTAR and well developed, without syndactyly. The tail is square, rounded, or occasionally emarginate (except in *Enicurus*, in which it is forked), and contains 12 (in one case, 14) rectrices. Rictal bristles are present. The young generally have a spotted first plumage. Adult plumages are generally patterns of black, grey, russet, earth- and olive-browns and white; a few species are largely blue or green, and several have bright patches of red or blue. Sexual dimorphism is marked in many species, the striking male patterns being less distinct or absent in females. There is a single annual moult following the breeding season (prebasic moult). In most species there is no pre-breeding (prealternate) moult; such colour change as occurs at that time is by abrasion or by casting the points of the feathers. There is, however, a partial prealternate moult, involving the body plumage, in some wheatears *Oenanthe* spp. and chats, in one of the rock-thrushes *Monticola* spp., and in White's Thrush *Zoothera dauma*. The syrinx is tracheobronchial. The tongue is non-tubular, with an extensive blade-like reedy tip.

Habitat. Many thrushes are largely terrestrial. Most are arboreal but feed, and in many cases also nest, to varying extents on the ground. They are found in almost every kind of terrestrial habitat, from arid desert or subarctic tundra to dense equatorial rain-forest. A few species occur primarily on open grassland or near water-courses. Many live in close association with man, in farmland and gardens.

Distribution. The subfamily has a world-wide distribution except for the Antarctic and New Zealand (Blackbird *Turdus merula* and Song Thrush *T. philomelos* introduced into the latter). Its approximately 300 species have been divided into several subgroups, of which the simplest arrangement comprises two: the chat-like thrushes and the true thrushes. The greatest number and variety of forms occurs in the Old World, and it may well be that the thrushes have a Palearctic centre of dispersal. Africa has also been an important evolutionary centre, particularly of the chat-like forms. From Eurasia there appear to have been several invasions into the New World, as well as into the Australasian Region and Polynesia. Remote oceanic islands such as Hawaii and Tristan da Cunha have evolved distinctive species of thrushes.


Seychelles Magpie-robin *Copsychus sechellarum*. (*D.W.*).

Chat-like thrushes. The chat-thrushes are small, with more slender legs, more varied nesting habits and plumage, and weaker song than the true thrushes. Many are highly specialized for tropical habitats. The group is diverse and presents the impression of containing more evolutionary end-lines and relict species. The exceptional cases of characters unusual for the family (e.g. unspotted young, scutellate tarsus, prominent bristles) tend to occur among the chat-like thrushes. Some genera approach the warbler family (Sylviidae), others the flycatchers (Muscicapidae). The most primitive chat-thrushes appear to be the shortwings *Brachypteryx*, small sedentary birds inhabiting tropical forest in India and south-eastern Asia through the Sunda Islands and Philippines to Sulawesi. (Another genus which has been thought to be primitive, the scrub-robins or rail-babblers *Drymodes* of Australia and New Guinea, was included in the Turdidae but has recently come under question, and is here included in the RAIL-BABBLER (see Sibley 1976)). From such rather warbler-like birds, including *Erythropygia* of Africa (see also WARBLER (1)), have perhaps come the complex of Old World robins *Erithacus* spp. and their relatives, a large group centred in Africa. Some authors separate these species of simply coloured, rather inconspicuous little birds into several genera—the nightingales, for example, in *Luscinia*. Others prefer to lump many of the genera together.

This group of robins and nightingales ranges from the taiga zone of northern Eurasia south to the Cape of Good Hope in Africa and to south-eastern Asia, the birds tending to prefer damp forest or forest edges, or well-wooded parks and gardens. Offshoots of this group are the robin-chats or forest robins of Africa *Cossypha* and *Alethe* spp., the magpie-robins (or 'shamas') *Copsychus* spp., bluish to black singers of south-eastern Asia; and the redstarts *Phoenicurus* spp., mainly rock-inhabiting birds, widely distributed in the Palearctic Region. The colourful North American bluebirds *Sialia* spp. are birds of semi-open country, and are perhaps not far removed from the solitaires *Myadestes* spp., magnificent singers of jungle and forest in western North America, the West Indies and the New World tropics. A distinct group sometimes treated as a subfamily are the forktails *Enicurus* spp., black and white birds of south-eastern Asia.

Next there are the open country or desert chats such as *Cercomela* spp., dull coloured and found primarily in Africa, and *Saxicola* spp., tending to be black and white, sometimes with brown; the latter include the Stonechat *S. torquata* and Whinchat *S. rubetra* of Eurasia. Near them come the redstarts, already mentioned, and the wheatears *Oenanthe* spp., found in deserts, tundra and meadows of Eurasia, Africa and India. They have rock-living relatives in Africa, the sooty chats ('ant-chats') *Myrmecocichla* spp., and in India the familiar Indian Robin *Saxicoloides fulicata*.

True thrushes. The true thrushes centre round the genus *Turdus*, the familiar one of Blackbird, Song Thrush, Redwing *T. iliacus*, Fieldfare *T. pilaris*, Ring Ouzel *T. torquatus* and American Robin *T. migratorius*. This central genus, distributed more widely than any other of the family, has about 63 species, many of them migratory. Round it we may group the rock-thrushes *Monticola* spp., chat-like birds of open country tending to bright blues or browns, of Africa and Eurasia, and the 'Whistling Schoolboy' or Whistling Thrush *Myiophonus caeruleus*, a plaintive and beautiful dark blue song-bird, found in south-eastern Asia. The *Zoothera* thrushes, with rounded wings and mainly non-migratory, have white bases to the primaries and underwing and are found in the Old World tropics, except for races of White's Thrush (or Golden Mountain Thrush) in the eastern Palearctic and Australia, the isolated Varied Thrush *Z. naevia* of western North America, and the Aztec Thrush *Z. pinicola* of Mexico. Near these are the forest thrushes of the West Indies *Cichlherminia* spp. and the Tristan Thrush *Nesocichla*; and finally the New World nightingale-like thrushes *Catharus* spp. (including the Hermit Thrush *C. guttata* and Veery *C. fuscescens*) and the North American Wood Thrush *Hylocichla mustelina*.

Two aberrant Asian genera, of uncertain relationships, may also be included here for convenience. The 3 species of *Cochoa* are forest-living birds with partly green, pale blue or mauve plumage, rather short-legged and with laterally expanded bills apparently adapted for taking large fruits. The single species of *Grandala*, a bird of high mountains, with very long wings, is highly aerial and social, a ground-feeder and more starling-like than thrush-like in general behaviour.

Food. Thrushes typically feed on both invertebrates and fruits. Many eat worms and snails, the Song Thrush *Turdus philomelos* in particular being a snail specialist with the ability to break open the shells by hammering them against an 'anvil'. Many of the larger thrushes can uncover hidden food by sweeping with the bill and at the same time scratching with one foot. The chats typically search the ground from a vantage point and drop down to take small exposed prey.

Behaviour and voice. Thrushes are typically monogamous, maintaining more or less strict pair bonds in the breeding season and exclusive breeding territories. Pair bonds may persist throughout the year, and from year to year, in resident species; migratory species generally live in loose flocks outside the breeding season, or may maintain feeding territories in their winter quarters (e.g. some wheatears). The loud and varied songs, for which the family is famous, proclaim ownership of territory; in addition there are in all species studied a variety of other calls, used in intraspecific interactions, and alarm calls which are often loud and staccato or, when the alarm is intense, high-pitched and drawn-out.

Courtship displays, performed during pair-formation and before copulation, involve stereotyped postures which tend to emphasize the more striking parts of the plumage, for example the red breast of the Robin *Erithacus rubecula* or the spotted breast of the Song Thrush. Feeding of the female by the male is regular in some species, for example the Robin, but does not normally occur in *Turdus* spp.

Breeding. The nest is cup-shaped and well built of grasses, moss, or kindred materials, the cup being strengthened with mud in *Turdus* spp. Nest-sites are very various: nests may be in a bush or tree, or in a recess or a deeper hole in a tree trunk, a bank or among rocks. Some species regularly build nests in niches or on ledges of man-made structures. The eggs are very variable according to the site used by the species; species nesting in deep holes tend to have immaculate white eggs; those nesting in shallow holes speckled white or blue eggs; those nesting on the ground grey or olive eggs; and those nesting in forks of trees and bushes blotched eggs with a pale greenish or bluish ground colour.

The clutch-size ranges from 2–6 eggs, occasionally more. The female is usually responsible for nest building, incubation, and brooding. The incubation period ranges from 12–15 (generally 13–14) days, and the fledging period is also typically 12–15 days, sometimes reduced in the Arctic in association with longer periods of daylight. Both sexes feed the young. Pairs usually make a succession of nesting attempts within the breeding season, which may last for only about a month at very high latitudes or, at the other extreme, for 9 months of the year in equable tropical regions.

See photos BILL ABNORMALITIES; COMFORT BEHAVIOUR; FEEDING HABITS; PARENTAL CARE; SEXUAL DIMORPHISM; SUNNING; VOCALIZATION.

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THRUSH, ANT-: see ANT-THRUSH; ANTBIRD.

THRUSH-BABBLER: *Ptyrticus turdinus* (see BABBLER).

THRUSH-FLYCATCHER: substantive name of *Namibornis herero*, alternatively called Herero Chat, a small THRUSH of restricted range in south-western Africa.

THRUSH, GROUND-; THRUSH, JEWEL-: names sometimes applied to Pittidae (see PITTA); the former is also used instead of QUAIL-THRUSH.

THRUSH, JAY-: substantive name of some laughing thrushes *Garrulax* spp. (see BABBLER).

THRUSH, LAUGHING: in the plural, general term for *Garrulax* spp. and also *Liocichla* spp. (see BABBLER).

THRUSH, NEW ZEALAND: substantive name of the probably extinct genus *Turnagra* (monotypic; 2 subspecies), the sole genus of the family Turnagridae (Passeriformes, suborder Oscines); also known by its Maori name, Piopio, for which the Forsters, on Cook's Second Voyage, introduced the vernacular 'thrush' that was adopted by the settlers. The Piopio was a thrush-sized bird with a short stout bill, emarginate at the tip, distinct rictal bristles, yellow iris, rounded wing with long first primary, its dorsal plumage olive-brown and rufous. The South Island subspecies (*T. c. capensis*) had a speckled breast (cream spots on brown), in plumage closely resembling the Tooth-billed Catbird or Stagemaker (*Scenopoeetes*) of Queensland. The North Island Thrush *T. c. tanagra* was unspotted, its throat white, breast and abdomen olive grey.

Piopio were somewhat gregarious, feeding on the forest floor, hopping with both feet together, building substantial cup-shaped nests in crutches of small trees, laying 2 spotted eggs. Calls included a triple piping whistle (recalling that of an oystercatcher *Haematopus*), a pipit-like song, a quick *chi-chi-chit* when males chased females, and low purring distress calls. Piopio were virtually omnivorous and occasionally predatory on other birds.

First classed in Turdidae (or Timaliidae), the New Zealand Thrush was confidently transferred to Ptilonorhynchidae by Finsch in 1875, a placing confirmed by Gadow after dissecting a specimen, with reservations based on its pterylosis. E. Mayr (in Fleming 1950) considered *Turnagra* to be an overgrown relation of the Australian whistlers (*Pachycephala*), but Oliver (1955) and Falla *et al* (1979) use the endemic family Turnagridae, citing possible relationship with Ptilonorhynchidae. In its emarginate bill, yellow iris, plumage pattern, diet, voice and habits, *Turnagra* seems to combine characters of several Australian BOWERBIRDS and catbirds *Ailuroedus*. Olson *et al* (1983) confirmed that *Turnagra* belongs to the bird-of-paradise/bowerbird assemblage and is apparently its most primitive member.

The New Zealand Thrush, originally abundant throughout both main islands of New Zealand, proved vulnerable to dogs, cats and other introduced predators. The North Island Thrush was last collected in 1908, and the South Island subspecies (which ranged to Stephens Island) was fast expiring in 1905 and last reported in 1921. Subsequent sight records are unconfirmed.

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THRUSH, QUAIL-: see QUAIL-THRUSH; RAIL-BABBLER.

THRUSH-TANAGER: *Rhodinocichla rosea* (see TANAGER).

THRUSH, WATER: see WATERTHRUSH; WARBLER (2).

THYMUS: a small glandular body of obscure function lying near the bronchi; as in mammals, it is best developed in the young and later diminishes.

THYROID GLAND; THYROXIN: see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM; also MOULT.

TIBIA: see below.

TIBIOTARSUS: a bone of the leg, in birds formed by the fusion of the tibia and the proximal tarsals; often loosely called the 'tibia' (see SKELETON, POST-CRANIAL; and LEG).

TICHODROMADIDAE: family of PASSERIFORMES, suborder Oscines; WALLCREEPER.

TICK-BIRD: see OXPECKER; STARLING.

TICKS: see ECTOPARASITE.

TIERCEL: special term for a male falcon, the latter word being used both generally and for the female only (see FALCON; FALCONRY).

TIGRIORNITHINI: see HERON.

TIMALIIDAE: family of PASSERIFORMES, suborder Oscines; BABBLER; PARROTBILL; RAIL-BABBLER.

TIME MEASUREMENT: see RHYTHMS AND TIME MEASUREMENT.

TINAMIDAE: see below.

TINAMIFORMES: an order, alternatively 'Crypturi', comprising only the Neotropical family Tinamidae (see TINAMOU). They are generally placed in taxonomic sequences next to the 'ratite' orders.

TINAMOTIS: generic name sometimes used as substantive name of *Tinamotis* spp. (for family see below).

TINAMOU: substantive name of the species of Tinamidae (Tinamiformes); in the plural, general term for the family. In the Neotropical Region, to which the family is restricted, the birds are known variously as 'perdiz' (*Rhynchotus*), 'codorna' (*Nothura*), 'inhambu' (*Crypturellus*), 'macuco' (*Tinamus*), and so on. Some of these names owe their origin to a superficial resemblance between these ground-dwelling birds and the Galliformes; in proportion and carriage some tinamous do indeed remotely resemble guineafowl (Numididae). It seems, however, that most of these similarities are the result of parallel evolution rather than phylogenetic relationship. Anatomically and biologically the tinamous are distantly related to the rheas (Rheidae). There are 9 genera and 45 species, ranging from southern Mexico to Patagonia.

Characteristics. The species of tinamou range in size (length 15–49 cm) from that of a Quail *Coturnix coturnix* to that of a male Black Grouse *Tetrao tetrix*. Male and female tinamous generally look much alike, but the females are slightly bigger and have more pronounced colouring. The bill is thin and slightly curved, the head is small, and the neck is thin. The rear part of the body seems to be high, owing to the enormous development of rump feathers; these often hide the very short and soft tail. The thick, heavy-looking legs are built for running; there are 3 short front toes, the hallux being either elevated or absent. Although tinamous are adapted for ground dwelling, running soon tires them; when chased they are apt to stumble and fall. The wings are short and rounded, with stiff, curved primaries. The flight is clumsy, and accompanied by a rumbling or whistling noise; they fly with the neck curved, and the head may be held slightly erect (*Nothura*). When frightened and flushed, tinamous sometimes collide with branches, tree-trunks, and other obstacles and may injure themselves fatally. It is strange that they fly so poorly, seeing that their flight muscles are as well developed as those of birds which fly very well; on the other hand, the heart and lungs are exceptionally small.

Tinamous succeed best in escaping the attention of their enemies by standing motionless, with the head stretched high, or by stealing away while cleverly using all available cover. They like to crouch, and rise only when one is almost upon them. Species living in open terrain sometimes hide in holes in the ground. All these modes of escape are very effective, as required, and contribute to the continued existence of a group which, in South America, is represented by a considerable number of species and individuals.

The coloration of the plumage is highly protective—brown, grey, or sand-coloured, depending on the environment, frequently with dark spots and bands. There is commonly a considerable quantity of powder down. The tinamous love to take a bath either in dust (*Eudromia*, certain of the *Crypturellus* spp.) or in water (*Tinamus*). With the exception of *Tinamus*, which uses trees, they sleep on the ground. In *Tinamus* the back of the tarsus is covered with roughened scales, which provide a firm hold when crouching down on a thick branch at night.

Food. The food is largely of vegetable origin, such as seeds and fruit, supplemented by insects and other small animals. The gape is wide enough to swallow, occasionally, even mice (*Rhynchotus*). Tinamous have a crop and large caeca. Certain species appear more inclined towards animal food (*Nothoprocta*), as are the young of some other species (e.g. *Crypturellus tataupa*). *Rhynchotus* digs for roots and termites.

Behaviour. Solitary life is the rule. With some species family groups or larger coveys are formed towards the end of the breeding period (*Eudromia*). Polygamy appears to preponderate in the family. The most general pattern seems to be that one or several females lay a clutch of eggs for a male, and then move on to mate with and lay a clutch for another male. The system is thus a combination of POLYANDRY and POLYGYNY, the conditions varying between species and probably also within species. Thus in the Ornate Tinamou *Nothoprocta ornata* a single male and female associate together for nesting, but in the Brushland Tinamou *N. cinerascens* up to 4 females may associate with a male. Unbalanced sex ratios have been reported: a preponderance of males has been noted more frequently, such as 4:1 in *Crypturellus variegatus*, but in other species such as *Nothoprocta ornata* the ratio is 1:1.

Voice. Their voice consists of a loud, melodious, usually polysyllabic whistle. In the breeding season they call often, some of them nocturnally as well as by day. They may be attracted by imitating their calls.

Breeding. The eggs are relatively large for the size of the bird, and beautifully coloured; they are indeed among the most handsome birds' eggs known. They are always unicoloured and heavily glazed as if polished. Colours include light chocolate, almost black, purple, dark bluish green, light yellowish green, and grey; the colour changes rapidly when exposed to light. The number of eggs in a clutch varies from 1–12 or more. The larger clutches are probably always the result of the efforts of more than one female. A flat, hollowed-out indentation in the ground serves as nest, and is protected by a bush, tufts of grass, or the base of a tree. The nest is poorly lined with dry matter, rarely well cushioned. Incubation is apparently done by the cock only; on the male of *Nothoprocta* an incubation patch has been noted. The cock may concentrate on brooding to such an extent that, on occasion, he allows himself to be picked up by hand. Sometimes (e.g. *Crypturellus tataupa*) the cock feigns lameness in order to distract the disturber from the nest. Some species cover the eggs with leaves (*Tinamus*) or feathers (*Nothoprocta*) when they leave the nest.

Incubation is short—in *Eudromia* 19 days, in *Crypturellus tataupa* and *Tinamus solitarius* 20 days. Led by the cock, the young leave the nest on their first or second day. The cock defends them, even against human beings. The young run very well and are guided by hearing; when danger threatens they crouch low and the colour of their down feathers blends with the ground so that they become almost invisible. While certain species (*Tinamus*) have a well-defined breeding period, others (some *Crypturellus* spp.) breed throughout the year.

Reproduction in captivity is frequently successful, even in Europe. Nevertheless, domestication has not succeeded, and the attempted introduction of the Argentine Tinamou *Rhynchotus rufescens*, e.g. into England, was a failure. All tinamous are in demand on account of their tender although oddly transparent meat. H.S.

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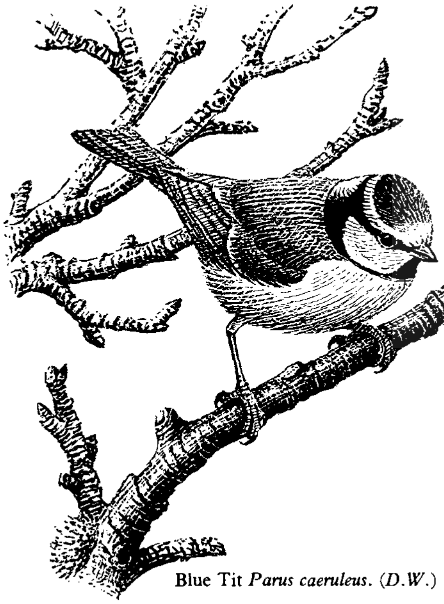
TINKER-BIRD: substantive name of *Pogoniulus* spp. (see BARBET).

TIPPET: name earlier given to a woman's cape made of the under feathers of grebes (Podicipedidae), but used ornithologically for the elongated facial feathers of typical grebes *Podiceps* spp., as distinct from other types of head-ornamentation in this group, e.g. 'facial disc' (well defined area of short feathers on the face) and 'auricular fan' (elongated feathers on side of head behind eye)—see under GREBE.

TISSUE: a more or less homogenous aggregation of cells (see CELL). Tissues form the structural basis of the organs and parts of the body. They are of four main kinds, each of which is divisible into various specialized types. (1) Epithelium occurs as a very thin covering layer, e.g. the external layer (epidermis) of the skin, or the lining of the alimentary canal (see SKIN). (2) Connective tissue has supporting and binding functions, and there may be an intercellular matrix (secreted by the cells); it occurs in many diverse forms, e.g. fibrous tissue, fatty tissue, cartilage, bone (see SKELETON, POST-CRANIAL). (3) Muscular tissue (see MUSCULATURE). (4) Nervous tissue (see NERVOUS SYSTEM).



Blue Tit *Parus caeruleus*. (*D.W.*)

TIT: substantive name, abbreviated from 'titmouse', of most species of Paridae (Passeriformes, suborder Oscines); in the plural, general term for the family. The name is strictly applicable only to the Paridae, although various unrelated but superficially similar birds are commonly called 'tits' or have names of which 'tit' forms part, e.g. Bearded Tit (see PARROTBILL), shrike-tit (see THICKHEAD), wren-tit (see BABBLER). In other cases 'tit' is a prefix with diminutive effect; it is also used as a substantive name for some Australian flycatchers. The long-tailed tits (Aegithalidae) and the penduline tits (Remizidae) were formerly classed as subfamilies of the Paridae. They are now treated as separate families; see PENDULINE TIT; TIT, LONG-TAILED.

Characteristics. Tits are small (lengths 11–14 cm except Sultan Tit *Melanochlora sultanea* which is *c.* 22 cm), active, woodland birds with stout, roughly conical bills; as in the crows the nostril is concealed by bristles. The plumage is typically olive, brown, grey or greenish above, and white, yellow or buff below. Many species have a striking black-and-white head pattern and a few have crests. The wing coverts and outer tail feathers are often pale edged and tipped.

Habitat. Tits are basically woodland species, deciduous, conifer or mixed, also occurring in more open habitats like gardens, where feeding tables attract many species especially Blue Tits *Parus caeruleus*.

Distribution. The typical tits comprise about 46 species distributed throughout North America (including parts of Mexico), Europe, much of Asia (including parts of south-east Asia), and Africa, wherever there is suitable woodland. They include such well-known species as the Great Tit *Parus major* and the Blue Tit. In North America some *Parus* spp. are called 'chickadees', the best known being the Blackcapped Chickadee *P. atricapillus* (formerly regarded as conspecific with the Willow Tit *P. montanus*). There are also some not very well known, mainly tropical, species: among them are the very large Sultan Tit of Eastern Asia, a black bird with a bright yellow crest and underparts; the local *Parus superciliosus* and *P. davidi* of the mountains along the eastern border of Tibet, unusual in having the underparts uniformly rufous; the very local *P. fringillinus* of central Africa, lacking the contrasting head markings found in all the other species of *Parus*; and the Mexican Chickadee *P. sclateri* from the mountains of Central America. There are also 2 Asian species of very atypical appearance: *Sylviparus modestus*, which resembles a warbler (Sylviinae), and *Cephalopyrus flammiceps*, which has a flame-coloured forehead and should perhaps not be included in the family at all.

Populations. The tit population of European woodlands fluctuates from year to year, but over longer periods remains remarkably constant. In Britain about 50% of adult Great Tits survive from one breeding season to the next. They are usually single brooded, and only an average of one juvenile from each brood survives to breed. In continental woods, where second broods are common, the mortality rate must be even higher. There is evidence of heavy losses of young birds soon after fledging, survival being closely linked with the supply of beech mast and other seeds which do not crop in successive years. Definite proof of 'density-dependent' mortality is hard to find, but high populations lead to reduced clutch-size, intensified predation by weasels and perhaps sometimes to food shortage in winter. The Great and Blue Tits are unusual for the family in that they reach very high breeding densities (occasionally more than 2 pairs per ha) in favourable habitats. All other species are much less abundant, a pair per 3 ha or less.

Movements. Although British tits are largely sedentary, some of the Scandinavian and North Russian populations are migratory and there are considerable local movements of juveniles elsewhere in northern Europe. Others winter even in very cold regions.

Food. In the breeding season tits feed largely on insects and other small invertebrates, but in winter some species rely mainly on seeds and other vegetable matter. Tits can open nuts by holding them down with the foot and hammering the shells, and several species, especially the northern ones, store food in times of abundance, hiding it under bark or elsewhere. Hiding places seem to be remembered for some days but recovery of food after longer periods may be fortuitous. Detailed research has been done on the diet of tits throughout the year and the interaction of predators and prey. Conclusive evidence for the control of insect pests is elusive, but abundant tits may check an incipient plague in spring and, at least in pines, reduce insect numbers significantly in winter. Some Great, Blue, Coal *Parus ater* and Marsh *P. palustris* Tits have proved surprisingly quick to solve food-finding problems involving the use of complex mechanisms, and there is at least a suggestion of 'insight learning' and imitation of other birds, e.g. in opening milk bottles.

Behaviour. Outside the breeding season Great, Blue and Coal Tits are strongly gregarious and move about in mixed flocks over a limited area through the winter with a few fellow travellers of other species. The other European tits are more sedentary and less sociable; some remain in their territories all the year round. In winter flocks break up at dusk when the birds go to their individual roosting places, usually small holes and crevices.

Voice. Flocks are kept together by a constant exchange of flight calls or alarm notes. The Great Tit has a particularly wide range of call notes and song variations which seem to be developed both by individual improvisation and by imitation. The tonal quality of the song even varies between forest and more open habitats. Some species have quite elaborate songs though most contain only a few syllables.

Breeding. All species are hole-nesters. The nest, typically a mass of moss or other soft material, with a hair, fur or feather lining, is placed in a hole in a tree or, less usually, in the ground or a wall. A few species, including the Willow Tit, excavate their own holes in rotten tree trunks. The eggs are white with small brown spots. In most species the female will cover an incomplete clutch with nest lining on leaving; she builds the nest and incubates the eggs but both parents feed the young.

Clutch-size varies from 3–4 in some tropical species to much larger in some temperate species. The average clutch of 11 (clutches of 15 are not uncommon) laid by Blue Tits in deciduous woodland in Europe is perhaps the largest of any nidicolous bird.

The fact that the Great Tit prefers nest-boxes to natural holes for breeding has enabled zoologists to make detailed long-term studies of variable factors such as date of egg-laying, clutch-size, hatching and fledging success and survival of juveniles. Although egg-laying is so timed that the nestling period roughly coincides with an abundance of caterpillars, the quantity and nutritional value of food in deciduous woods tends to decline before the fledglings are self-supporting, so earlier breeding would be an advantage. But even with the help of 'courtship feeding' female tits seem unable to produce their rather large clutches any earlier. The date of egg-laying varies with latitude, altitude and habitat, and with winter and spring temperatures. Older females lay earlier than first-year birds, small females earlier than big ones, and small tit species earlier than larger ones. Clutch-size is affected by an even more complex interaction of factors. Most tit species lay smaller clutches in southern latitudes of Europe, in less favourable habitats, when laying is later than usual, when the nest chamber is small, when one or both parents are first-time breeders, and there is a high population density of the same species. In general these variations result in tits' families being the largest that the parents can successfully raise, but the mechanism by which the females adapt their clutch size to a food supply some 5 weeks ahead is not yet understood. The incubation period is 13–14 days and fledging varies from 15–20 days, with the young continuing to be fed for a week or so after leaving the nest.

See photo MAMMALS, ASSOCIATION WITH. J.A.G.B.

Barnes, J.A.G. 1975. The Titmice of the British Isles. Newton Abbot.
Hinde, R.A. 1952. The behaviour of the Great Tit *Parus major* and some other related species. Behav. Suppl. 2. Leiden.
Kluijver, H.N. 1951. The population ecology of the Great Tit, *Parus m. major* L. Ardea 39: 1–135.
Lack, D. 1958. A quantitative breeding study of British tits. Ardea 46: 91–124.
Perrins, C.M. 1979. British Tits. London.
Snow, D.W. 1954. The habitats of Eurasian tits (*Parus* spp.) Ibis 96: 565–585.

TIT-BABBLER: in the plural, a general term for the Timaliini (see BABBLER); also an alternative name for TIT-WARBLER; (see WARBLER (1)); also accepted name, in South Africa, of *Parisoma* spp. (see TIT-FLYCATCHER; FLYCATCHER (1)).

TIT, BEARDED: see BEARDED TIT; for family see PARROTBILL.

TIT-FLYCATCHER: name applied to *Parisoma* spp. (for family see FLYCATCHER (1)).

TIT-HYLIA: *Pholidornis rushiae*, a very small bird found in West African forests, of uncertain affinities. Superficially it is like a flowerpecker, with a pointed, slightly decurved bill, short tail, streaked head and breast and olive-yellow rump and belly; it has variously been associated with the sunbirds, estrildid finches and warblers. A recent appraisal (Vernon and Dean 1975) shows that in many ways it is closely similar to the penduline tits, and suggests that it is either a member of the Remizidae or a remarkable case of convergence.

Vernon, C.J. & Dean, W.R.J. 1975. On the systematic position of *Pholidornis rushiae*. Bull. Br. Orn. Club 95: 20.

TITLARK: popular name applied in Britain to *Anthus* spp., particularly the Meadow Pipit *A. pratensis* (see under WAGTAIL).

TIT, LONG-TAILED: *Aegithalos caudatus*; in the plural, general name for the family Aegithalidae (Passeriformes, suborder Oscines), consisting of the 2 genera *Aegithalos* (6 species) and *Psaltriparus* (Bushtits, 1 species, sometimes regarded as 2). The genus was previously placed close to the true tits (Paridae), or as a subfamily of the heterogeneous Muscicapid assemblage. Recent research has placed the long-tailed tits closer to the babblers (Timaliidae) on the basis of structural and biochemical characteristics. This rearrangement makes good sense from a behavioural point of view as the long-tailed tits have much in common with babblers, being almost entirely sedentary and living in persistent small groups which defend common territories and frequently indulge in co-operative breeding.

Long-tailed Tit *Aegithalos caudatus*. (*A.H.*).

Characteristics. Long-tailed tits are very small, 10–12 cm in length and averaging about 10 g in weight, with compact bodies, short wings and long narrow tails; the latter character being more pronounced in *A. caudatus* than in the other members of the genus. The body plumage is loose and fluffy, again resembling babblers, and the legs are fairly long and very slender. Bills are short, conical and somewhat laterally compressed, resembling those of the smaller PARROTBILLS (Timaliidae).

Distribution and habitat. *A. caudatus* extends over most of the boreal Palearctic region, from Britain to Japan, but the genus *Aegithalos* is otherwise confined to the Sino-Himalayan subregion, with 3 species occurring only in the Himalayas and associated ranges, one extending through China to Taiwan, and one being confined to the mountains of west and central China. The other genus, *Psaltriparus*, occurs in western North America from southern British Columbia southwards, and extends into central America as far as Guatemala. The disjunction between the 2 genera is reminiscent of the situation in the babblers where the isolated genus *Chamaea* occupies a similar range to *Psaltriparus*, while the rest of the family is concentrated in the Oriental and Sino-Himalayan regions (see BABBLER); in both cases the North American populations probably crossed from Asia via the Bering Straits during a period of climatic amelioration. In the Himalayas long-tailed tits are found in the temperate and sub-alpine forest zones between 1,800–3,400 m, descending somewhat in winter. The widespread *A. caudatus* is mainly a bird of temperate and boreal forests but also occurs in scrub, particularly where there are patches of woodland nearby, and extends into Mediterranean vegetation in southern Europe. The American species *Psaltriparus minimus* occupies dry forest near the west coast and semi-desert woodland and scrub in the interior.

Food. All species feed principally on small insects gleaned from leaves and twigs, using particularly the terminal branches of shrubs and trees and behaving very acrobatically, frequently hanging upside-down.

Behaviour. The family appears to be extremely uniform in behaviour, all species living in discrete groups of 5–20 birds, roving constantly, often in association with other small passerines, but probably occupying group territories, which have been extensively studied in *A. caudatus* (Nakamura 1969, Gaston 1973). Helpers have been recorded at the nests of 3 species and these other birds probably belong to the same winter territorial group as the breeding pair. Groups roost together, huddled in contact with one another on a branch.

An unusual display, observed in both *A. caudatus* and *A. concinnus*, consists of hovering repeatedly close to the nest after delivering food to the young. This occurs only at nests with helpers in attendance and presumably constitutes a communication between breeders and helpers, although the exact significance is not known; it facilitates finding nests with young.

Members of the family do not have a recognizable territorial song. Instead, a variety of vocalizations, mainly churring and high-pitched nasal squeaks, are given, which apparently serve to communicate within the group. Territorial confrontations between groups are accompanied by loud vocalizations on the part of all group members.

Breeding. Nests are characteristic, being domed, with a single small entrance at one side near the top. They are built largely out of moss and usually covered outside with lichens and cobwebs. The cup is lined with a dense mat of feathers and other soft material which confers very good insulation. These complex nests take a long time to build compared with many passerine nests; up to 20 days in the case of early nests of *A. caudatus* and a minimum of 5 days later in the season. Nest sites range from just above the ground in low bushes to more than 20 m up in trees, sometimes close to the main trunk, sometimes in the terminal twigs of side branches.

Eggs are laid at daily intervals and clutch sizes range from 4–12; the eggs are white with faint markings. Incubation is carried out entirely by the female and takes 13–14 days. Both members of the pair contribute more or less equally to feeding the young which fledge at 15–16 days old. Predation pressure is very heavy on populations of *A. caudatus* that have been studied, making the fledging period, close to that of the hole-nesting Paridae, somewhat surprising. Family parties remain together for at least a month after the young fledge and may form the nucleus of winter flocks.

See photo ROOSTING. A.J.G.

Gaston, A.J. 1973. Ecology and behaviour of the Long-tailed Tit. Ibis 115: 330–351.

Nakamura, T. 1969. Structure of flock range in the Long-tailed Tit, I. Winter flock, its home range and territory. Misc. Rep. Yamashina Inst. 5: 1–29.

TITMOUSE: name now usually abbreviated to 'tit' (see TIT); still used to some extent, but more often as a group term ('titmice') than as a substantive name of species.

TIT, PENDULINE: see PENDULINE TIT.

TIT, SHRIKE: alternative name of *Calicalicus madagascariensis* (see VANGA).

TIT-TYRANT: substantive name of the small South American tyrant-flycatchers of the genera *Anairetes* and *Uromyias* (see FLYCATCHER (2)).

TIT-WARBLER: substantive name, sometimes 'tit-babbler', of *Leptopoecile* spp. (see WARBLER (1)).

TIT, WREN-: see WREN-TIT; BABBLER.

TITYRA: generic name used as substantive name of *Tityra* spp. The three species of *Tityra* were formerly included in the Cotingidae, but are now placed in a subfamily of the Tyrannidae (see FLYCATCHER (2)). They are heavily-built birds of medium size (18–21 cm), the male largely pale grey or white with black crown, wings and tail, and the females duller, partly brownish or streaked. They are Neotropical forest birds, living strictly in pairs and nesting in tree holes; their calls have a peculiar grunting or croaking quality. Their closest allies are probably the BECARDS; in both, the 9th primary of adult males is much reduced and attenuated.

TOBOGANNING: in respect of penguins (Spheniscidae), see LOCOMOTION, TERRESTRIAL.

TOCOCO: *Chilia melanura* (see OVENBIRD (1)).

TODIDAE: see CORACIIFORMES; TODY.

TODY: substantive name of the 5 species of Todidae (Coraciiformes, suborder Alcedines); in the plural 'todies', general term for the family. Todies are confined to the Greater Antilles of the West Indies and form a compact group in the order Coraciiformes, where they are allied to motmots (Momotidae) of tropical America, and more distantly to kingfishers (Alcedinidae).

Characteristics and distribution. The 5 species—one each on Cuba, Jamaica, and Puerto Rico, and 2 on Hispaniola—in the single genus *Todus*, are morphologically very similar. All are small (11 cm), shining green above, with pale underparts, a prominent scarlet gorget (bib), stout bodies and long, flat, red bills. The Jamaican Tody *Todus todus* is locally called the Robin Redbreast. Differences in flank colour (pink or yellow), the presence or absence of a small blue subauricular patch, vocalizations and courtship behaviour distinguish the species. A recent large fossil, *Palaeotodus emryi* (Oligocene, Wyoming), indicates that the present range of the family is only a remnant of that found formerly, and may have included Europe as well as North America and the West Indies during the early stages of tody evolution.

Habitat. Inhabiting all major habitats from dense, moisture-saturated, mossy, elfin forest (as high as 3,200 m) down to xeric lowland forest bordering sea-level, todies prefer shady and brushy areas, generally where there is an abundance of branches, twigs and leaves, and a suitable embankment for burrow-excavation.

Food. Foraging usually occurs within a few metres of the ground. Todies are primarily insectivorous, but also eat spiders, small seeds and rarely, minute lizards. They feed opportunistically, capturing insects in an unusual manner from virtually all available substrates. They feed primarily from the undersides of leaves and twigs. They sit quietly but alertly on twigs or branches, constantly moving their heads and eyes with rapid and jerky movements, and occasionally flick their wings. Typically the bird perches with its bill pointing upwards (at angles up to 45°) and scans the lower surfaces of leaves above it. On spying an insect the tody flies up to the leaf, snaps its bill audibly, and continues in an unbroken arc to another perch. Less than 10% of the time they sally out in flycatcher fashion to capture insects on the wing. A detailed analysis of feeding behaviour reveals striking character displacement in the 2 Hispaniolan species, the Broad-billed *Todus subulatus* and Narrow-billed Todies *T. angustirostris*, over a sympatric zone of at least 1,265 m (between 465 and 1,730 m). These 2 species have diverged from other *Todus* in morphology, vocalizations, and egg-dimensions, as well as exhibiting striking behavioural divergence between themselves because of their sympatry. One can recognize either species immediately in the field merely by observing its foraging height and feeding behaviour, regardless of morphology.

Behaviour. Their flight is often accompanied by wing-rattling, a loud whirring noise probably produced by air rushing through the attenuated outer primary; this noise is under the control of the tody, and is used generally during territorial encounters and courtship. Todies are non-social birds, normally remaining paired in their home-ranges throughout the year, although the bonds are looser in the non-breeding season.

Voice. Each species has at least 6 different vocalizations, of which one is distinctive and different from the other species. The Puerto Rican and Jamaican todies utter short, loud, nasal *beeps*, whereas the other 3 species whistle much clearer two- (or more) part calls. These vocalizations, even though mostly unmusical, and the peculiar bobs that accompany them, constitute some of the most characteristic qualities of todies.

Breeding. During the nesting season (which may cover 10 months each year), todies excavate narrow, curved (usually right-angled) burrows in earth banks, using their bills and feet. These burrows are dug out in natural bare or sparsely vegetated banks, often under sheltering roots or rocks, but todies will also utilize road- or trailside cuts. Neither the banks nor burrows are high above the lower ground level (in the Puerto Rican rain forest, the average bank height is 1.6 m, and average burrow height is 0.9 m). These burrows are defended vigorously; rarely are they used more than one season. Many nests are abandoned; for example, in Puerto Rico's rain forest, todies begin three times as many burrows as are ultimately used for egg-laying. As the bird is tiny, the burrow-opening averages 3.4 cm in diameter at the exterior, but the eggs are laid in an enlarged, unlined chamber approximately 11 × 10 cm and 7 cm high. The glossy, ovate, fragile eggs (clutch size averages 2.4) are very large for such a small bird. In the Puerto Rican Tody *T. mexicanus*, each egg represents 39% of the bird's body weight (birds average 5.4 g and eggs 1.4 g). This relative heaviness is due to the large yolk reserve required for the rather long incubation period (21–22 days), which is longer than any similar-sized hole- or cup-nester, either in the tropical or temperate zones. Adults are unusually inattentive during incubation, each spending less than one-quarter of its time brooding, and only then for periods averaging 13 min at a time. However, during the nestling period they feed their chicks with remarkable speed and energy expenditure, result-

Jamaican Tody *Todus todus*. (*N.A.*).

ing in the highest rates recorded for any bird (up to 140 feeds per chick per day!). Even in the non-breeding season, todies feed constantly from early dawn to dusk to maintain their own metabolism.

Todies are often assisted at the nest by helpers, who are usually pairs from adjacent territories whose breeding has been curtailed. Breeding pairs willingly accept helpers after a few days of aggressive behaviour, and when fed by 4 adults, the nestlings emerge sooner than the normal (which is 19–20 days). Nestlings emerge with pale grey throats and short black bills; after about 6 weeks adult coloration and behaviour are attained. A.K.K.

Kepler, A.K. 1977. Comparative Study of Todies (Todidae): with Emphasis on the Puerto Rico Tody, *Todus mexicanus*. Cambridge, Mass.

TODY-FLYCATCHER, TODY-TYRANT: alternative substantive names of *Todirostrum* spp. (see FLYCATCHER (2)).

TOE: see under LEG; SKELETON, POST-CRANIAL.

TOMIUM: the cutting edge of a mandible; the upper and lower mandibular tomia on either side meet, in the closed position, in a line known as the commissure (see BILL).

TOMTIT: *Petroica macrocephala*, a small forest bird native to New Zealand (for family see FLYCATCHER (1)); also a common (but decreasing) vernacular name for the Great Tit and Blue Tit (see TIT).

TONGUE: a mobile, muscular organ situated in the floor of the mouth. It is covered with epithelium, often thick and horny, particularly towards the tip, and is supported by the entoglossum, which is often partly or entirely cartilaginous. Muscles attached to the hyoid skeleton (see SKULL; MUSCULATURE) provide for the organ's mobility. The tongue in birds is highly variable in size, form, and function. This applies particularly to the horny epithelium; its tendency to fray at the tip has been increased by selection to produce complex structures. The varied papillae and serrations are also developments of this layer.

While it is possible to describe many adaptations according to function, particularly feeding habits, there are many apparent contradictions. Thus, the penguins (Spheniscidae) have long, pointed tongues, the upper surface being covered with conical papillae pointing backwards to hold and direct slippery fish towards the oesophagus, whereas the auks (Alcidae), divers (Gaviidae), and grebes (Podicipedidae) have similarly sized and shaped tongues that are quite smooth. Other fish-eating birds, notably the Pelecaniformes and certain kingfishers (Alcedinidae), that swallow their food whole, possess only rudimentary tongues; so do the spoonbills and ibises (Threskiornithidae) and the storks (Ciconiidae), all of which feed on small animals. Any attempts to classify types of tongue are therefore bound to be unsatisfactory, and it is more helpful to consider the various functions of the organ.

Functions of the tongue. Although the tongue can be seen to move when a bird is singing, it does not in fact play any part in the production of the song (see SYRINX). The actual functions can be grouped as follows:

Collecting food. Included here are those few species that use the tongue instead of the bill for the collection of food. Selection has produced the most remarkable adaptations among these species.

Woodpeckers and wrynecks (Picidae) possess exceptionally long 'tongues' which can be thrust out for a considerable distance. These structures in fact consist of a tiny true tongue (entoglossum and associated epithelium) on the end of a greatly lengthened basihyal. Protrusion is made possible by the elongated hyoids. The highly developed salivary glands cover it with a sticky secretion. The surface of the tongue proper is roughened with hair-like papillae, and a few backward-pointing barbs near the tip. This results in increasing the thickness of the salivary coating in which the insects become stuck. The tongue of the Wryneck *Jynx torquilla* lacks barbs. The tongue is most strikingly elongated in genera taking large quantities of ants, e.g. *Picus*, *Colaptes* and *Jynx*; in the Wryneck, the tongue is nearly two-thirds the length of the bird's body (excluding tail).

Other tree woodpeckers have shorter tongues in which the terminal barbs are more developed and are of use in extracting larvae from their crevices. The sap-sucking woodpeckers have still shorter tongues, the tips of which are covered with fine hair-like processes, which draw up sap by capillary traction.

The tongues of snipe and woodcock (Scolopacinae) play an important part in extracting prey such as earthworms from soft substrates. However, long-billed waders such as curlews *Numenius* which feed in harder substrates with more vigorous actions have the bill so reinforced that only a small tongue can be accommodated, and prey are removed by bill action alone.

The tongues of sunbirds (Nectariniidae) and hummingbirds (Trochilidae) are long and bifid, folded over in the form of two tubes, the ends of which are greatly frayed and feather-like. The tongue is worked in and out of flowers at great speed, nectar and contained insects being forced into the tubes. The resemblance of this tongue to that of the nectar-sucking bee has been remarked upon. The brush-tongue characteristic of the Meliphagidae is notably different from that found in most other families of birds with like habits (see HONEYEATER), but a similar structure is found in the Zosteropidae and the Loriinae (see WHITE-EYE; PARROT).

Eating. In general, those species with relatively thick, fleshy tongues, closely conforming to the inner margin of the lower mandible, use the tongue as an eating organ, but without protruding it to take in food. The flattened tongues of the grazing geese *Anser* spp. bear serrations along the edge, corresponding with those of the lower mandible, and serve to fix and break the vegetation. Dabbling ducks *Anas* spp., with a more varied diet, have on the tongue a series of serrations and papillae that serve additionally as a sieve, this condition reaching maximal development in the Shoveler *Anas clypeata* and allied species. The slender backward-pointing barbs of the tongues of saw-billed ducks *Mergus* spp. assist in holding and swallowing slippery prey, as in the case of the penguins.

In the flamingos (Phoenicopteridae) the tongue fills the whole cavity of the lower mandible and is capable of moving only backwards and forwards. It bears many soft papillae and has closely serrated edges, being used to sift food from soft mud (see FLAMINGO).

Seed-eating species tend to have thick, fleshy tongues, that of the crossbills *Loxia* spp. playing an important part in extracting seeds from fir cones. The tongue is used by these species for discarding unwanted husks. The fleshy tongues of parrots (Psittacidae) are capable of sophisticated and versatile movements due to a highly modified and refined musculature.

Swallowing. There are a number of adaptations in the tongue that facilitate swallowing. In many species that swallow their food whole, as has already been mentioned, the tongue is very small. Many other tongues possess backward-pointing spiny papillae to direct the food towards the oesophagus, the papillae becoming more numerous around the glottis, guarding it from any obstruction.

The raised edges of the tongues of some seed-eating species give such tongues a scoop-like form in which the seeds are directed towards the oesophagus. The bifid tongues of the owls (Strigiformes), larks (Alaudidae), and swifts (Apodidae) are probably concerned with swallowing.

Taste and touch. The sense of taste seems to be poorly developed in birds, with the possible exception of the parrots, the thick, fleshy tongues of which possess more taste-buds than any other species. In birds, however, many of these are situated elsewhere in the mouth (see TASTE). Tactile end-organs are much more widespread and the tongue is definitely an organ of touch, as would be expected (see TOUCH). The tongue has possibly a temperature-perceiving function in Megapodidae (see MEGAPODE).

Nest building. In the swiftlets *Collocalia* spp. the musclaginous salivary secretion used to build their nests is deposited by the tongue (see EDIBLE NESTS).

There remain many tongues in which it is not possible to correlate function with form, e.g. the long, thin horny tongues of the toucans (Ramphastidae).

Tongue and mouth markings. A widespread characteristic of the mouths of nestling birds is that they are brightly coloured, often with a variable number of contrasting spots on the tongue and soft palate. These are considered to be directive marks or targets, revealed by the gaping response on the arrival of the parent with food. A more primitive arrangement is seen in the enlarged, light-coloured margins of the gape, as in the nestlings of thrushes (Turdinae) and many other passerines. Nestlings of some birds, e.g. the parrot-finches *Erythrura* spp., possess semi-luminous blue warts on the sides of the mandible, again to direct the parents in placing food.

It has also been suggested that the bright mouth-colouring in adult birds may serve as threat and warning coloration, the gaping response being induced as a last resort when the bird is attacked and cornered. It is also a factor in display, revealed particularly by certain sea birds, notably the auks (Alcidae). (J.G.H.) P.J.K.B.

TOOLS, USE OF: 'the use of an external object as a functional extension of the body, in attaining an immediate goal'. A recent closer definition is 'the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool' (Beck 1980). This somewhat tortuous definition points to its being a decidedly indistinct category of behaviour. It is best considered as just one aspect of object manipulation and may not necessarily be the 'highest' form.

The number of wild bird species which use tools as an established and regular piece of behaviour is extremely few. The classic case is the Woodpecker Finch *Cactospiza pallida* of the Galapagos which was observed as early as 1901 to wield a cactus spine or twig as an implement (see DARWIN'S FINCHES). The closely related Galapagos Mangrove Finch *C. heliobates* has once or twice been seen to behave similarly. The Woodpecker Finch has been studied in captivity in some detail in West Germany and the USA. When looking for prey this species first searches like a true woodpecker, using its bill to prise off bark, thus uncovering insect holes. It will then pick up accessible prey directly with the bill. If no prey is within reach the bird flies off to fetch a cactus spine which it may then use in one of three ways: as a goad to drive out an active insect (without necessarily touching it); as a spear with which to impale a slow-moving larva or similar creature; or as an implement (best named a poker?) with which to push, drag, nudge or otherwise manoeuvre an inactive insect from a crevice or hole.

In Australia several wild Orange-winged Sittellas *Daphoenositta chrysoptera* were seen successfully to insert strips of wood into cavities containing insect larvae; the probe was first held in the bill and later under toes while dislodged larvae were eaten. In the Serengeti, Tanzania, a Grey Flycatcher *Bradornis microrhynchus* was on more than one day seen to 'fish' winged termites out of holes in a concrete verandah using a grass stem. In Texas a similar method was successfully used by an adult Green Jay *Cyanocorax yncas*, and unsuccessfully by a juvenile. Each bird flew with a twig into a tree and inserted it under the bark of a branch. The adult on pulling the stick out of the small cavity found a prey item adhering to it that it then consumed. Brown-headed Nuthatches *Sitta pusilla* in North America detach bark scales and use them as levers (?crow bars) to prise other pieces of bark and thus expose invertebrate prey. The nuthatches carry their implements from tree to tree. Particularly well-known is the stone-throwing behaviour of the Egyptian Vulture *Neophron percnopterus* used to break open the eggs of the Ostrich *Struthio camelus*. These depredations are believed to be serious. The much-quoted case of the Australian Black-breasted Buzzard *Hamirostra melanosterna* dropping stones from a height on to the eggs of the Emu *Dromaius novaehollandiae* and other large ground-nesting birds has been discredited, having a basis only in Aborigine legend. White-winged Choughs *Corcorax melanorhamphus*, also in Australia, use pieces of mussel shell as thrown or dropped missiles and as hammers to break open other mussels. An apparently unique case of a wild species using an aggressive weapon concerns the Australian Brush Turkey *Alectura lathami* which will kick barrages of sandy stones and litter at monitor lizards *Varanus varius*, that compete for the birds' food.

All other cases of apparent tool use by wild birds are single instances involving an individual bird. Three of the more convincing concern a Double-crested Cormorant *Phalacrocorax auritus* that used a moulted secondary feather to 'paint' preen oil on its wings, an American Robin *Turdus migratorius* that used a twig to rake aside leaves, and an Egyptian Vulture in Israel that used a stone as a cudgel to kill a young monitor lizard. Many of the other cases scattered in the literature need to be treated with caution.

ANTING by birds can reasonably be held to be true tool use, but not the use of anvils by the Song Thrush *Turdus philomelos* and others; nor the dropping of hard-shelled objects from a height by crows and others.

A borderline case concerns the use of bait to attract prey. This behaviour is well-established for the Green Heron *Butorides virescens* in both the Old and the New Worlds; one individual used dummy bait, luring fish within range with a feather—a 'fly' placed carefully on the water surface. There is one fully authenticated case from Kenya of a Pied Kingfisher *Ceryle rudis* baiting with bread over a longish period of time.

To sum up, wild birds use the following: goad, poker, lever, rake, fishing stick, hammer, brush, thrown missile, dropped missile and kicked missile; plus bait and dummy bait. The functions include the finding, opening and moving of food; the care of the body; and the deterrence of food competitors; also the attraction of prey.

Tool use by birds in captivity is more commonly observed than among wild birds. In particular, parrots of several species use objects with which to scratch themselves; almost invariably they are specimens caged individually and which cannot indulge in mutual preening. One or two parrots use hollow objects as bailers to lift water to their bills. A Common American Crow *Corvus brachyrhynchos* filled a plastic cup by dipping in a water trough and then transported the water 5 m to tip it into a container of dried mash. At London Zoo an Oystercatcher *Haematopus ostralegus* regularly used a stick with which to probe cracks in the concrete surround of its cage; on one occasion it flushed an insect. A caged North-western Crow *Corvus caurinus* has been seen to use a probe. A detailed study of a captive Rook *C. frugilegus* showed how the bird would use a plug in a drainage hole to flood the floor of its aviary for a bath! A female Eclectus Parrot *Eclectus roratus* used a segment of palm frond to excavate a burrow in which it later laid eggs.

Tool-making (manufacture) is 'any modification of an object by the user or a conspecific so that the object serves more effectively as a tool'. Thus the simple detachment by the bird of part of an object is held to be tool making. The 2 Geospizids detach twigs and *pallida* will remove 'awkward' branching stems from a chosen twig. Similarly the Brown-headed Nuthatch detaches the flakes of bark. Certain crows and Starlings *Sturnus vulgaris* combine ants into wads to enhance their effectiveness. A remarkable case of tool-making among captive birds concerns Blue Jays *Cyanocitta cristata* that tore off strips of newspaper and used them to draw food toward themselves.

The rarity of tool use and tool-making among birds may be more apparent than real; the passage of time will bring to light additional implement-wielding birds. But it seems that only in exceptional circumstances is the employment of an external object a more parsimonious path for natural selection than the evolution of body structures or behavioural traits (other than tool-using), to solve the same problem.

J.H.R.B.

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TOOTH: see (plural) TEETH; also EGG-TOOTH.

TOOTHBILL: *Androdon aequatorialis* (for family see HUMMINGBIRD).

TOPAZ: substantive name of *Topaza* spp. (for family see HUMMINGBIRD).

TOPOGRAPHY: as applied to a bird, the definition of, and the terminology applied to, the various external areas and features of its plumage and bare parts. Some parts of the plumage, for example most of those on the head and underparts, are named after the approximately equivalent areas on the human body, and are thus incapable of close definition. Other parts of the plumage, for example those on the wings, are named from clearly defined groups of feathers. Topographical terms also include the names for particular plumage marks, for example the variously positioned stripes on the head of some species. Other terms refer to what are known collectively as the bare parts—the bill, the legs and feet, the orbital ring and the externally visible parts of the eye, and various unfeathered areas or specialized structures of some species; these are dealt with in separate articles (see BILL; INTEGUMENTARY STRUCTURES; IRIS COLORATION; LEG; SKIN), as also are certain of the plumage areas (see TAIL; WING; also PLUMAGE). There remain the areas, usually feathered, of the head, neck and body, and the various openings in the body surface.

Head and neck. From the base of the bill backwards, the areas are named as follows, any special adjectives referring to them being also given.

Dorsally: forehead (adj. frontal); crown (adj. coronal); occiput (back of head, adj. occipital); nape (adj. nuchal); hindneck. The forehead, crown, and occiput (the whole top of the head) are sometimes collectively called the pileum.

Laterally: (the terms are more commonly used in the plural, the two sides being similar): lore (between the upper mandible and the eye, adj. loral); ear-coverts or auriculars (behind and immediately below eye); malar region (the adjective malar, although strictly relating to the cheeks, is applied in ornithology to the area from the base of the lower mandible bordering the lower edge of the ear-coverts); side of neck.

Ventrally: chin or mentum; throat (adj. gular); foreneck or jugulum.

The whole side of the head may be referred to as the cheek and its upper part is sometimes called the temple. Other terms derive from particular plumage marks or colour patterns: some of these are shown in the chart, and there may also be a HOOD, or a CAP, or a COLLAR. Elongated feathers may constitute a CREST on the top of the head or hackles on the hindneck.

Body. Between the neck and the tail the areas are:

Dorsally: mantle or interscapular region (upper back); back; rump or uropygium.

Laterally (on each side): scapulars (between the mantle/back and wing); axillaries (between the flank and underwing); flank.

Ventrally: breast or chest (adj. pectoral); belly or abdomen; ventral region (sometimes vent, although literally this applies to the anus); crissum (vent and undertail-coverts together, adj. circumcloacal).

The need for naming different areas of the body may also depend largely on the requirements for describing a particular plumage mark or pattern. A band of colour on the upper breast may be called a breast-band or gorget. When the mantle, back and scapulars together present an area of distinctive colour, this may be called a saddle. The term mantle (pallium) is often also used when the mantle, back, scapulars and wing-coverts are uniformly coloured.

Openings. The openings in the body surface are the nostrils (anterior nares) on the upper mandible; the mouth (adj. buccal), at each side of which, at the junction of the upper and lower mandibles, is the gape (adj. rictal); the auditory meatus on each side of the head (usually hidden by feathers); the openings of the oil gland (sometimes absent) above the root of the tail; and the vent or anus, the external end of the cloaca (see ALIMENTARY SYSTEM; HEARING AND BALANCE; NARIS; OIL GLAND; TONGUE).

The primary practical application of topography is in compiling precise descriptions of birds, so that identification, ageing or sexing criteria may be clearly defined. The charts reproduced here are intended as a basis for this purpose, and show the standard terminology for the common areas and features of plumage and bare parts. All flying birds have the same basic 'map' of plumage components, but the prominence or extent of some feather groups (and the number of feathers in each group) may vary considerably from one species or family to another. A.L.T.

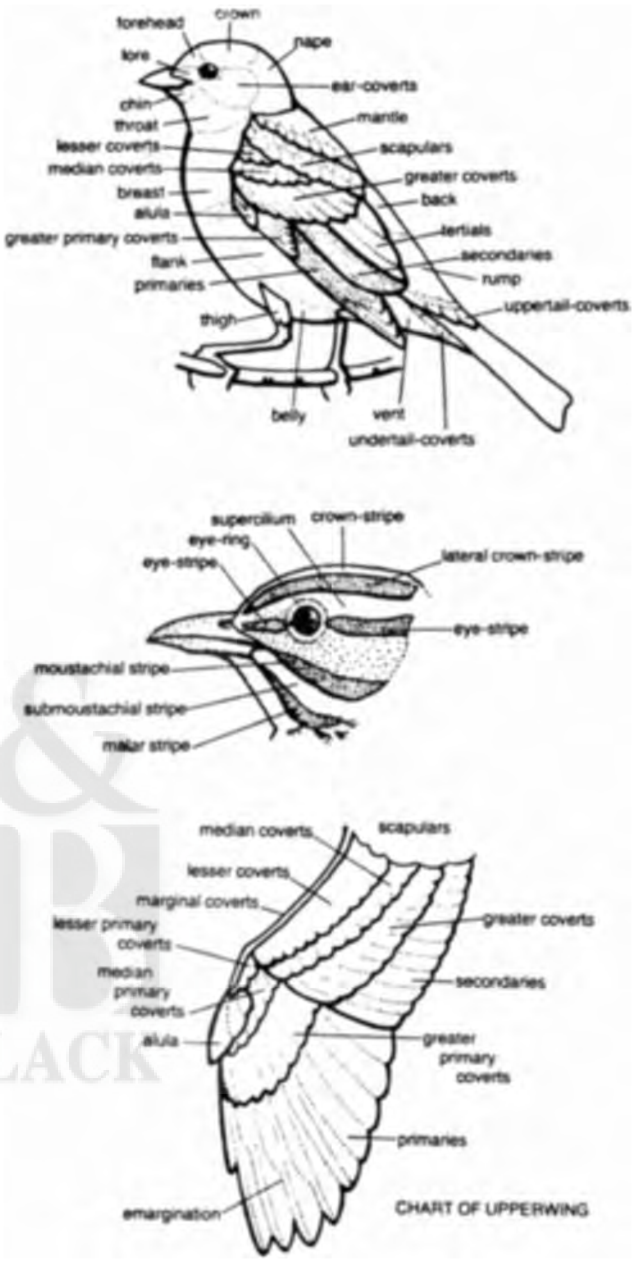


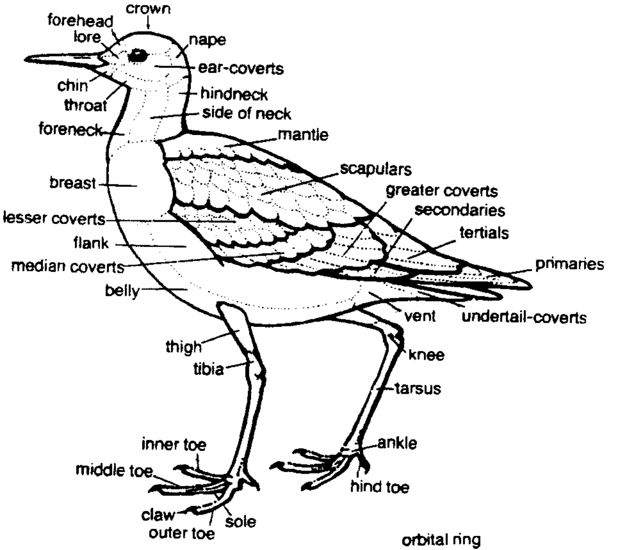
Fig. 1. Topography (above and opposite) of typical birds as published in the journal British Birds.

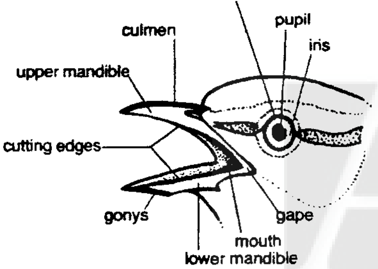
TOPOTYPE: term sometimes applied to a specimen, not forming part of the original type series, collected at the type locality of the species or subspecies concerned.

TOQ TOQ: *Foudia sechellarum* (for family see WEAVER).

TORPIDITY: a state of dormancy and lowered body temperature (hypothermia) that enables a bird to conserve energy during periods of energy shortage, and from which it can arouse by means of endogenous heat production. Birds of at least 3 orders (Apodiformes, Caprimulgiformes, and Coliiformes) can undergo daily cycles of torpidity, but prolonged dormancy of the type characteristic of mammalian hibernation has been demonstrated only in nightjars (Caprimulgidae) (see HEAT REGULATION; METABOLISM).

In the 18th century and earlier it was widely believed that swallows *Hirundo rustica* became torpid and passed the winter in hollow trees and crevices, or even in the mud at the bottom of ponds. When the actual





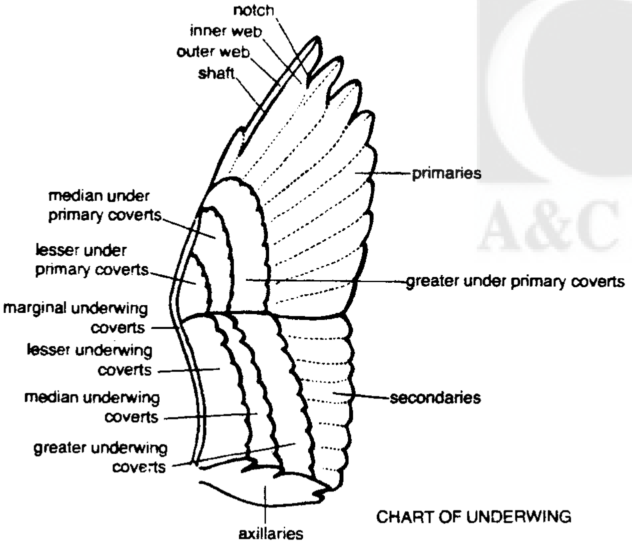


CHART OF UNDERWING

whereabouts of swallows during the winter became known, the hibernation theory was discarded as myth. The idea of avian hibernation was so completely discredited that the anecdotal accounts of the occurrence of dormancy in swifts and hummingbirds which were published during the first third of the 20th century by Hanna (1917) and by Chaplin (1933) attracted little interest. During a cold wave in January, 1913, in San Bernardino County, California, Hanna found a large number of dormant White-throated Swifts *Aeronautes saxatilis* in a rock crevice. He concluded that these birds might experience intermittent hibernation because they disappeared for many days in cold weather and during one such period he found them in substantial numbers among the rocks in a torpid state. Chaplin, in 1933, noted that in the 19th century Gould had observed torpidity in hummingbirds; he also reported that he had himself found *Chrysolampis mosquitus* and *Eupetomena macroura* torpid at ambient temperatures of 17–21°C. The birds sat on their perches with the head drawn down on to the shoulders, and 'showed to all appearances no spark of life.' Chaplin also observed that torpidity was not a direct response to cold because hummingbirds were often active at low temperatures. He suggested that swifts, nightjars, and colies might also experience torpidity. Six years later Huxley, Webb, and Best, apparently in ignorance of the literature, published similar although less detailed observations on hummingbirds.

In 1947 McAtee reviewed the literature on torpidity in birds and found few records, beyond those just mentioned, in which reliable witnesses reported first-hand observations. His review was published shortly before the remarkable discovery of a hibernating Poorwill *Phalaenoptilus nuttallii*, a caprimulgid which breeds in the arid and semi-arid parts of western North America. In December 1946 Jaeger (1949) found a Poorwill hibernating in a rock crevice in the Chuckwalla Mountains of the Colorado Desert in California. The bird was inert, its respiration and heart rate undetectable with the apparatus available in the field. The bird was ringed and in subsequent winters was found repeatedly in the same spot in a dormant condition with a body temperature of 18–20°C. Fewer than half a dozen torpid Poorwills have subsequently been found in nature but many aspects of the physiology of both normally alert and torpid Poorwills and other caprimulgids have been studied in captive birds (Withers 1977).

In torpid caprimulgids low body temperature, and a greatly reduced metabolic rate allow prolonged survival in a dormant state. Calculations indicate that normal fat deposits can easily sustain a torpid Poorwill for 100 days at a body temperature of 10°C. In captivity Poorwills have remained in torpor for as long as 4 days. However, the other kinds of birds which experience dormancy appear to remain dormant only overnight (hummingbirds) or at most for only a few days (swifts and colies).

The mass-specific energy metabolism of hummingbirds is extremely high, not only because of their small size, but because they characteristically feed on the wing and flight is energetically expensive. As long as hummingbirds maintain a high body temperature they are never more than a few hours from death by starvation. This would be a formidable hazard in periods of inclement weather or food shortage were it not for their capacity for becoming torpid at night during periods of energy shortage. They hold body temperature at a typical avian level (approximately 40°C) during daytime, but after going to roost at night they may allow it to fall to near ambient, which in some cases involves a decrease of more than 30°C. This pattern of heterothermy is central to the success of hummingbirds and has been extensively documented both ecologically and physiologically (see Bartholomew 1972; Calder 1974; Hainsworth and Wolf 1978).

At present two primary generalizations can be made about hummingbird torpidity. (1) Torpor occurs only when energy is in short supply. If food is readily available hummingbirds maintain normally high body temperatures. (2) Body temperature during torpor is in a regulated state; the level of hypothermia about which temperature is controlled varies from species to species, and appears to be related to the environment in which the birds live. This level is near 20°C in *Eulampis jugularis* which occurs in the lesser Antilles in mountainous areas where the altitude is generally less than 1,500 m. It is near 10°C in *Eugenes fulgens* which occurs on mountain slopes from Arizona to Panama, and near 7°C in *Oreotrochilus estella* which occurs at altitudes from 3,800 to 4,200 m in the Andes.

Torpidity occurs in the Apodidae but it has not been extensively studied either physiologically or ecologically. The nestlings of the Swift *Apus apus* become torpid during temporary food shortages. Adults of the White-throated Swift *Aeronautes saxatilis* will undergo torpor both in the laboratory and in the field and can spontaneously arouse from body temperatures near 20°C.

A nocturnal decline of body temperature of 10°C or more (usually not accompanied by complete torpor) has been reported in several sunbirds in the genera *Nectarinia* and *Anthreptes* kept in captivity at an altitude of 3,350 m in East Africa (Cheke 1970). Like hummingbirds, sunbirds feed on nectar and insects. A capacity for nocturnal hypothermia could afford them significant energy savings during periods of inclement weather.

Torpor also occurs in birds that do not depend primarily on nectar or insects for food. The Speckled Mousebird *Colius striatus* can enter into and arouse from a state of nocturnal torpor in which body temperature falls 15°C or more below normal levels. These birds, which belong to the Order Coliiformes, are widely distributed in Africa south of the Sahara. They weigh about 50 g and are almost exclusively vegetarian. Thus, they do not face the necessity of sustaining extremely high rates of mass-specific metabolism nor do they have to deal with the problem of temporary shortages of insect food during bad weather. Moreover, they readily maintain normal high body temperatures (about 39°C) at ambient temperatures near 0°C. Consequently, the precise ecological role of torpor in colies remains obscure.

It is of interest that a similar but less profound nocturnal hypothermia occurs in at least 2 species of tropical passerines which feed primarily on fruit, the Red-capped Manakin *Pipra mentalis* and the Golden-collared Manakin *Manacus vitellinus*. During periods of reduced food intake these manakins allow body temperature to fall to as low as 30°C at night and then gradually warm up to normal levels in the pre-dawn hours. However, they do not enter a completely dormant state. Similar but less extreme nocturnal hypothermia has been reported in the Willow Tit *Parus montanus* and Siberian Tit *P. cinctus* in northern Europe and in the Black-capped Chickadee *P. atricapillus* in north-eastern United States, but it apparently does not occur in Arctic populations of this species.

Avian torpidity and the associated condition of marked nocturnal hypothermia have so far been examined in only a few species. However, their occurrence may be much more widespread than currently documented. One can predict that they are most likely to be found in species that have unusually well sheltered roosting sites or live in warm regions. For example, in the lowland tropics where night time air temperatures rarely fall below 18–20°C, a nocturnal decline of body temperature of 10°C halves the difference between body and ambient temperatures. This reduces the rate of heat loss to the environment by 50% and results in a concomitant saving in metabolic energy which could be ecologically important during periods of reduced food availability such as occur during the dry season for both insectivorous and frugivorous species. (L.H.M.) G.A.B.

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TORRENT-LARK: *Grallina bruijni*, the New Guinea member of the MAGPIE-LARK family.

TORRESIAN: see AUSTRALASIAN REGION.

TOTIPALMATE: having all 4 toes connected by webs (see LEG).

TOUCAN: substantive name of species of Ramphastidae (Piciformes, suborder Galbulae); in the plural, general term for the family. The name comes from 'tucano' in the language of the Tupi Indians of Brazil. The family consists of 6 genera and 42 species.

Characteristics. Toucans are middle-sized or large birds (34–66 cm long) confined to the tropical parts of the American continents. Wholly arboreal, they occur only in wooded regions, chiefly at low and middle altitudes. The outstanding feature of these ungraceful birds is the bill, which in all species is enormously enlarged, while in some it almost equals the body in length and bulk. Nearly always it is coloured with several bright and contrasting hues. Although in some species it appears almost too heavy for the bird to support, lightness combined with strength is obtained by a network of bony fibres ramifying through the space within the horny outer shell. Nevertheless, these bills are sometimes conspicuously broken; birds lacking half the mandible or maxilla often survive a long while in the free state. In size the toucan's bill compares with that of the hornbills of the Old World tropics, but it always lacks the dorsal out-growth or casque; the 2 families are not closely related.

Collared Araçari *Pteroglossus torquatus*. (*P.J.K.B.*).

The toucan's tongue is also remarkable. It is a long, narrow, horizontally flattened, thin lamina, which may attain a length of 15 cm in the largest species. Its distal part is on both sides obliquely notched by indentations that become progressively deeper toward the apex, where it has a bristly aspect. The wings are short and rounded; the tail tends to be long; the legs are strong and the feet zygodactylous. Each eye is surrounded by an area of bare skin that is usually brightly coloured.

Distribution and habitat. The largest toucans belong to the genus *Ramphastos*, which contains 12 species, up to 66 cm long. The Rainbow-billed or Keel-billed Toucan *R. sulfuratus* ranges through the forests from southern Mexico to northern South America. As in most toucans, the sexes are alike in coloration, but the males average larger than the females, with considerably longer bills. About 43–50 cm long, this stout bird is largely black, slightly glossed with green on the upper parts and washed with maroon on the hindneck. The upper tail coverts are white. The cheeks, throat, and foreneck are bright yellow, and the under tail coverts are bright poppy red. The coloration of the great, swollen bill varies somewhat with individuals and, with the exception of violet, all the colours of the rainbow are found on it. The tints blend rainbowlike into each other, and the basal margin of the bill is deep black. Other members of this genus have fewer but more strongly contrasting colours on their bills.

The genus *Pteroglossus* consists of 13 long-tailed, middle-sized or small toucans usually called araçaris. The Collared Araçari *P. torquatus* is a slender bird, about 42 cm long, which is found in wooded country at lower altitudes from southern Mexico to Colombia and Venezuela. In both sexes, the upper plumage is generally blackish, glossed with green on the back, with a bright red rump and upper tail coverts. The throat and foreneck are black, and the more posterior under plumage is largely yellow, with a band of black and red across the upper abdomen. The bill, less vividly coloured than in certain other araçaris, is whitish, grey, and black. The cutting edge of the maxilla has widely spaced, toothlike projections. The bright yellow eyes are surrounded by red bare skin. In this genus the curious Curl-crested Toucan *P. beauharnaesii* of the upper Amazon valley is sometimes placed. The feathers of its head consist largely of the broadly expanded horny shafts. Those on the pileum are curled forward and resemble shavings of glossy black horn.

The 7 toucanets of the genus *Aulacorhynchus* are largely green in plumage and reach higher altitudes than the 2 preceding genera, to about

3,000 m in the Andes and the highlands of Middle America. The Blue-throated Toucanet *A. prasinus caeruleogularis*, confined to the mountains of Costa Rica and western Panama, is about 30 cm long. In both sexes, the green plumage which covers most of the body lacks metallic lustre. The cheeks, chin, and throat are dark blue, and the under tail coverts are chestnut. The bill is yellow, white, red, and black, with yellow predominating. Toucanets perform vertical migrations, but other members of the family seem not to migrate.

Likewise found at high altitudes are the 4 species of the Andean genus *Andigena*, known as mountain toucans. The 56 cm long Black-billed Mountain Toucan *A. nigrirostris* is glossy black on crown and hindneck and olive-brown on back and wings. The rump is yellow, throat white, under tail coverts crimson, rest of under parts light blue, and thighs chestnut. The 5 small toucanets of the genus *Selenidera* have intricately patterned plumage and are the only members of the family in which the sexes differ in coloration. They inhabit warm forests of the Tropical Zone. The Saffron Toucanet *Baillonius bailloni* of south-eastern Brazil is the only member of its genus.

Food. Toucans eat many berries, arillate seeds, and other small fruits, and they vary their diet with such insects, spiders, small lizards, small snakes, and the like as they can catch, including slowly fluttering termites on evenings when the air is full of the winged sexual brood. Seizing the food in the tip of its great bill, the toucan tosses its head upward to throw the piece backward into its throat. Large items are first torn by the bill while held against the perch with a foot. The toucan that Humboldt and Bonpland carried on their historic canoe voyage up the Río Orinoco liked to fish in the river. Species of *Ramphastos, Pteroglossus, Aulacorhynchus*, and doubtless other genera, devour eggs and nestlings of small birds.

It is in connection with the toucans' feeding habits that their peculiar bills must be considered. The long bill enables these heavy, rather clumsy birds to reach fruits that grow at the slender tips of branches while they perch farther inward, where they find more adequate support. But to give a longer reach, the bill need be neither thick nor brightly coloured.

Behaviour. Toucans are sociable birds that are often found in small flocks of a few to more than a dozen individuals, yet they are almost devoid of group impulses. When they travel, one flies away and then another follows; and so they straggle on, one by one, until the whole flock has moved. The larger species fly with alternate flapping and gliding, tracing undulatory courses; but the flight of some of the smaller kinds is swift and direct. Toucans bathe in water that collects in hollows in crotches of trees or in the upper side of thick horizontal limbs, often high above the ground. They evince curiosity, and in remote forests they may look down with interest at the activities of a botanical collector or other human intruder. They are frolicsome birds, jumping about and sometimes playfully striking their great bills together in a sort of fencing, or grasping each other's bills and pushing, with no display of antagonism. Sometimes they preen one another's plumage with the tips of their bills. At least in *Ramphastos*, *Pteroglossus*, and *Aulacorhynchus*, one individual often passes food to another, doubtless its mate. Sometimes pair members feed each other reciprocally. Like other piciform birds, toucans scratch their heads by raising a foot outside the closed wing rather than over the drooped wing, as passerines commonly do.

The size and vividness of toucans' bills probably serve them well when they make predatory visits to the nests of other birds; they are so intimidating that even small hawks and the boldest of the American flycatchers (Tyrannidae) fear to attack a toucan perching beside its nest. But when the pirates are flying and cannot turn their heads to defend their backs, the outraged parents sometimes buffet them. Since the bills of conspecifics often differ more strikingly in coloration than their plumage, they probably serve for specific recognition among sympatric forms. The vivid bill may also enter into courtship, although little is known about toucans' nuptial displays. It has been suggested that the long bill may also help an incubating or brooding toucan to repel enemies from the doorway of its hole, but toucans hurry forth from their nests at the first hint of danger.

Sleeping. Araçaris roost throughout the year in holes of woodpeckers or other cavities, usually high in trees. Each flock seems to have a number of these lodgings; if their suspicions are aroused as they approach one, they may retire into another. Five or 6 adults may sleep in the same hole, folding their tails over their backs to save space in crowded quarters. In captivity, *Ramphastos* spp. roost with the bill laid among the plumage of the back and the tail folded forward over the bill, so that they become featureless balls of feathers. Bourne (1974) noticed 5 Red-billed Toucans *R. tucanus* sleeping side by side in close contact high in a tree in Guyana. As far as known, only *Pteroglossus* spp. and (at least occasionally) the Guianan Toucanet *Selenidera culik* sleep in holes when not nesting.

Voice. Toucans are poorly endowed vocally. Their monotonous calls have been compared to the croaking of frogs, the mewing of gulls, and the yelping of puppies. They produce rattling, castanetlike notes that seem to be mechanical but are actually vocal. Araçaris utter high, sharp notes, surprisingly weak for such large birds. The *dios te de, te de, te de* of the Chestnut-mandibled Toucan *Ramphastos swainsonii* is, however, not unmelodious as it floats down from distant treetops. These birds sing much at nightfall, swinging their heads up and down as they emit their notes.

Breeding. Toucans nest in trees, in hollows resulting from decay or, in the smaller species, in woodpeckers' holes, of which they may dispossess the makers. They may remove rotten wood from a hole, or enlarge the doorway if the surrounding wood is soft; but their occasional attempts to carve a nest cavity seem always to be ineffectual. *Ramphastos* spp. prefer living trees and may nest in the same cavity in successive years, but smaller toucans are often content with dead trees. Toucans' nests are often at a great height, but exceptionally they choose one near the ground. Rainbow-billed Toucans take a few green leaves into their holes and may carry them away after they wither. Otherwise, toucans take no lining into their nests; but the many large seeds which they regurgitate while they sit soon form a pebbly bed beneath the eggs. These number 2–4 in a clutch; they are broadly ovate, white or pinkish, and unmarked.

Incubation is performed by both parents, who are surprisingly restless for such large birds. They seldom sit for more than an hour at a stretch; and often they leave the eggs uncovered for up to an hour or more, while both attendants go off to forage. Even if, as in the araçaris, both parents had slept in the nest hole before laying began, only one stays with the eggs at night. A male Red-billed Toucan incubated by night and also brooded the young on most nights, but the female sometimes brooded through the night. However, only the female of a pair of Blue-throated Toucanets was seen to occupy a nest with eggs at night. Nocturnal incubation and brooding by the male is usual in the related woodpeckers and has also been found in puffbirds, but it is not invariable in the order Piciformes. The incubation period of the Red-billed Toucan is approximately 15.5 days; that of the Blue-throated Toucanet, 16 days.

Toucans are hatched perfectly naked, with no trace of down. Their eyes are tightly closed, and the mandible is both longer and broader than the maxilla. Their heels are equipped with prominent thickened pads, from which project a number of strong tubercles, arranged in a peripheral ring in species of *Ramphastos*. These heel pads, along with the abdomen, bear the nestling's weight; their function appears to be to prevent abrasion of the heel joint by the nest's rough floor. The nestling's uropygium is extraordinarily long and prominent and is often held with a strong upward tilt. Young toucans develop with extreme slowness. They are over 2 weeks old before their eyes begin to open, and at this age they are still naked.

Both parents brood and feed the young, nourishing them largely with fruits, insects especially while they are younger, and occasionally a lizard, small snake, or the nestling of some other bird. Much of the food is carried to the nest in the throat or stomach, but usually a final item is held prominently in the parent's bill and given to a nestling before the remainder of the load is brought forth. Waste material is removed from the nest in the parents' bills. In the Blue-throated Toucanet and species of *Ramphastos*, a single parent sleeps with the nestlings until a few days before their departure, but in the araçaris both parents pass the night with them. In Panama, 6 Collared Araçaris roosted in a very high hole that was afterward used for breeding. Only one parent slept in it while incubation was in progress, but after the eggs hatched 5 adults roosted in the nest hole each night. All 5 of them fed the nestlings, of which there were at least 3. The nestling period of this species is 43–46 days; that of the Blue-throated Toucanet, 43 days; and that of *Ramphastos* spp., about 47–49 days. Fledgling araçaris return to sleep in the nest hole with their parents, and the helpers when these are present; but apparently young of *Ramphastos* spp. and *Aulacorhynchus* spp. do not return. In the highlands, Blue-throated Toucanets rear 2 broods in a season, but the larger toucans of the lowlands apparently attempt only a single brood. A.F.S.

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TOUCANET: substantive name of *Aulacorhynchus* spp. (see TOUCAN).

TOUCH: the 'sense of touch' is understood to mean the faculty to perceive mechanical deformation of the body surface (or internal structures) which can be caused by autogenic movements as well as by external influences. Exposed regions, like finger-tips or lips in man, are particularly touch-sensitive; the same is true of bill-rim, bill-tip, palate and tongue in birds. Tactile perception is, however, found distributed over the whole avian body as well, though it has but rarely been studied. Tactile perception, combined with temperature and pain sensitivity, constitutes in all vertebrates the so-called 'somato-sensory system'. In birds too, certain slow-adapting mechanoreceptors are at the same time strongly temperature sensitive; as in mammals, 'genuine' thermoreceptors are also found.

Receptors for tactile stimuli are, in most cases, the endings of sensory nerve fibres which are partially equipped with small organs and originate from the ganglia of the cranial nerves (trigeminal for bill, glossopharyngeal for tongue) and the spinal ganglia. Direct participation by elements of the sympathetic system in tactile perception is questionable, but the tactile corpuscles of birds also appear to receive additional sympathetic innervation. A great variety of sensory endings is known from the skin of mammals; in birds these concern free nerve-endings, Merkel and Grandry's corpuscles and also the lamellated Herbst's corpuscles (see SKIN). These contain, as the sensitive element, a central axon-process surrounded by several myelinated layers of Schwann cell derivatives and an outer capsule of connective tissue; they are essentially comparable to the somewhat larger mammalian Pacinian corpuscles but differ a little in enzymatic respect. Grandry's corpuscles are found only in birds, predominantly in the bill region of Anatidae. They may be understood as a higher development of the Merkel corpuscles also known in mammals, but are distinguished above all by the capsule and a larger number of 'tactile cells'; furthermore, they are positioned within somewhat deeper subepidermal layers. As in the Merkel corpuscles, flattened segments of afferent nerve fibres enter between at least two, frequently more cushion-like differentiated cells ('tactile cells'), the neurofibrils forming a dense plexus in the unmyelinated nerve segments. Synaptoid ultra-structures are found in the very narrow contact-zones with the 'tactile cells'. The interpretation of the latter as excitable secondary sense-cells is controversial.

Responsible, as a somato-sensory region for the processing in the central nervous system of sensory information from avian tactile receptors, is on the one hand an electro-physiologically detected region in the Neostriatum caudale adjoining the auditory region (Field L). On the other hand, anatomical studies have shown that not only the main sensory trigeminal nucleus but correspondingly also the frontal fore-brain region (Nucleus basalis) increases in size depending on the degree to which the bill is used as a tactile organ. The frontal fore-brain region is connected to the trigeminal nucleus by the Tractus quintofrontalis. From the size development of these two regions a functional order can be derived leading from *Merops* through *Strix*, *Aix*, *Melopsittacus* to *Capella* and *Ibis*. Finally, somato-sensory input is also clearly represented in the cerebellum, especially within folium V1.

Some insight into the functional importance of the touch-sensitive nerve-endings can be gained by considering their distribution over the avian body. Free nerve-endings are found in all regions but are apparently less densely distributed than in mammals. They alone can also enter epidermal cell layers. Merkel corpuscles have been found superficially beneath the epidermis and also the keratinized sections of tarsus and foot. Herbst's corpuscles occur at the base of the contour feathers, abundantly in the region of the bill-tip, e.g. in Scolopacidae and Anatidae (bill-tip organ), in the palate, and, with particular concentration, in the tongue-tip of woodpeckers; they are not found, however, on the plantar surface of the foot. In the especially well studied bill of ducks and geese (Anatidae), Herbst's corpuscles are somewhat more numerous and, importantly, they show a different distribution from that of Grandry's corpuscles. Overall, the supply with tactile endings of certain sections of the anatid bill considerably exceeds that of the human finger-tip. Larger numbers of Herbst's corpuscles occur furthermore on the metacarpus and between radius and ulna, attached to the remigial follicles. As on the bill-tip, alveolar isolating structures are formed around the corpuscles. A special 'cord' of numerous Herbst's corpuscles is protectively located between the tibia and fibula where it is exposed only towards the M. flexor-digitorum profundus. The distribution and special arrangement of the endings permit general conclusions to be drawn regarding the respective functions in the taking up and processing of food and also control of movements. Only a few experimental studies give direct information on receptor efficiency. According to these studies, the Herbst's corpuscles, like the more exactly known Pacinian corpuscles of mammals, may be numbered amongst the fast-adapting endings which are especially sensitive to dynamic tactile and vibratory stimuli. The fluid-filled cushion, enclosed in the capsule of connective tissue, functions as a low pass filter and, in accordance with their small size, the Herbst's corpuscles of birds react to slightly higher frequencies of vibratory stimuli than the mammalian Pacinian corpuscles. In the Bullfinch *Pyrrhula pyrrhula*, behavioural experiments have shown an optimal sensitivity to vibration (localized in the lower leg) lying between 400 and 800 Hz. Neurophysiological studies on ducks have demonstrated corresponding preferential frequencies. The threshold amplitude lies one order of magnitude below that of the human finger-tip. Vibrations of the remiges are presumed to be perceived in flight; air currents directed onto the breast feathers release reflex flight-movements.

The Grandry's corpuscles also belong to the fast-adapting 'phasic' receptors which are particularly suited to the processing of tactile stimuli. Here it is not amplitude or frequency but rather the speed of deformation which is decisive for stimulus efficiency. The Merkel corpuscles and free nerve-endings are employed as receptors for more persistent (tonic) pressure stimuli.

The behaviour of birds with widely differing ecological adaptations, well known from a great variety of ornithological observations, shows the slightly varying but always paramount importance of the bill in obtaining, tactilely investigating and dealing with food. This is true for the bill of snipe (Scolopacidae) which 'probe blindly' into the substrate, for dabbling ducks (*Anas* spp.), but also for the palate and tongue of granivorous birds in the 'shelling' of seeds. The function of the tongue-tip of woodpeckers becomes particularly clear when these birds explore insect tunnels in wood. The sensitivity of birds to vibrations, occasionally described as mysterious—e.g. swallows Hirundinidae leaving their nests in advance of earthquakes—can be explained by the efficiency of vibration receptors in the lower leg. Tactile sensations, translated by way of the feathers or the feet, are also involved in preening and in contact between eggs or chicks ready to hatch and the brooding parent. J.S.

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Saxod, R. 1970. Étude au microscope électronique de l'histogenèse du corpuscule sensorial cutané de Herbst chez le canard. J. Ultrastructure Res. 33: 463–482.
Schwartzkopff, J. 1973. Mechanoreception. Pp. 417–477. *In* Farner, D.S. & King, J.R. (eds.). Avian Biology, vol. 3. New York.

TOURACO: see TURACO.

TOWHEE: substantive name of species of *Pipilo* (see BUNTING; also HYBRIDIZATION, ZONE OF SECONDARY).

TOXIC CHEMICALS: considered here as a hazard to birdlife. Any chemical can be toxic; whether it is depends on the dose. The term 'toxic chemicals' is used to describe those substances which are put into the environment by man on a scale and at concentrations which have or are likely to have deleterious effects on organisms. They include pesticides used in agriculture, forestry and public health, and industrial pollutants such as polychlorinated biphenyls (PCB) and heavy metals. Fertilizers can have profound effects on terrestrial and aquatic ecosystems and so may affect bird populations, but they are not usually classified as toxic chemicals, nor are oils (see OIL POLLUTION). The most important toxic chemicals from the ornithological point of view are pesticides, PCBs and mercury.

Pollution is principally a consequence of industrialization and has been a significant factor for many decades, but the extensive use of pesticides only began in the 1940s and 1950s. They became an integral part of farming throughout the developed world and much of the developing world in the 1960s. Growth in the use of pesticides in the United Kingdom is shown by the following: 15 chemicals were listed in the Ministry of Agriculture's List of Approved Products for Farmers and Growers in 1950, 47 in 1960, 163 in 1970 and 198 in 1980.

Thus, pesticides are a new and important ecological factor. They include herbicides, fungicides, insecticides, rodenticides and growth retardants. No pesticide is specific to a particular pest or weed, therefore their use always involves some risk to some other organism, though in practice it may often be ecologically negligible. Hazards to birds depend on the toxicity of the compound, its dose rate and on the way it is applied. Very dilute formulations of very toxic substances may be less dangerous than more concentrated formulations of less toxic substances. Less toxic substances which are very persistent (e.g. DDT) may be more dangerous than very toxic ones which break down quickly (e.g. several organophosphorus insecticides). If seed dressed with very toxic insecticides (e.g. aldrin, dieldrin and certain carbamates such as aldicarb) or fungicides (certain mercury compounds) is left exposed on the ground it can be particularly hazardous to birds since it acts as poison bait. The deliberate misuse of pesticides, notably mevinphos, α-chloralose and strychnine as poison baits has caused the deaths of numerous predatory birds in Great Britain.

Pesticides affect individual birds either directly by poisoning them, or indirectly by reducing their food supply or cover. The prediction of the effects of pesticides on bird populations is extremely difficult. First, because species vary considerably in their response to the same pesticide, for example, grey geese *Anser* are much more susceptible to the organophosphorus seed dressing carbophenothion than are Woodpigeons *Columba palumbus* or Canada Geese *Branta canadensis*. Secondly, because the interaction between lethal and sub-lethal toxic effects with environmental factors (which may include indirect effects of pesticides) are extremely complicated. Thus it is not yet possible to assess the impact of pesticides on most species of birds.

In the 1950s the use of dinitrocresol and the more toxic organophosphorus insecticides such as parathion, was responsible for the death of numerous birds in Great Britain, continental Europe and the USA. The deaths drew attention to the dangers of pesticides to wildlife and stimulated authorities to seek ways of reducing harmful side-effects of pesticides. The British Pesticides Safety Precaution Scheme was introduced in 1953. During the late 1950s and early 1960s attention was focussed on the persistent organochlorine insecticides. These vary in toxicity, aldrin, dieldrin and heptachlor being much more toxic than DDT and TDE. They or their metabolites are soluble in lipids and hence become stored in animal fats. This enables them to accumulate in animals and so to be transferred from prey to predator. Although the amounts of these chemicals in water are so small that they often cannot be detected, fish and molluscs can concentrate them through their gills and so can pass persistent pesticides on to fish-feeding birds such as pelicans, cormorants, herons and grebes. DDT breaks down extremely slowly below the surface layers of the soil. Thus, owing to their persistence, organochlorine insecticides can circulate within ecosystems for a long time. Much is now known about the amounts of organochlorine insecticides present in air, water, soils and organisms and about their transfer from one level or organ to another. Persistent organochlorine insecticides have numerous physiological effects, but the most significant is their effect on the central nervous system. Stress occasioned by migration, reproduction and starvation causes depletion of the fat reserves and so results in an increase of pesticide in the blood, which in turn affects the brain. DDE, the principal metabolite of DDT, causes EGGSHELL THINNING and dieldrin affects reproductive behaviour in birds.

Lethal and sub-lethal effects of persistent organochlorine insecticides on predatory and fish-feeding birds have been studied in the laboratory and in the field, notably in the British Isles, North America and in central and northern Europe. Pesticide residues can be considerable and yet little effect on populations can be discerned. For example, large residues and associated reproductive failure have been reported in the Heron *Ardea cinerea*, yet effects on the total English population of this species appear to have been negligible. Different pesticide practices have had different effects in different regions. The well documented declines in populations of Peregrines *Falco peregrinus*, Sparrowhawks *Accipiter nisus* and Kestrels *Falco tinnunculus* in the United Kingdom were primarily due to acute poisoning by dieldrin, as was the decline in the breeding success of the Golden Eagle *Aquila chrysaetos*. By contrast in the USA, the declines of the Peregrine Falcon, Osprey *Pandion haliaetus*, Bald Eagle *Haliaeetus leucocephalus* and Brown Pelican *Pelecanus occidentalis* and American White Pelican *P. erythrorhynchus* appear mainly to have been caused by DDT. The sub-lethal effects of DDE appear to have been more serious in the USA than in the United Kingdom.

Little is known about the indirect effects of pesticides on birds. However, the elimination of reeds from large areas of the English Fens through the use of dalapon must have affected the numbers of Reed Warblers *Acrocephalus scirpaceus* there, and there is some evidence that low numbers of Kestrels and Barn Owls *Tyto alba* may be due to lack of food caused by pesticides as well as to habitat loss. Extensive studies on the Grey Partridge *Perdix perdix* have shown that its decline in Great Britain is due primarily to a diminution of the insect food which is necessary for its chicks in summer. The decline of insects is due to herbicides which kill the weeds on which the insects depend, to insecticides and insecticidal fungicides applied to cereals, and to a decline in the practice of under-sowing. The great reduction in populations of many weed species by herbicides must have had profound effects on many other bird species but they have been little studied.

PCBs, which have numerous industrial uses, are like DDT in being fat-soluble and very persistent in the environment. Large residues of PCBs have been recorded in many birds, particularly sea-birds, in many parts of the world. Little is known about their effects on bird populations. They were probably a contributing factor in the sea-bird disaster in the Irish Sea in 1969 when many thousand Guillemots *Uria aalge* died.

Organic mercury compounds are used extensively as fungicides. Fungicides based on methyl mercury caused many farmland bird deaths and population declines in Sweden in the 1950s. Phenyl mercury was also used extensively in that country in order to preserve wood pulp. This compound is broken down into inorganic mercuric compounds but in bottom muds the latter can become converted into methyl mercury, which is commonly found in fish in Sweden. Little is known about the effects of secondary poisoning of fish-feeding birds by mercury in Sweden or elsewhere. It is often difficult to separate the effects of mercury from those of organochlorine insecticides since birds are frequently exposed to both types of chemical at the same time.

Demonstration of deleterious effects of pesticides on bird populations has resulted in restrictions or total bans on certain pesticides in developed countries and to a growing sophistication in the methods of controlling pesticide use. Large-scale mortality due to DDT, dieldrin, aldrin and methyl mercury ceased when restrictions were placed on these substances. As a result, British populations of Peregrines, Kestrels and Sparrowhawks have shown marked recoveries and reproduction in the Golden Eagle has returned to normal. Nevertheless, considerable DDE residues are still found in Sparrowhawks and the recovery of this species has been relatively slow. Elsewhere in Europe and in the USA recoveries of affected species have been slower or non-existent. Partly, this appears to be due to birds migrating in winter to areas where persistent organochlorine insecticides are still widely used. Restrictions on the use of the organophosphorus seed dressing carbophenothion in Scotland was agreed between industry and Government in the 1970s and removed a serious hazard to Greylag Geese *Anser anser* and Pinkfeet *A. brachyrhynchus* in that country.

Pesticides will continue to be used extensively in the developed world and their use in the developing world is likely to increase. Despite advances in their control they are likely to remain a significant factor in relation to bird populations in the years to come. N.W.M.

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Moriarty, F. 1975. Pollutants and Animals. A Factual Perspective. London.

Newton, I. 1979. Population Ecology of Raptors. Berkhamsted.
Ratcliffe, D. 1980. The Peregrine Falcon. Calton.

TRACHEA: the windpipe, an air passage leading from an opening (glottis) at the back of the mouth, running down the neck (ventrally to the oesophagus), and dividing into the two bronchi leading to the lungs (see RESPIRATORY SYSTEM). The anterior part, surrounded by the cricoid and other cartilages, is known as the larynx but is without vocal cords. At the posterior end and commonly also involving the bronchi (but wholly tracheal in some species, and wholly bronchial in some others) is the syrinx, an organ peculiar to birds (see SYRINX). The whole tube is reinforced by cartilaginous or bony rings, and dilatations or enlargements are found in some species, notably among ducks. In certain species, either in the males only or in both sexes, the tube is elongated by being coiled; different versions of this character are found in a wide diversity of birds, but its presence may not be constant even within a genus. In some swans and cranes the bone of the sternal carina is extensively excavated to accommodate the tracheal loops. (Fig. 1.)

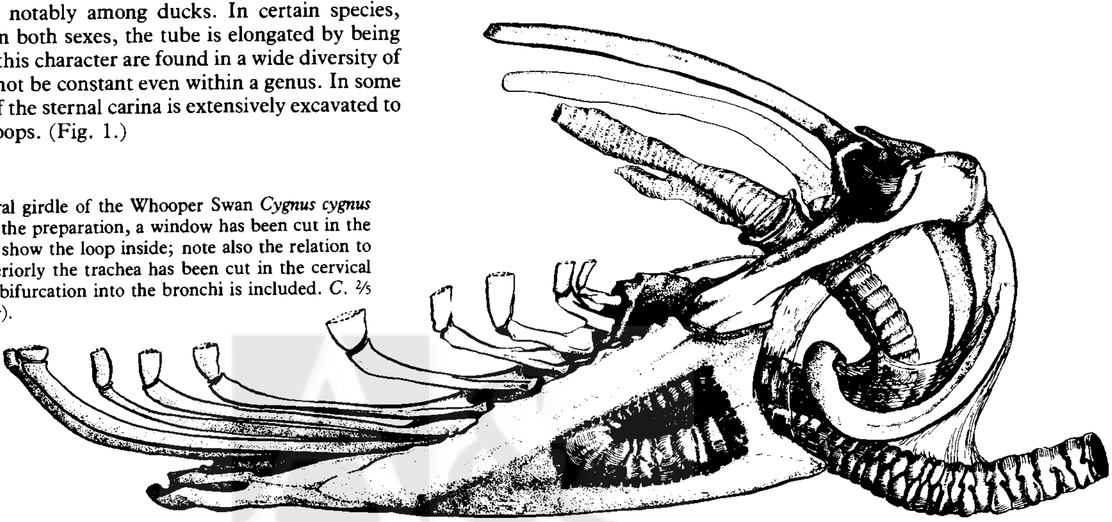


Fig. 1. Sternum and pectoral girdle of the Whooper Swan *Cygnus cygnus* showing looped trachea. In the preparation, a window has been cut in the side of the hollow carina to show the loop inside; note also the relation to the furcula (clavicles). Anteriorly the trachea has been cut in the cervical region, and posteriorly the bifurcation into the bronchi is included. *C.* ⅖ Natural size. (*Saida Symons*).

TRACHEOPHONAE: see under PASSERIFORMES.

TRACK: the path of a flying bird relative to the earth's surface; the resultant (allowing for speeds) of the bird's heading and the local wind (see MIGRATION, Flight performance).

TRACKS AND SIGNS: footmarks and other evidence of their presence left by birds. Foot and wing marks show on soft ground (mud, sand) and snow, and vary with the shape of foot, length of leg and gait (see LOCOMOTION, TERRESTRIAL). Signs include DROPPINGS, PELLETS, plucking places of birds-of-prey, food remains, shrikes' larders.

Ennion, E.A.R. & Tinbergen, N. 1967. Tracks. Oxford.
Urner, C.A. 1943. *In* Hickey, J.J. Guide to Bird Watching. London.

TRAGOPAN: substantive name of *Tragopan* spp. (see PHEASANT).

TRAIN: term sometimes applied to a long tail or tail-coverts e.g. of a Peacock *Pavo cristatus*, or by falconers to tail of a bird-of-prey (see TAIL).

TRAINBEARER: substantive name of *Lesbia* spp. (see HUMMINGBIRD); also formerly of several *Pharomachrus* spp. (see QUETZAL; TROGON).

TRANSECT: see BIOSTATISTICS; CENSUS.

TRANSIENT: perhaps the most precise term for a species or subspecies (on occasion applicable to individual birds) that appears on migration in the area under reference but neither breeds nor over-winters there; also 'passage migrant' (see MIGRATION, Time of year).

TRANSILIENT: term for a mode of moulting the primary feathers, proceeding by forward or backward leaps across one or more adjoining quills. The term was coined by Stresemann and Stresemann (1961) to describe the mode of primary moult of some cuckoos. Orderly transilient moult is apparently confined to some of the Old World parasitic members of the family (see MOULT).

Stresemann, V. & E. 1961. Die Handschwingen-Mauser der Kuckucke (Cuculidae). J. Orn. 102: 317–352.

TRAPPING: in the present context, the catching of wild birds for ringing and other study purposes. In the UK trapping is only permitted under licence (except for certain pest species by authorized persons); but no methods that might cause suffering are countenanced (e.g. bird-lime, stupefying baits, tethered decoys), and a special permit is required to use lights for catching birds at night. The position naturally varies from country to country, and in some the trapping of birds for food or caging is still practised on a large scale.

Static cage-type traps. The traditional method employed until the mid 1950s, when mist nets, rocket/cannon nets, and clapnets began to be widely used. Still utilized but now mainly in special circumstances e.g. Heligoland traps, duck traps, waders in the Baltic, corvids (see OBSERVATORY, BIRDS).

The Heligoland trap is a long permanent wire-netting cage, up to 4 m high at the mouth and 20 m wide between wings (Fig. 1), narrowing and beset by baffles as it gives access beyond a swing-to door to a 'lock-up', and finally to a windowed catching-box whence birds are removed through a sleeve. Migrants on Heligoland in the early part of the century were driven into such traps from low cover in the catching area ahead, or were attracted by water or bait provided. At the other extreme are the small Potter and Chardonneret traps used in suburban gardens, operating automatically on the tripped-door principle.

Intermediate types include aviary-sized crow-traps, where ingress is by wide-mouthed funnel from above and a tame crow used as 'bait'; garden house-traps, entered either through a drop-door worked by trip or pullstick or through little tunnels at ground level; duck-traps, straddling the water margin, with adjustable slit entrances let in on 3 sides, employed with excellent results for both ducks and waders (Charadrii) on reservoirs; floating duck-traps moored on endless cable, and sparrow-traps, both constructed on lobster-pot principles; and a variety of smaller automatic wire-netting traps with maze or creep-in funnel entrances, baited for finches (Fringillidae) etc., or set with low lead-in 'fences' between them on shores for pipits and waders—these have proved most successful on tideless rotting seaweed beds infested with shore-fly larvae in Scandinavia. For removal from these larger traps a catching-box (like the Heligoland's) is built-in, or a landing-net is used; in the smaller types, a flap opens to let the bird pass through a corresponding opening into an independent carrying-box.

Clap nets. Large double clap nets used formerly by bird catchers relied for their high efficiency on the tethered decoy—now illegal in Britain but still used extensively by ringers in the Netherlands (often in conjunction with a 'tape lure'—see later). A variety of smaller versions—some with elastic or spring aids to increase catching efficiency—are now used by ringers in Britain. A simple version, with net area up to 6 × 2.5 m (but often less) and thrown by a single pole, has been developed successfully for use on a wide variety of species—from waders on the tide

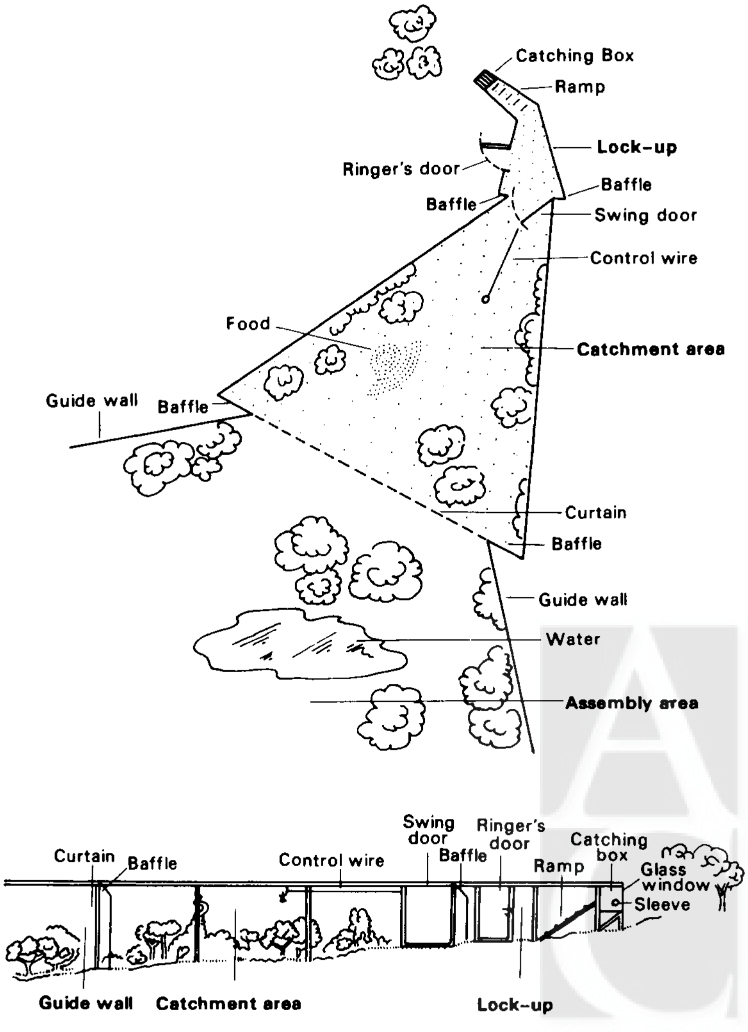


Fig. 1. Heligoland trap.

line to garden birds (baited to attract them to the catching area).

Small oval automatic spring-nets of soft netting string on stout wire frames, baited (e.g. with mealworms) and set like breakback mousetraps, will catch individual wheatears *Oenanthe*, shrikes etc. and—with care in expert hands—ground-nesting birds.

Rocket/cannon nets. Rocket nets—each measuring 60 × 20 m—were developed around 1950 by the Wildfowl Trust for catching geese *Anser* spp., with up to 400 being captured in a single throw. These have also been used to capture waders at large high tide roosts. However, since the mid-1960s cannon nets—typically 30 × 15 m and propelled by projectiles fired from 4 mortar-like barrels—have been more extensively used on waders, revolutionizing the study of this group. Catches average 200 per firing of the nets—but much larger catches have been made, including one of over 4,000 (3,500 Knot *Calidris canutus* and 600 Oystercatchers *Haematopus ostralegus*). Stuffed decoys may be used to lure birds into the catching area of cannon nets.

More recently cannon nets have been increasingly and successfully used on a wider range of species—ducks, coots, gulls (rubbish tip feeding areas as well as loafing and pre-roosting sites), corvids, passerines (including Snow Buntings *Plectrophenax nivalis*) in the UK; parrots, ibises in Australia and even vultures (Aegypiinae) in Africa.

A smaller, highly portable, net propelled by compressed air—a 'phut' net—has also been successfully developed in the 1970s for use on similar species.

Mist nets. The most important development in trapping techniques ever to take place was the invention of mist nets in Japan. These were first used in Britain in 1956 and very soon became the predominant method of capturing many species, especially passerines. These nets greatly increased the range of species which could be caught in significant numbers and provide the opportunity of ringing samples of birds in habitats/situations not previously possible (e.g. reed beds, roosts).

The fine nylon or polyester nets, hung upright between supporting poles, are almost invisible against a dark background, even in full daylight. The principle on which they work is very simple. On a rectangular 'framework' of 4–6 taut horizontal cords is threaded a significantly larger rectangle of netting. The surplus netting is apportioned vertically so that it hangs in folds, one beneath each horizontal 'shelf' string (other than the top one). A bird striking the wall of netting slithers down, to be pocketed in the surplus hanging beneath the nearest shelf string. A process of tethering maintains an even distribution of slack along the length of the net and permits catching in moderate winds. Strong winds greatly reduce the efficiency of mist nets.

Nets are normally 3 m high (divided into 3 to 5 panels) and 6–20 m long. Single panel nets (i.e. only 1 m high) are less visible and hence more effective in open conditions; alternatively, night-time mist netting is used on shores and marshes for waders etc.

Close supervision of nets needs to be maintained and, with birds being removed at regular intervals, catches in a single net rarely exceed 10–20 birds at a time. However, at hirundine roosts, where many birds may be caught over a short period, up to 100 have been captured at one time in a 20 m net. Tape recordings of bird calls, the so called 'tape lures', have been successfully used to attract birds into mist nets.

Other methods. Other traditional specialized methods for trapping birds now used for ringing include:

(i) For sea birds. The Fleyg, a long-handled outsize butterfly-Y-net is wielded by experts to intercept flying Fulmars *Fulmarus glacialis* and Puffins *Fratercula arctica*; wire crooks adjusted to their leg diameters are used to take Puffins, Kittiwakes *Rissa tridactyla*, etc. on the rock; 'stopped' snares to take Shags *Phalacrocorax aristotelis* and Gannets *Sula bassana* on their nests.

(ii) For ground feeding birds. Drop-nets of various patterns and dimensions worked by pull-cord and smaller drop-cages sprung automatically by trip-line or trigger.

(iii) For roosting birds. 'Bat-fowling' with tall folding nets clapped together to take birds as they fly out when disturbed from their roosts at night, or dropping nets over ground-roosting birds dazzled by strong light are other useful techniques, particularly at communal roosts of finches, gulls or Starlings *Sturnus vulgaris.*

(iv) For flightless wildfowl. Geese and swans during their 3–6 weeks flightless period can be rounded up and herded, generally with the aid of boats, into netting corrals erected on the surrounding shore. Catches of several hundred birds at a time have been made.

(v) For swans. A shepherd's crook on the end of a long (up to 6 m) pole can be most effective in catching individual swans, sometimes baited to attract the birds within range. The 'swan hook' is engaged round the bird's neck.

(vi) For birds of prey. A framework of foot snares on the outside of a small cage containing a live pigeon—known as a Bal chatri—has been used extensively for catching birds of prey in the Middle East and North America.

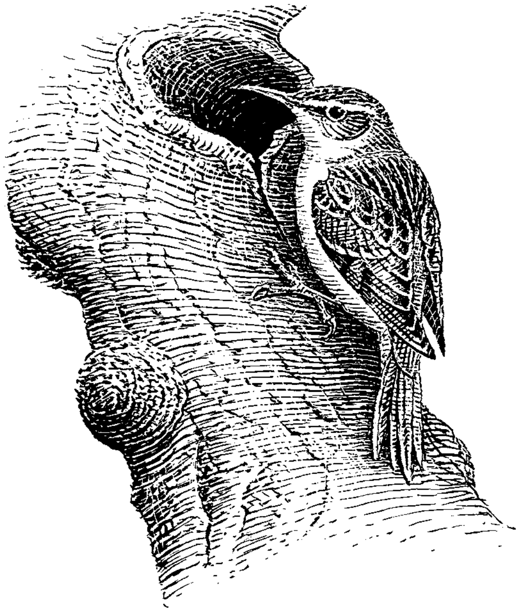
(vii) For birds breeding in nest boxes. A variety of devices attached to the entrance hole of nest boxes has been developed for catching the adult breeding birds. This technique has particularly been used on e.g. Pied Flycatchers *Ficedula hypoleuca* and tits (Paridae); see NEST-SITES, MAN-MADE. (E.A.R.E.) C.D.T.M.

Spencer, R. 1972. The Ringer's Manual (revised edn.). Tring.

TREAD: verb used, with the male as subject and the female as object, to signify the act of copulation in birds.

TREECREEPER (1): substantive name ('creeper' in American usage) of the species of Certhiidae (Passeriformes, suborder Oscines), all placed in the genus *Certhia*; in Britain commonly used without qualification for the sole native species; in the plural, general term for the family (see also under CREEPER and next entry below).

Characteristics. Mostly only 12–13 cm long (though *C. discolor* is 14–15.5 cm), treecreepers are small, brownish birds, streaked above and varying from almost white to grey-brown below, with slender decurved bills, long curved claws, and stiff pointed tails. They have short, rounded



Treecreeper *Certhia familiaris*. (*D.W.*).

wings and their flight is undulating, rather weak and usually only for short distances. They share with nuthatches and certain other families the habit of climbing about on trees, creeping up vertical trunks and along the undersides of branches; they will also move head downwards, but much more rarely than nuthatches. Unlike nuthatches, but like woodpeckers, they use their stiff tails as supports pressed against the bark.

Habitat. Treecreepers are birds of both broadleaved and coniferous forests, or well-timbered woods and parkland. Several species are restricted to mountain forests at 2,000–4,000 m.

Distribution and systematics. The family is confined to the Northern Hemisphere. There is confusion and disagreement over its taxonomy: some authorities recognize 6 species, and most 5, but the validity of 2 of these 5 as distinct species has also been questioned. All but one have restricted ranges in the Old World. The exception, *C. familiaris* ('Treecreeper' of Britain and Ireland, and 'Brown Creeper' of North America), is circumglobal between extremes of 70° and 15°N, if one accepts the concept of 5 species rather than 6, but the Brown Creeper is sometimes separated as *C. americana*. There is considerable variation in this species; a dozen or more races are recognized in a series of clines in Eurasia and another 10 or so in North and Central America. In different parts of its range it occurs in various types of woodland at all levels, but over much of continental Europe to the south of Britain and Scandinavia it overlaps with the very similar Short-toed Treecreeper *C. brachydactyla*, which also extends to north-west Africa (Morocco to Tunisia). In the area of overlap *C. brachydactyla* seems largely to have taken over the lowland broad-leaved niche and *C. familiaris* has become primarily a montane bird of dense conifer forest. Racial differences within both these birds cause much confusion in parts of their ranges, and it has even been suggested that *C. brachydactyla* should no longer be treated as a separate species. The other 3 species are all partly or exclusively Himalayan, and one of those also—the Rusty-flanked or Nepal Treecreeper *C. nipalensis*, found up to about 3,600 m from central Nepal to north-east Burma—may be only a high altitude race of *C. familiaris*. The larger Brown-throated or Sikkim Treecreeper *C. discolor* likewise occurs eastwards from Nepal, extending into semi-tropical montane regions of Thailand and Laos; and the Bar-tailed or Himalayan Treecreeper *C. himalayana*, which has a rather longer bill, breeds from Turkestan and Afghanistan to western China and Burma.

Movements. All treecreepers are largely non-migratory, although the northernmost populations tend to move south in winter and those nesting in high mountain regions descend to lower levels.

Food. Treecreepers are almost exclusively insectivorous, although they occasionally take tiny seeds, and their method of feeding is to work in a series of jerks up one tree and then fly diagonally down to the base of the next, to climb that in a similar manner.

Behaviour. Treecreepers are not gregarious, but outside the breeding season they may join parties of tits (Paridae). Also, while they generally roost alone behind the bark of trees, or excavate small cavities in soft bark or wood on the trunks of trees, they sometimes huddle together communally in very cold weather.

Voice. The calls and songs of most of the treecreepers tend to be thin and high-pitched, but, for example, *C. brachydactyla* utters a louder, shorter, more emphatic and slightly lower song than the initially hesitant but accelerating phrase of *C. familiaris*, while *C. discolor* sings a series of rather loud double notes with the emphasis on the second. Calls, singly or sometimes in series, vary from thin, plaintive and very faint, through soft, piping or shrill, to loud, explosive and penetrating.

Breeding. The nests are typically built behind loose bark or ivy stems or in deep cracks or crevices, but also occasionally in nest-boxes, wall crevices, or accumulations of dead leaves and twigs. They are untidy structures of twigs, roots, grasses, and mosses, but have a neat cup lined with feathers and bits of bark. The eggs are commonly 5–7 in number, but *C. familiaris* may have as few as 3 or as many as 9 in a clutch, while the Himalayan forms (especially *C. discolor*) apparently often produce only 3–4; they are white, marked with red-brown, varying between species from a zone of fine spots at the large end to a fairly even distribution of spots and blotches. Incubation commonly lasts 14–15 days and fledging usually 14–16, though the young of the Himalayan forms may apparently spend about 3 weeks in the nest. While the eggs are mainly or entirely incubated by the female, the young are fed by both parents; there is normally only one brood in the season. I.J.F.-L.

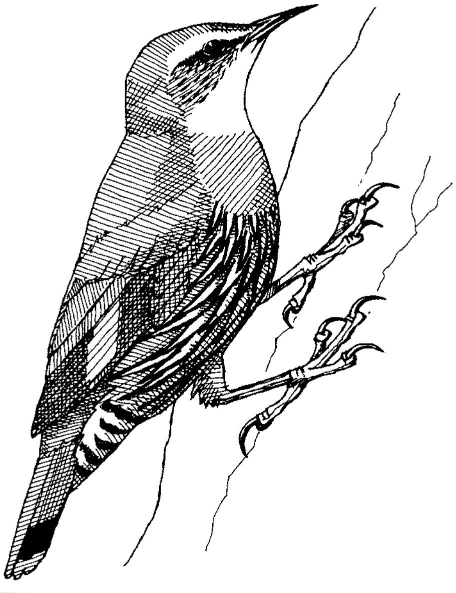
Mead, C.J. 1975. Variation in some characters of three palearctic *Certhia* species. Bull. Br. Orn. Cl. 95: 30–39.

Vaurie, C. 1957. Systematic notes on Palearctic birds. No. 30. The Certhiidae. Amer. Mus. Novitates 1855: 1–14.

TREECREEPER (2): substantive name of the species of Climacteridae (Passeriformes, suborder Oscines); in the plural form 'Australian treecreepers', general term for the family. The single genus *Climacteris* contains 3 species groups (Keast 1957), typified by the Red-browed Treecreeper *C. erythrops*, the Brown Treecreeper *C. picumnus*, and the White-throated Treecreeper *C. leucophaea*, all of eastern Australia. The *leucophaea* species group has been placed in a separate genus *Cormobates*.

Classification and distribution. Seven of the 8 species recognized by Schodde (1975) are confined to Australia, with representatives in all of its recognized faunal subdivisions. The Papuan Treecreeper *C. placens* occurs in New Guinea, where 4 apparently relict subspecies are discontinuously distributed in mountain forests between 1,250 and 3,050 m.

Although *Climacteris* was formerly included in either the Certhiidae (see TREECREEPER (1)) or Sittidae (see NUTHATCH), its resemblance to other climbing birds is superficial. This association was questioned long



White-browed Treecreeper *Climacteris affinis*. (*N.W.C.*).

ago, and Mathews (1923–24) placed the genus in its own family. *Climacteris* possesses apparently unique features in its syringeal and limb musculatures (Orenstein 1977). Affinities have been proposed with the Acanthizidae (Mayr 1963; see WARBLER, AUSTRALIAN) and the Meliphagidae (Harrison 1969; see HONEYEATER). DNA–DNA hybridization studies support maintaining the Climacteridae as a separate family within a superfamily Menuroidea, allied to bowerbirds, lyrebirds and scrub-birds (Sibley *et al* 1984).

Characteristics. The Australian treecreepers are about 15 cm in total length, and have a fairly uniform dorsal coloration (grey-brown to rufous or blackish) with an off-white to rufous bar across the flight feathers. Most species have streaked underparts, and several have a pronounced superciliary line. The tail is rounded, with no stiffening of the rectrices. The bill is moderately long and somewhat decurved. The legs and toes are long, with the claws, especially that of the hallux, greatly developed and curved. There is some sexual plumage dimorphism, most noticeably in the Black-tailed Treecreeper *C. melanura*. Usually, reddish marks on the heads or breasts of females are blackish or absent in males.

Habitat. The several species frequent timbered country, and range from montane rain forest to dry savanna and semi-arid mulga *Acacia aneura* country in the interior.

Movements. Treecreepers are rather sedentary, although the White-throated Treecreeper may join mixed flocks of other species (Bell 1980).

Food. Treecreepers forage on the trunks and limbs of trees, on fallen logs, and, to varying degrees, on bare ground, with rare visits to leaves and flowers. Ants are the most important item in their diet. On trees, the birds normally start at the base of the trunk and climb upwards, following large limbs into the crown, before taking undulating flight to the base of another tree. When climbing, their legs are widely staggered, with one foot held well above the level of the other. The tail is not used for support. Treecreepers do not adopt the upside-down postures of nuthatches or sittellas (Neosittidae; see SITTELLA) (see Noske 1979).

Voice. The song of most species is a series of shrill, high-pitched whistles.

Breeding. Four species of treecreepers, the Red-browed, Black-tailed, Brown and Rufous *C. rufa*, are known to breed communally (Dow 1980; Noske 1980). One or more auxiliary birds, usually males, assist in feeding the incubating female and the nestlings. Of the other species, the White-throated Treecreeper apparently always breeds in simple pairs. Treecreeper nests are made of grasses, plant down, soft bark and animal fur, placed, often deep down, inside the hollow spout of a tree, or sometimes in a hollow log or other cavity. The clutch consists of 2–3 eggs (occasionally 1 or 4), which are white or of a pale flesh tint in ground colour, freely spotted with reddish-brown. Two broods may be raised in a season. (D.L.S.) R.O.

Bell, H.L. 1980. Composition and seasonality of mixed-species flocks of insectivorous birds in the Australian Capital Territory. Emu 80: 227–232.

Dow, D.D. 1980. Communally breeding Australian birds, with an analysis of distributional and environmental factors. Emu 80: 121–140.

Harrison, C.J.O. 1969. The possible affinities of the Australian treecreepers of the genus *Climacteris*. Emu 69: 161–168.

Keast, J.A. 1957. Variation and speciation in the genus *Climacteris* Temminck (Aves: Sittidae). Austr. J. Zool. 5: 474–495.

Mathews, G.M. 1923–24. The Birds of Australia, vol. XI. London.

Mayr, E. 1963. Comments on the taxonomic position of some Australian genera of songbirds. Emu 63: 1–7.

Noske, R.A. 1979. Co-existence of three species of treecreepers in north-eastern New South Wales. Emu 79: 120–128.

Noske, R.A. 1980. Cooperative breeding by treecreepers. Emu 80: 35–36.

Orenstein, R.I. 1977. Morphological adaptations for bark foraging in the Australian treecreepers (Aves; Climacteridae). PhD thesis, University of Michigan.

Schodde, R. 1975. Interim List of Australian Songbirds. Passerines. Melbourne.

Sibley, C.G., Schodde, R. & Ahlquist, J.E. 1984. The relationships of the Australo-Papuan treecreepers Climacteridae as indicated by DNA–DNA hybridization. Emu 84: 236–241.

TREEHUNTER: substantive name of *Thripadectes* spp. (see OVENBIRD (1)).

TREE-PARTRIDGE: substantive name of some species of *Arborophila*, a genus of south-east Asian gamebirds inhabiting forest and scrub (see PHEASANT).

TREE-PIE: or written 'treepie', substantive name of *Dendrocitta* spp. (see CROW).

TREERUNNER: alternative substantive name of *Daphoenositta miranda*, and (alternative to 'sittella') of *Neositta* spp. (see SITTELLA); also substantive name of *Margarornis* spp., *Premnornis guttuligera*, and *Pygarrhichas albogularis* (see OVENBIRD (1)).

TREKDUIKER: Afrikaans name, sometimes used as if English, for *Phalacrocorax capensis* (see CORMORANT).

TREMBLER: substantive name of *Cinclocerthia ruficauda* and *Ramphocinclus brachyurus* (see MOCKING-THRUSH).

TRERONINAE: see PIGEON.

TRIAL AND ERROR: see LEARNING.

TRIBE: see under FAMILY; NOMENCLATURE; TAXON.

TRILL: a rapid succession of notes.

TRILLER: substantive name of some species of Campephagidae (see CUCKOO-SHRIKE).

TRINGINAE: see SANDPIPER.

TRINOMIAL or TRINOMINAL SYSTEM: see NOMENCLATURE.

TRIP: see ASSEMBLY, NOUN OF.

TRIUMPH CEREMONY: a type of display which follows a successful aggressive encounter, usually given by a pair of birds.

TRIVIAL NAME: see NAME, TRIVIAL; NOMENCLATURE.

TROCHANTER: a process on the head of the femur (see SKELETON, POST-CRANIAL).

TROCHILI; TROCHILIDAE: see APODIFORMES; HUMMINGBIRD.

TROCHLEA: pulley-shaped process at the distal end of each metatarsal element of the tarsometatarsus (see SKELETON, POST-CRANIAL).

TROGLODYTIDAE: a family of the PASSERIFORMES, suborder Oscines; WREN (1).

TROGON: substantive name of most species of the Trogonidae (sole family of the Trogoniformes); in the plural, general term for the family and order.

Characteristics. Trogons rank among the most beautiful birds. Considering their distribution in 3 widely separated tropical regions (America, Africa and Asia), they are surprisingly similar in colour pattern and shape. In all species adult males have the lower breast and abdomen bright red, pink, orange or yellow, usually contrasting with the colour of the chest and upper parts. The tail, rather long and graduated, tends to be carried closed so that it looks square-tipped and from below may show a specifically distinctive pattern of black and white. In the American and African species, adult males have most of the upper parts, and often the entire head and chest, brilliant metallic green (sometimes with a golden or bronzy gloss) or metallic blue or violet. The Asian species generally lack metallic colour, but males may have red or pink on the head, rump, chest or tail. Females are considerably duller, with metallic colour reduced or absent; but in many species (including all American and African ones) they have much the same bright carotenoid tints on the lower underparts as the males. In size they range from medium to large for arboreal birds (length 23–33 cm). The bill is short, broad at base, with a curved culmen. The tarsus is short; the weak feet have 2 toes directed forward and 2 backward, an arrangement unique in that the first and second digits are directed backwards (see LEG). The skin of trogons is delicate and easily torn; in museum specimens the bright red or orange colours tend to fade, and feathers drop off readily.

Most systematists are uncertain as to the closest relatives of the trogons, but alliance with the kingfisher group of the Coraciiformes has support. Fossil bones from southern France, believed to date from the Upper Eocene or the Oligocene, have been attributed to the Trogonidae.

Narina's Trogon *Apaloderma narina*. (*N.A.*).

Habitat. Trogons are primarily inhabitants of forest or woodland, but a few favour secondary growth, or clearings and coffee plantations. While almost restricted to tropical latitudes, they are not confined to the warm lowlands; some species occur only in cool mountains, even reaching elevations of 3,500 m, and a few extend into temperate latitudes.

Distribution. In America, where the family is best represented (5 genera usually recognized), they are all breeders in the Neotropical Region from Mexico to northern Argentina, and the Greater Antilles (2 monotypic genera), although one subspecies of the Middle American *Trogon elegans* does nest north to southern Arizona. The 3 African species (2 genera) are found south of the Sahara; one being widespread in evergreen forests of various kinds, one confined to humid equatorial forest and one to montane forest above *c.* 1,500 m. In Asia the sole genus, with 11 species, breeds from western India to south-eastern China, the Indo-Malayan Peninsula, many Indonesian islands, the Philippines and Sri Lanka. From 35 to 40 species of Trogonidae are recognized—the number varying according to taxonomic opinion. Because of similarity in appearance between some species and our ignorance as to details of distribution and behaviour, defining specific limits is hard in the American genera *Trogon* and *Pharomachrus*. The latter (whose members were formerly called 'trainbearers' because of greatly elongated upper tail-coverts) includes the Resplendent Quetzal *P. mocinno*, sacred to the ancient Mayas and Aztecs, which ranges in mountain forest from southern Mexico to western Panama.

Movements. Most trogons appear to be sedentary, although it is probable that younger individuals wander until they establish a breeding territory. Species or populations nesting in temperate latitudes, such as the Coppery-tailed Trogon *Trogon elegans* in Arizona, evidently may be partly migratory.

Food. Insects and other arthropods form the main part of their diet, mixed with small fruits (at least among American species). The Resplendent Quetzal is notably fond of the fruits of *Ocotea* spp., wild relatives of the avocado, which it swallows whole, regurgitating the large seed; it also takes arboreal snails, insects, small frogs, and lizards. The characteristic trogon way of feeding is aerial; the bird darts out and, fluttering vertically before a twig or leaf, or tree bark, picks off the prey (in Africa often a caterpillar); some insects are taken in flight.

Behaviour. Trogons are usually seen alone, in pairs, or in small family groups, perched on a horizontal branch or liana, well below the top of the tree canopy, often staying in the same spot for long periods. They sit rather erect, with tail hanging almost vertically. In some species a number of males gather during the courtship season, calling loudly within sight, or at least within sound, of each other. Displays have been recorded for only a few species.

Voice. Vocalizations, while often resonant and rhythmic, are simple in structure. What seems to function as 'song', recorded for many American and African species, may be described as a series of hollow whistles, hoots, caws or coos, varying, according to species, in pitch, timbre, loudness, rhythm, speed, and number of notes. Some species also have chirring, squeaky, or guttural notes. The tail may be raised or lowered slowly when calling, perhaps an indication that the bird is apprehensive. In some species the female has been reported to give vocalizations much like those of the male.

Breeding. Nests are in cavities, usually of a tree or decayed stump; some excavate holes in occupied arboreal nests of termites or wasps, or use the hollows formed by epiphytes. Both sexes share in nest-building, incubation, brooding and feeding the young. The clutch is usually 2 or 3, sometimes 4; eggs are immaculate white, cream, buff, brown, pale blue, or pale green. Incubation periods (reported for only a few American species) have ranged between 17 and 19 days. Young hatch naked, and are altricial and nidicolous. Fledglings resemble females, but usually lack bright abdominal colour and show some spotting on the wings. E.E.

Chapin, J.P. 1939. Birds of the Belgian Congo. Pt. 2. Bull. Amer. Mus. Nat. Hist. 75: 479–488.

Meyer de Schauensee, R. 1966. The Species of Birds of South America and their Distribution. Philadelphia.

Peters, J.L. 1945. Check-list of Birds of the World, vol. 5. Cambridge, Mass.

Skutch, A.F. 1944. Life history of the Quetzal. Condor 46: 213–235.

Skutch, A.F. 1959. Life history of the Black-throated Trogon. Wilson Bull. 71: 5–18.

Stuart-Baker, E.C. 1934. The Nidification of Birds of the Indian Empire 3. London.

Wheelwright, N.T. 1983. Fruits and the ecology of Resplendent Quetzels. Auk 100: 286–301.

TROGONIDAE: see below.

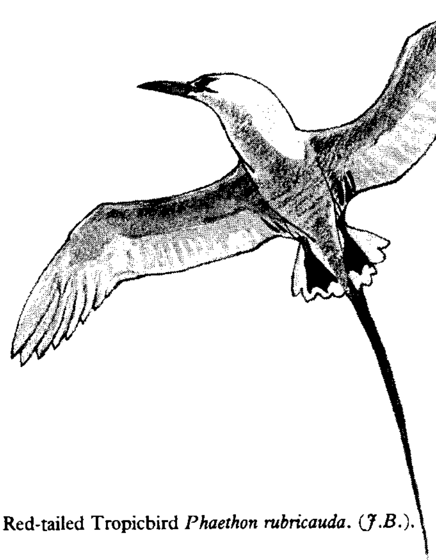
TROGONIFORMES: order comprising only the Trogonidae (see TROGON).

TROPICBIRD: substantive name of the species of Phaethontidae (Pelecaniformes, suborder Phaethontes); in the plural, general term for the family. The one genus *Phaethon* has 3 species.

Characteristics. Tropicbirds (lengths 25–45 cm) are typically white with a black bar across the eyes and solid black markings on some or all of the flight feathers. The plumage may, however, be flushed with delicate or richer roseate pink, and one subspecies, *P. lepturus fulvus*, is distinguished by plumage of strong apricot or orange-pink. The bill, which is stout and slightly decurved, is orange red, crimson or yellow according to species. The long central tail feathers (which may exceed the length of the body) give tropicbirds an unmistakable flight outline, and have prompted such vernacular names as 'marlin spike', 'paille-en-cul' and 'paille-en-queue'. First-year juveniles of all species lack the elongated central tail feathers and are more or less heavily barred and speckled with black on head, back, wings and tail. Barred plumage occurs also in adult Red-billed Tropicbirds *P. aethereus*. The short legs are set far back and cannot support the weight of the body on land. The webbed feet are used for paddling, for shuffling over the ground, and in digging the shallow nest scrape.

Habitat. Tropicbirds range over warm tropical and sub-tropical waters, nesting mainly on oceanic and off-shore islands and wandering far from land between breeding seasons.

Distribution and characteristics. Three species of tropicbirds are currently distinguished. The Red-tailed Tropicbird *P. rubricauda*, with several doubtful subspecies listed, is known from the south tropical Indian Ocean and the tropical Pacific. Largest of all the tropicbirds, this species may reach a length of 46 cm (excluding the central tail feathers) with wing-span of 88–100 cm. The narrow vanes of the 2 central rectrices are red, and the plumage of newly-moulted adults may be flushed with pale roseate pink. The bill is generally orange-yellow or red. Red-billed Tropicbirds, slightly smaller (length *c.* 35 cm), are distinguished by their barred adult plumage and coral-red bill. This species extends from Tower I (Genovesa) in the Galapagos group through the Caribbean Sea and tropical Atlantic Ocean, and into the Red Sea and northern Indian Ocean. The Indian Ocean and Gulf of Aden birds are slightly smaller than those of the Atlantic, and by some authorities are regarded as a separate species *P. indicus*. Yellow-billed (or White-tailed) Tropicbirds *P. lepturus* range through the Caribbean Sea, Atlantic and Indian Oceans, and south-western Pacific Ocean. This is the smallest species, about 25 cm long. The adult plumage is generally clear white or tinted but never barred; among the birds of Ascension Island, some of which are



Red-tailed Tropicbird *Phaethon rubricauda*. (*J.B.*).

flushed with salmon-pink, males tend to be more strongly tinted than females. In the subspecies *P. l. fulvus* of Christmas Island (Indian Ocean) both sexes are vividly coloured.

Studies of all 3 species of tropicbirds, especially breeding studies, have been made at several island sites. The 2 larger species tend toward annual breeding; the smaller Yellow-billed Tropicbirds are more likely to breed less-than-annually at intervals of 6 to 9 months, though climatic fluctuations and the amount of inter- and intra-specific competition (which is often high) may exert over-riding influences.

Behaviour and food. Tropicbirds may be numerous about the breeding grounds, where groups of 6 to 12 birds are often seen together in noisy courtship flight. At sea they fly alone or in silent pairs, swooping low over the water and plunging for small fish and squid.

Voice. The name 'bo'sun bird', common among British seafarers, may be derived from the shrill, trilling calls of the larger species, which strongly resemble the calls of a boatswain's pipe.

Breeding. Tropicbirds usually nest high on steep cliffs or in similar places from which they can take-off without walking or springing. The nests are hidden in cavities or under overhanging rocks, in sites that afford shade and can readily be defended against intruders.

Tropicbirds are gregarious in courtship, flying in excited groups along the cliff-faces, swooping, circling and calling in close line-astern formation. The tail-streamers are undulated during courtship flight. Pairing may involve fights, lasting several days, over nest-sites and partners, especially at the peak of the breeding season when many pairs are nesting at the same time. The birds grip each other with their bills and, with feet and wings spread to gain anchorage, strive to eject each other from the chosen site. Many adults bear scars and gashes about the head and neck. Coition occurs in the nest. A single egg is laid, and is incubated by both parents in watches of 2–5 days. The eggs are oval, varying in shade between pale and deep purple-brown and usually becoming paler in the course of incubation as the surface pigment rubs off. Incubation lasts from 41 days in the smaller, to 44–45 days in the larger species. Newly-hatched tropicbird chicks are covered with heavy grey or fawn down between 1 and 3 cm thick. They are left alone at the nest shortly after hatching while both parents are away foraging. In breeding colonies in which the laying season is spread over many months the small chicks are vulnerable to attack by adults of the same or a related species in search of nest sites, and many are killed by intruders during their first week of growth. Juvenile plumage starts to appear about the 10th or 12th day. The chicks grow slowly and leave the nest as fully-fledged juveniles some 11–15 weeks after hatching. B.S.

Stonehouse, B. 1962. The tropicbirds (genus *Phaethon*) of Ascension Island. Ibis 103b: 124–161.

Harris, M.P. 1969. Factors influencing the breeding of the Red-billed Tropicbird in the Galapagos Islands. Ardea 57: 149–157.

Prŷs-Jones, R.P. & Peet, C. 1980. Breeding periodicity, nesting success and nest site selection among Red-tailed tropicbirds *Phaethon rubricauda* and White-tailed tropicbirds *P. lepturus* on Aldabra Atoll. Ibis 122: 76–81.

TROPISM: in the most general sense, a tendency (at the simplest level) to react in a certain way to a particular kind of stimulus—compare TAXIS.

TROUPIAL: *Icterus icterus*; in the plural, sometimes used in place of 'oriole' as a group name for the genus, or even the family (see ORIOLE (2)).

TRUMPET-BIRD: *Phonygammus keraudrenii*, a BIRD-OF-PARADISE so named because of its loud trumpet-like calls.

TRUMPETER: substantive name of the 3 species of Psophiidae (Gruiformes); in the plural, general term for the family, which is purely Neotropical; the name is given on account of the trumpeting call note.

Characteristics and distribution. Trumpeters are about the size of a domestic fowl (45–52 cm in length), with a rather long neck and long legs, a small rounded head, and a stout and short, somewhat curved bill. The tail is short and the wings rounded. The plumage is largely velvety black with purplish gloss on the foreneck. The sexes are alike. They have a somewhat hump-backed appearance especially when calling, so the local name in Surinam, 'Kamikami' (camel back), is well chosen.

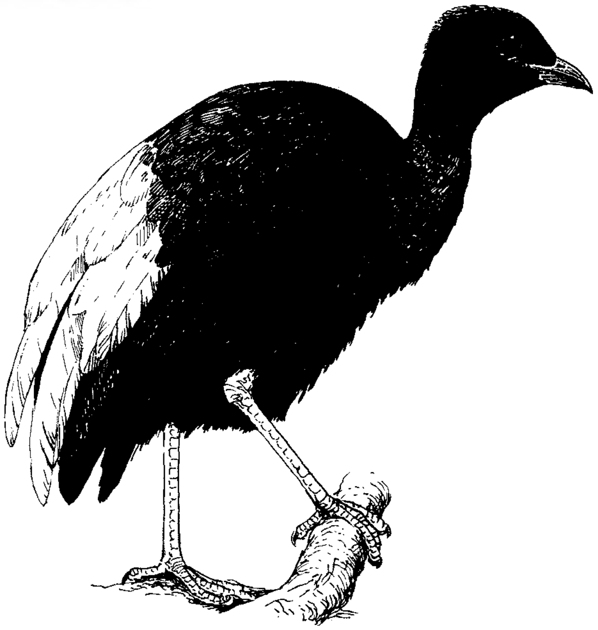
The single genus, *Psophia*, contains 3 species which replace one another geographically. All are mainly black, and of about the same size (weights of the Common Trumpeter *P. crepitans* from Surinam: 1 male, 1,019 g; 4 females, 1,000–1,500 g, average 1160 g). In the Common Trumpeter the secondaries and the tertials are ash grey. This species is found in northern South America east of the Andes south to the Amazon river. The White-winged Trumpeter *P. leucoptera* has white or ochraceous inner secondaries. It inhabits eastern Peru, eastern Bolivia, and north-western Brazil. The Green-winged Trumpeter *P. viridis* has the mantle and the secondaries green or brownish olive and lives in northern Brazil, south of the Amazon river.

Habitat. Trumpeters live on the ground of dense tropical rain-forests in South America.

Food. Their food is partly vegetable (berries and other fruits) but also includes many insects—Formicidae (Hymenoptera) and Tabanidae (Diptera) are recorded for *Psophia crepitans*.

Behaviour and voice. Trumpeters are gregarious, living in flocks on the ground. They run fast, fly laboriously and seldom, and roost in trees. They like bathing in shallow water, after which they sink down on the ground with widely spread wings to dry their feathers in the rays of the sun.

The ordinary call of *P. crepitans* when in a group is a long drawn-out *uh uh uh uh ooooo ooooo oooo*, the *uh*s in quick tempo, followed by 2 or 3 long-drawn *ooooo*s. When the bird is uttering this call, the feathers on the back are somewhat raised and the bill is opened and shut with each note. The birds are easily lured (and shot) by imitating this call. A loud trumpeting call is given with the wings widely spread, when birds



Common Trumpeter *Psophia crepitans*. (*C.J.F.C.*).

threaten other members of the flock; a soft *wheet wheet* is heard when they are at ease.

Breeding. Very little is known about their life in the wild and most of our knowledge comes from captive *P. crepitans*. In Guyana C.A. Lloyd found a nest of this species with 7 eggs in a large hole in a tree, and there is a reliable record from Surinam of a sitting bird in a large tree hole. The eggs are dirty white with a rather rough shell; in shape they resemble, in miniature, the eggs of the Ostrich *Struthio camelus*. The average dimensions of 5 eggs of *P. crepitans* laid in Surinam in captivity on 9, 10 and 12 December and again on 25 and 27 May were 58.5 × 47.55 mm. These eggs were incubated by the female alone. The incubation period is not known. According to Beebe (1917) the nestlings of this species are nidifugous. In Guyana, H. Whitely found downy nestlings on 10, 11 and 12 February, and Beebe on 21 April. The downy plumage was rufous with grey streaks on head and back. F.H.

Beebe, W. 1917. Tropical Wildlife in British Guiana. New York.
Blake, E.R. 1977. Manual of Neotropical Birds, vol. 1. Chicago.
Chubb, C. 1916. The Birds of British Guiana. London.
Haverschmidt, F. 1952. Beobachtungen an einem frei gehaltenem Trumpetervogel *Psophia crepitans*. Vogelwelt 73: 168–170.
Haverschmidt, F. 1963. Die Eier von *Psophia crepitans*. J. Orn. 104: 443.
Haverschmidt, F. 1968. Birds of Surinam. Edinburgh.

TUBENOSES: general term for the Procellariiformes (Tubinares) (see PETREL).

TUBINARES: see PROCELLARIIFORMES.

TUFTEDCHEEK: substantive name of *Pseudocolaptes* spp. (for family see OVENBIRD (1)).

TUI: *Prosthemadura novaeseelandiae* (see HONEYEATER).

TURACO: substantive name of most species of Musophagidae (Cuculiformes, suborder Musophagi); in the plural, general term for the family. The word has been spelt Touraco or Tauraco, and the names Loerie (in South Africa), Go-away Bird (one genus), and Plantain-eater have been used for some species.

The turacos are endemic to the Afrotropical region and have been considered by most authors to be closely related to Cuculiformes. Others have linked them to gallinaceous birds through similarities of their Mallophaga, and they have been raised to a distinct order Musophagiformes. Recent work on their egg white proteins shows that the turacos Musophagi are related to the cuckoos Cuculi and should be placed in the same order Cuculiformes (see Sibley and Ahlquist 1972 for details and historical review). In this article the groupings and nomenclature of Snow, Clancey and Read (Snow 1978) are adopted. They recognize 22 species in 5 genera: *Corythaeola* (1 species); *Crinifer* (2); *Corythaixoides* (3); *Musophaga* (2) and *Tauraco* (14). To highlight the distribution of the family and possible relationships, a number of superspecies are identified by Snow *et al*; one each for *Crinifer*, *Corythaixoides* and *Musophaga*, and 4 for 12 species of *Tauraco*.

Systematic characteristics. Apart from the Giant (or Great Blue) Turaco *Corythaeola cristata* (size about 76 cm), all turacos are medium sized birds of length in the range 35–51 cm. Throughout the family the sexes are alike. Turacos have rather long tails (10 rectrices), and most of them have short rounded wings. Their flight is weak but they move easily and with great agility along branches and through vegetation. Bills are strong and decurved often with a 'keel'. A peculiar feature of the family is the exceptional variability of the position of the nostril and its shape (anything from circular to slit shaped). In 2 species which are difficult to distinguish in the field the nostrils are circular (Red-crested Turaco *Tauraco erythrolophus*) and slit-shaped (Bannerman's Turaco *T. bannermani*). The adaptive basis of these differences is unknown.

Another unusual feature is that in most species the feathers of the head and breast are largely deficient in barbules, so that they seem hairy. Their feet are also unusual; the outer toe is most often approximately at right angles to the main axis of the foot, but it may be moved further back or directly forward (semi-zygodactyl). In addition, the claws are short and abruptly curved. The family is also unique in the chemistry of the green and/or red pigments which occur in *Tauraco* and *Musophaga* species. Whereas green is in most birds produced by a combination of melanin and yellow carotenoid, in turacos it is due to turacoverdin. The red colour is due to turacin which contains copper, a pigment unique in the whole Animal Kingdom. Turacoverdin exists in several species of turaco that do not have turacin, but the reverse does not hold. The amount of green pigment is directly correlated with the luxuriance of the habitat, being most developed in the species of evergreen forest and least or absent in those living in deciduous woodland, especially thornbush.

Field characteristics, habitat and distribution. The Giant Turaco is blue above and green and brown below. It is found throughout the forests of western and west-central Africa and also in secondary growth and gallery forest in savanna that adjoins the main forest block.

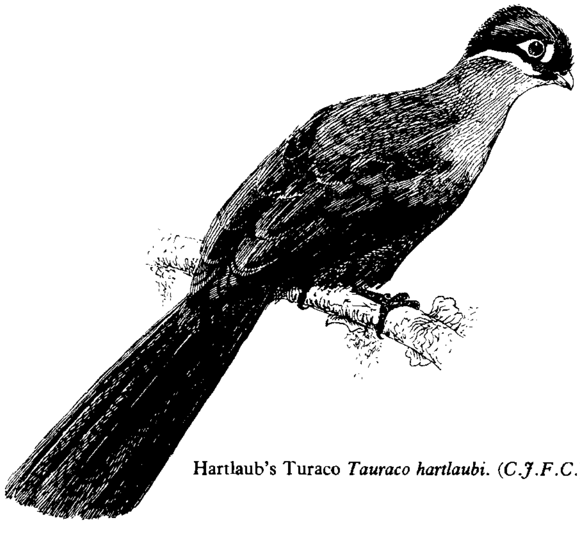
The remaining turacos divide into 2 groups; those mainly green-plumaged (*Tauraco*) or violet-plumaged (*Musophaga*) species which inhabit more or less thick woodland; and those mainly grey-plumaged birds (*Crinifer* and *Corythaixoides* species) inhabiting drier and more open vegetation. The Grey Plantain-eater *Crinifer piscator* occurs in the savanna of western and north-central Africa and its place in the savanna of central and north-eastern Africa is taken by the Eastern Grey Plantain-eater *C. zonurus*. They are predominantly grey but are streaked below; the most conspicuous difference between them is the presence of a white tail bar in *zonurus* which is absent in *piscator*.

The 3 species of *Corythaixoides* are grey-plumaged but they do not have streaked underparts and the position of their crests is different from the *Crinifer* species. Their distribution in acacia savanna ranges from north-east and central Africa (White-bellied Turaco *Corythaixoides leucogaster* and Bare-faced Turaco *C. personata*) to southern Africa (Grey Loerie *C. concolor*). The Bare-faced Turaco is of interest, as there are 2 populations separated by a gap of 1,000 km in northern Uganda and Kenya. In the northern population the foreparts of the neck and undersides of the wings and tail are pale yellow-green and the partially feathered throat brown; in the southern population the green is deeper in shade and restricted to a pectoral patch, and the throat is blacker.

The 5 species of *Tauraco* forming the superspecies *Tauraco persa* mainly differ from each other in their head ornamentation. The Guinea Turaco *Tauraco persa* has a green pointed crest which lacks white tips, the body plumage has a violet gloss and the bill is red. It is found at low altitudes from Gambia to Cameroun and south to northern Angola. A black-billed version, the Black-billed Turaco *T. schuetti* occurs in the Congo basin and eastwards to southern Sudan and the northern side of Lake Victoria. In contrast to these and others in this group Fischer's Turaco *T. fischeri*, the common turaco of the evergreen forests of the coastal zone of north-east Africa, has a red crest tipped with white, and a red bill. Another of this group, the Knysna Turaco *T. corythaix*, has a mainly coastal distribution in South Africa.

Three species of *Tauraco*, forming the superspecies *Tauraco hartlaubi*, inhabit montane evergreen forest in north-east Africa. Two of them have a larger patch of white on the face than other species in *Tauraco* but the third, Prince Ruspoli's Turaco *Tauraco ruspolii*, has a strikingly different head colouring of grey, green and pink. It also has a very restricted range in the southern Ethiopian highlands.

There are 2 isolated species of *Tauraco*. One, the White-crested Turaco *T. leucolophus*, has a mainly white head, and is found in gallery forest north of the Congo forest. The other, the Black-tip Crested Turaco



Hartlaub's Turaco *Tauraco hartlaubi*. (*C.J.F.C.*).

T. macrorhynchus, has a green crest and inhabits heavy forest in Upper Guinea and western parts of the lower Guinea forest. It is of interest as its range is split by the dry Dahomey gap; the western form has a black tip to its crest and the eastern form a red tip.

The *Musophaga* species differ from the other turacos in having an enlarged frontal plate. Except for the red area in the wings and a red crown, the plumage is mainly deep glossy violet produced by melanin which swamps the green turacoverdin. The Violet Plantain-eater *Musophaga violacea* is found in lightly wooded areas throughout western Africa. Its place in eastern and south-central Africa is taken by Lady Ross's Turaco *Tauraco rossae*. They differ mainly in beak shape and head ornamentation; the Violet Plantain-eater has no crest whereas Lady Ross's Turaco has a conspicuous erectile crest.

Movements. All species, as far as is known, are sedentary or make only short-distance movements which may be governed by the availability of food.

Food. Turacos are almost exclusively vegetarian, feeding mainly on fruits and to a lesser extent on foliage, flowers and buds. Some are known to eat snails (Chapin 1963). Although the English name plaintain-eater is used for several species, neither plantains nor bananas are part of their diet.

Behaviour. The whole family is more or less gregarious, usually met in pairs (breeding season) or small parties, often involved in feeding or associated with roosts at certain seasons. The Giant Turaco appears to be gregarious throughout the year. Often when one turaco calls, others in a group reply until all turacos in earshot are calling; this is particularly so in the forest species. As they are difficult to observe, little is known of their habits. Nuptial displays appear to vary much within the family. In the Grey Plantain-eater one bird of a pair (the male?) makes a noisy vertical ascent and dive just before perching near the other. A somewhat similar display occurs in *Corythaixoides* species. In others, displays involve raising of the crest, bowing and flirting of the tail and wing, which reveals the brilliant red patches.

Little is known of their breeding behaviour. They breed in pairs, as far as is known. Courtship feeding has been observed in the Blue-crested Plaintain-eater *Tauraco hartlaubi* and its young are fed on regurgitated fruit pulp; in the nest their faeces are swallowed by the parents.

Voice. One of the sounds associated with the African forest is the loud resounding chorus of calls of turacos. The most haunting and memorable are those of a party of Giant Plantain-eaters in which the chorus may last several minutes. It begins with a series of plaintive *oo-ers*, changing to a rapid series of staccato notes *kok-kok-kok-kok* . . . and ending with a series of vibrating *kurruk-kurruk-kurruk* notes. All species in *Musophaga* and *Tauraco* utter a series of hoarse grunting notes, *kraw-kraw-kraw*, often combined with repeated *coos* and barking calls. The savanna species also have loud calls but are not as resonant as those of the forest species. The Eastern Grey Plantain-eater is said to have considerable powers of mimicry. The calls of *Corythaixoides* species are onomatopoeic, hence the English name Go-away Bird.

Breeding. All members of the family build flat and often flimsy nests made of twigs, like those of pigeons, placed in trees or low bushes between 5–20 m above ground. The clutch size is 2–3 for species of *Crinifer* and *Corythaixoides* and 2 for the remaining species of turaco. The rounded eggs vary in colour from white or greyish-white to cream, glossy blue or bluish-white or even pale ivory-green. Incubation lasts about 18–20 days but exact data are few. The young on hatching are covered in thick down and the wing claw is well developed at least in some species. They are fledged after about a month, but they frequently move out of the nest and clamber about the nest tree long before they are able to fly. The breeding season of the forest species normally coincides with the rainy season, whereas the savanna species may be found breeding in all months of the year, in both dry and wet seasons. D.A.T. and L.L.G.

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TURBINAL CARTILAGE: in each nasal cavity (see SKULL).

TURCO: substantive name of *Pteroptochos* spp. (see TAPACULO).

TURDIDAE; TURDINAE: family and subfamily of PASSERIFORMES, suborder Oscines (see THRUSH).

TURKEY: substantive name of 2 species of Phasianidae (Galliformes, subfamily Meleagridinae), *Meleagris gallopavo* and *M. ocellata* (formerly classified as a separate genus *Agriocharis*); in the plural, general term for the genus. Historically the name turkey has been used in reference to cranes (*Grus* spp.), vultures (*Cathartes* spp.), Capercaillie (*Tetrao urogallus*) and various Phasianidae.

Characteristics. *Meleagris gallopavo* is among the largest North American birds. Wild males may be *c.* 110 cm long and weigh 10 kg; females average 90 cm and 4 kg. While plumage of domesticated turkeys is white, red or brown, that of wild birds is primarily dark brown and black. Colours of the rump feathers and the terminal band on the rectrices vary from chestnut to cream. Birds of more arid environments tend to be lighter coloured. Males are generally darker in colour and feathers are more iridescent than in females. Males (and 5–10% of the females) possess a tuft of long, pendulous, bristle-like feathers on the breast called the 'beard'. The head and neck of the female are more fully feathered. Turkeys undergo 2 moults each year, a partial prenuptial moult in late winter and a complete postnuptial moult in late summer. There is no flightless period. Seven subspecies of *gallopavo* are recognized: *M. g. gallopavo, intermedia, merriami, mexicana, silvestris, oneusta* and *osceola*. Distinctions are based primarily on plumage characteristics and geographic location. Domestic varieties were derived from *M. g. gallopavo*.

M. ocellata is similar to *gallopavo* except that it is generally smaller (males average 4 kg; females, 2 kg), the plumage and head of males are more colourful, and males lack a beard.

Habitat. Turkeys are general in their habitat requirements and inhabit temperate, subtropical and tropical forests and prairie brushland. *M. gallopavo* is closely associated with mature forests that include oaks *Quercus* spp. or pines *Pinus* spp. Areas containing an interspersion of forest and open fields are preferred and high population densities occur in areas of 50–80% forest cover. Forests provide protection, night roosting sites and feeding areas. Open fields provide important feeding sites, especially for broods. Agricultural fields are used extensively in some regions. Edge areas along forest and field borders appear to be important for nesting.

Distribution. Turkeys are indigenous to North America, probably originating in Mexico, and are known as far back as the upper Pliocene. Pre-Columbian populations were distributed across the south-eastern third of the North American continent. The distribution and abundance of *M. gallopavo* declined during 1800–1950 from an estimated 10 million individuals to remnant populations totalling 300,000. Changes in land-use patterns during the period 1950–1980 allowed for the development of extensive areas of suitable habitat. Active management efforts, including live-trapping and transfer of wild birds, hunting regulation and modification of forestry practices have resulted in the restoration of the species to many portions of its original range and establishment in many areas beyond. At present, populations occur in nearly all of the American states and several Canadian provinces. Attempts to introduce the species to Europe have met with only limited success. The species is estimated to number approximately 1.8 million individuals. As with *gallopavo*, populations of *ocellata* declined because of habitat destruction and over-hunting. Present populations are patchily distributed from Peten, Guatemala and adjacent Belize, north through the Yucatan Peninsula and west into eastern Chiapas.

Populations. The number of females hatched per female in the population varies greatly. The maximum average documented for *gallopavo* is 3.8 females hatched per year. Annual survival is also variable but averages 30% and 50% for juvenile and adult birds, respectively. Natural (non-hunting) mortality is heaviest during the first few weeks after hatching and during the breeding season. Mortality is often high during the winter months in northern regions when deep snow persists more than 6 weeks. Survival beyond 7 years is uncommon in the wild. The maximum finite rate of growth (λ) reported for the species is 2.15 in an introduced population. Population densities of 4–8 birds/km^2 are common and 27 birds/km^2 has been reported. Population statistics for *ocellata* are generally unknown although rough estimates suggest densities are 1 bird/km^2 in Peten, Guatemala.

Movement. Turkeys are not long distance migrants; altitudinal migrations occur in mountainous regions. Movement patterns are marked by intensive use of relatively small areas with periodic shifts to other areas. The annual range of *gallopavo* includes 200–2,000 ha. Movement is most extensive in the spring and, in southern regions, during the winter. In northern regions, deep snow may limit winter home range sizes to less than 10 ha. Summer movements of females with broods may cover 100–400 ha. Dispersal occurs in early spring when young birds are 9 months old. These birds may move 1–50 km from their natal areas; females tend to disperse farther than males. Annual movements of *ocellata* have not been investigated.

Food. Turkeys are omnivorous; the diet appears to be limited primarily by size of food items. The diet during the first 8 weeks after hatching is approximately 80% insects. Adults feed primarily on fruits, seeds, succulent vegetation and invertebrates. Mast, such as acorns (*Quercus* spp.) and waste grains (e.g. *Zea mays*), is especially important during fall and winter months.

Behaviour. Turkeys are diurnally active, cursorial birds. Nocturnal periods are spent off the ground, roosting in trees (or sometimes on man-made structures). Flock members roost together and, in areas where roost habitat is limited, several flocks may roost in close proximity. The bird is gregarious and spends most of the year in flocks. Females with broods begin to aggregate at midsummer and flocks may include as many as 100 individuals. These flocks generally remain intact through the winter. Adult males are not usually associated with the brood flocks and move in segregated flocks of 4–20 individuals. Within the flock a social hierarchy exists, though it is not always linear; larger individuals tend to be dominant. Brood flocks disintegrate in spring and male flocks split into small groups thought to be composed of siblings. The breeding system is best described as harem polygyny (see POLYGYNY). Males are non-territorial and movements during the breeding season cover 150–2,000 ha. Females associate with the males for brief periods of time. The breeding display of the male, called 'strutting', is characterized by tail-fanning and wing-dragging typical of other galliforms. The body is inflated, the body contour feathers erected, and the head is drawn in against the back. The frontal caruncle is distended and chromatophores in the head and neck are activated making the head appear white, blue and red. Associated with this visual display are several short range sounds.

Voice. Turkeys begin vocalizing immediately following hatching. The repertoire of young birds includes 3 calls; adults possess approximately 15 calls. Calls are graded, with information content dependent upon pitch, number and spacing of call elements. When in flocks, birds vocalize very frequently. Calls commonly given by birds of either sex include *kyelps*, *putts* and *purrs*. The breeding vocalizations, given only by the male, include the 'gobble', a long range call, and the barely audible 'pulmonic puff'.

Breeding. The age of first reproduction is variable: where population densities are low or habitat conditions are unusually good, female *gallopavo* will breed in their first year. Male *gallopavo* may reach maturity in their first year but are apparently inhibited from breeding by older males. This pattern is thought to occur in *ocellata* as well. Copulation occurs in early spring. Female *gallopavo* begin nesting in February in southern regions and April in northern areas; nesting for *ocellata* begins in April. The nest consists of a simple scrape on the ground. The average clutch size for both *gallopavo* and *ocellata* is approximately 11 eggs (range 7–18). Eggs weigh approximately 65 g. Sex ratios in clutches approximate unity. Incubation requires 26–28 days and hatching rates exceed 90%. Renesting occurs commonly following unsuccessful nesting attempts. PARTHENOGENESIS is known to occur among *gallopavo*, producing males only. The young are nidifugous. W.F.P.

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TURKEY, BRUSH: see BRUSH-TURKEY; MEGAPODE.

TURKEY, WATER: popular misnomer (USA) for the Anhinga *Anhinga anhinga* (see DARTER).

TURNAGRIDAE: see EXTINCT BIRDS; THRUSH, NEW ZEALAND.

TURNICES; TURNICIDAE: see under GRUIFORMES; BUTTON-QUAIL.

TURNING DOWN: releasing captive-bred birds into the wild.

TURNOVER RATIO: the species present in a particular habitat (for example a woodland, an island or a nature reserve), are rarely identical from one year to the next. Each year some species may be expected to disappear and others to colonize. Over several years an individual species may enter and disappear from a community several times, particularly if its total population, when present, is small (one or two pairs) and/or the habitat is marginally suitable or near the edge of the species' geographic range. The 'turnover ratio' is defined as the number of species entering and leaving a community over some specified time period (e.g. one year), divided by the total number of species present at the start of that time period. For example, turnover ratios for birds on islands vary between 0.2 and 20% per year of the species initially present, for islands ranging in size from 400 to 0.4 km^2.

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TURNSTONE: substantive name of the 2 species of *Arenaria*; used without qualification, in Britain, for *A. interpres* (see SANDPIPER). See photo FEEDING HABITS.

TURUMTEE: name applied in India to *Falco chicquera* (see FALCON).

TWIN-SPOT: substantive name of some *Clytospiza* spp. and *Hypargos* spp. (see ESTRILDID FINCH).

TWITE: *Carduelis flavirostris* (see FINCH).

TYPE: general term embracing TYPE GENUS, TYPE SPECIES, and TYPE SPECIMEN; used without qualification for any of these, in appropriate context, but especially the last mentioned—for the concept see NOMENCLATURE.

TYPE GENUS: the nominal genus that is the type of a taxon in the family group and that provides the stem of the name of such taxon (or taxa of different ranks within the group). The mere naming of the higher taxa after the included genus selects the latter as the type. The names of the higher taxa are not affected by subsequent disuse of the generic name as such, whether by reason of the nominal genus being merged in another for taxonomic purposes or (after 1960) by rejection of the generic name as a junior synonym; new names given to higher taxa before 1961 for the second reason are to be retained if they have meanwhile been generally accepted. The rejection of a generic name as a junior homonym invalidates names based upon it for family-group taxa. See FAMILY GROUP; NOMENCLATURE.

TYPE LOCALITY: that from which a species or subspecies was described by the author of its name, or—failing that in the case of early names—one subsequently designated; where applicable, that at which the type specimen was collected. The type locality of a nominate subspecies is that of the species. A type locality may be changed if the original geographical attribution is definitely shown to have been erroneous; and where a type locality was too vaguely defined (e.g. only the country being named), a subsequent author may determine a 'restricted type locality'. See NOMENCLATURE; TYPE SPECIMEN.

TYPE SERIES: see TYPE SPECIMEN.

TYPE SPECIES: the nominal species that is the type of a genus or a subgenus (or of both in the case of a nominate subgenus). The term 'genotype' (also 'generitype', 'generotype') is inadmissible as an equivalent, and has in fact quite a different meaning. The 'fixation' of a type species is obligatory, and the author of a generic or subgeneric name proposed after 1930 must himself designate a type.

In the case of older generic names there may likewise be a 'type by original designation'; but failing this there may be a 'type by indication', and the latter may take various forms. If the author established the genus with a single nominal species, that species becomes the 'type by monotypy'; if he established it with an included species having its specific name or a subspecific name the same as the generic name, that species becomes the 'type by absolute tautonymy'; if he established it with only one of its species having in its synonymy a pre-1758 name (single word) identical with the generic name, that species becomes the 'type by Linnean tautonymy'. In the absence of original designation or indication, it is necessary to fix a 'type by subsequent designation'; any zoologist may do so, in accordance with rules contained in the International Code (see NOMENCLATURE).

It may be noted that a species with a tautonymous name is not necessarily the type of its genus. It may have been ineligible as a type by indication through not being expressly included in the nominal genus when that was established; or some other species might conceivably have been designated in preference.

TYPE SPECIMEN: the single specimen that is the 'type' of a nominal species or subspecies, or of both in the case of a nominotypical subspecies (see NOMENCLATURE). If the specimen was expressly designated at the outset by the author of the name (the recommended course) it is a 'holotype'; if it was designated later, from an original 'type series', it is a 'lectotype'; if it was designated later in special circumstances to replace a holotype or lectotype that, with all other members of any original type series, had been lost or destroyed, it is a 'neotype'.

If there was an original type series on which the author of the name based his description, all of them are 'syntypes' unless one has been expressly designated. If a holotype or lectotype has been designated, the remainder are 'paratypes' or 'paralectotypes' as the case may be. The term 'cotype' is no longer recognized.

As type specimens are of particular and permanent value as standards of reference in nomenclature, they should be regarded as 'the property of science'. A special responsibility rests on museums for the custody and proper labelling of type specimens, and for the publication of a catalogue of all type specimens held by them.

A type specimen, however, is no longer regarded as necessarily typical in any but a nomenclatural sense; it may in fact happen to be unrepresentative of the norm of the population from which it was drawn. The old type concept in biological thought has given way to a population concept, in which mean values and range of variation are what have real, as opposed to conventional, significance.

TYPICAL: apart from the ordinary meaning of the word, an adjective relating to TYPE; see also under NOMENCLATURE. Sometimes inappropriately used in the sense of NOMINOTYPICAL.

TYPICAL INTENSITY: see DISPLACEMENT ACTIVITY.

TYRANNI: see PASSERIFORMES.

TYRANNIDAE; TYRANNINAE: family and subfamily of PASSERIFORMES, suborder Deutero-Oscines; FLYCATCHER (2).

TYRANNULET: substantive name of small tyrant-flycatchers in *Camptostoma, Tyrannulus*, and other genera (see FLYCATCHER (2)).

TYRANT: substantive name (alone or in compounds such as 'ground-tyrant' and 'water-tyrant') of species in many genera of tyrant-flycatchers (Tyrannidae). Many other members of the family have 'flycatcher' as substantive name (the two names being also to some extent interchangeable), still others having various special names (see FLYCATCHER (2)).

TYSTIE: alternative substantive name of the guillemots of the genus *Cepphus* (see AUK).

TYTONIDAE: see under STRIGIFORMES; OWL.

U

ULNA: a bone of the forelimb (see SKELETON, POST-CRANIAL; WING).

ULNARE: one of the proximal carpal bones (see WING).

ULTIMATE: applied to factors that are remotely causative but do not lead immediately to the effect—contrasted with PROXIMATE.

ULTRASOUND: sounds of a frequency too high for the human ear to detect; above about 15–20 kHz (1,000 waves per second). Such sounds can be detected by most other mammals and by many insects. They have short wavelengths, which endow the echolocation systems of bats and dolphins with a high resolution. It seems unlikely that birds can hear 15 kHz so that the echolocation of swiftlets and oilbirds can only give a 'coarse-grained picture' of their surroundings. (See ECHOLOCATION; INFRASOUND).

UMBILICAL CORD: connection between the embryo and transitory structures within the egg.

UMBILICUS: term applied to each of the two ('inferior' and 'superior') openings in the shaft of a feather (see FEATHER, Contour feathers).

UMBRELLA-BIRD: substantive name of *Cephalopterus* spp. (see COTINGA).

UNCINATE PROCESS: a projection found on most of the ribs (see SKELETON, POST-CRANIAL).

UNDER TAIL-COVERTS: see TOPOGRAPHY.

UNDER WING-COVERTS: see TOPOGRAPHY.

UNGUAL: term applied adjectivally to the terminal phalanx of a digit, bearing the claw if any.

UPENDING: immersing the forepart of the body, head downwards, in the water, this causing the hind part to stick up into the air. This position is maintained by paddling movements of the feet.

See photo FEEDING HABITS.

UPPER TAIL-COVERTS: see TOPOGRAPHY.

UPPER WING-COVERTS: see TOPOGRAPHY.

UPUPIDAE: see CORACIIFORMES; HOOPOE.

URBANIZATION: with reference to birds, adaptation to an urban environment. As an area becomes increasingly urbanized, the process of adaptation by birds to the new environment can be observed. The process is usually spontaneous, starting from temporary invasions and leading to the establishment of permanent breeding populations. This is the most advanced stage of the birds' 'synanthropy'.

Conditions in city centres are continually changing under human impact, causing rapid changes in the composition and structure of urban bird communities. These contain fewer species than elsewhere, but total bird density may be up to three times higher than in forests (Tomiałojć and Profus 1977), and a dozen or more times higher than in grassland or desert, whereas single species can reach densities several hundred times higher than elsewhere. The degree of isolation between urban and 'natural' populations of a species is usually low but variable, depending both on the species and on the size and structure of the urban areas. These areas contain a higher proportion of 'adaptable' forms than the surrounding 'natural' habitats.

No essentially new qualities emerge in the course of urbanization, but differences do develop: there is greater tameness in relation to humans; diurnal and annual activity patterns change somewhat; prolonged breeding occurs and there is an inclination to adopt resident status; there may be deviation from traditional nest-sites and partial reliance on new types of food as well as increased overlap in diet with other species; territories are smaller and breeding densities higher. These are mostly the opportunistic consequences of abatement of the pressures of natural selection.

In cities interspecific interactions are less marked, as a result of fewer competing and fewer predatory species, a feature common to insular, man-made or other simple ecosystems.

According to most authorities, superabundance of food is the main reason for the invasion of cities by wild birds, which is especially true in winter. During the breeding season, however, very few species visit cities merely in search of food, though the Black-headed Gull *Larus ridibundus* is one example. At least for birds capable of long feeding flights—swifts *Apus*, some raptors, Rooks *Corvus frugilegus*, Jackdaws *C. monedula*, Woodpigeons *Columba palumbus*, American nighthawks *Chordeiles minor* and, in smaller habitations, many finches *Carduelis*, swallows and martins (Hirundinidae), owls and White Storks *Ciconia alba*—the crucial advantage of human settlements seems to be their greater safety for adults and young. Released from predation pressure, for example, Woodpigeons from Silesian urban parks produce yearly 4 times as many fledgelings per pair as in the country, in spite of relying on the same food sources, though this is apparently not so in London. In most species both extra food and better security under the protective influence of human presence are responsible for high densities in urban areas. These are achieved through a prolonged breeding season, despite smaller clutch-sizes, by lower mortality in the nest, and a longer adult life-span.

There are three types of response by a species to increasing urbanization.

Retreat from the urban area. Some species occur on the periphery of cities as relict remnants of the previous fauna. These include most ground- or bush-nesting species, e.g. buntings, pipits, some warblers (Sylviidae), Skylarks *Alauda arvensis*, some water birds and most large, shy and hunted birds. They will continue to retreat because even if they could adapt to the general conditions, there will be an increasing lack of nest-sites.

Adaptability to thrive equally well in cities as in natural habitats. These urban populations form integral parts of 'natural' populations of the same species. They are usually upper canopy forest dwellers and are able to penetrate urban areas easily. They include nuthatches *Sitta*, treecreepers *Certhia*, tits *Parus* and kinglets *Regulus*.

Re-entering urban areas after initial retreat. These are originally dwellers in the lower forest layers, nesting low down and feeding on the ground. At first it seems they retreat, but later on form a new truly urban population, though only in some parts of the breeding range; two more or less distinct populations, urban and 'natural', differing in several respects can be recognized. Pigeons (Columbidae), thrushes (Turdidae) and starlings (Sturnidae) furnish examples. Sometimes such urban populations extend their existing breeding range and invade new areas, e.g. Collared Dove *Streptopelia decaocto*, House Sparrow *Passer domesticus*, Black Redstart *Phoenicurus ochruros*, as well as European species introduced into other continents.

An intriguing aspect of bird urbanization lies in the changes which occur as the invading population develops into the urban one. For Mallard *Anas platyrhynchos* and Woodpigeon there is some indirect evidence of secondary tameness acquired by learning (Tomiałojć 1976). In the case of the Blackbird *Turdus merula*, some authors suggest that the reduced shyness of urban birds is inherited, although their experiments are open to doubt (Graczyk 1963, 1974).

Historical aspect of bird urbanization. Analysis leads to the conclusion that the sequence in which species enter urban areas reflects both the form urbanization takes in cities and changes in human attitudes to birds. The first urbanized birds were small passerines or scavengers tolerated by man. The latest species to invade cities represent birds once persecuted by man; but as urban man no longer behaves as a predator, except to superabundant species or individual birds causing a nuisance, it is likely that cities in future will accommodate more species, including some which now avoid them.

Geographical aspect of bird urbanization. This can be exemplified by the most advanced adaptations to urban life which have occurred recently in the north-western parts of Europe, as a result partly of the greater new urbanization in this region and partly of the more positive attitude there of humans to birds. A further factor is that large populations of first-year birds winter in the area traditionally, and have attached themselves to the urban environment. The early and almost total deforestation of the region forced these birds to adapt themselves to an agricultural landscape, including villages, from which it was only a small step to adapt further to the towns. All these reasons have presumably contributed to the apparent eastward expansion of some urban bird populations, e.g. of Blackbird and Woodpigeon. It is far from sure, however, that this has been a real expansion of West European populations as opposed to expansion due to the whole complex of reasons causing urbanization: the second possibility does not exclude the first. The exchange of avifauna between cities is possible, especially when they are not separated from each other by long distances of open country and ecological barriers such as vast forests or mountains.

As a rule, an urbanized population first occurs in an area with a dense natural population of the species involved. This initial high density can be either primeval and general, as in dense parts of the quantitative centre of the species' natural breeding range, or it may be secondary and local, as in areas where human activity has driven the species to concentrate in remnants of natural habitat. Only exceptionally does a species start to colonize urban areas on the periphery of its range. Even wide-ranging but sparse species like the Rock Sparrow *Petronia petronia*, Snow Finch *Montifringilla nivalis* and Blue Rock Thrush *Monticola solitarius*, have urban populations, but only where they were relatively common in natural habitats turned urban. Some species are more urbanized in north-eastern Europe: the Redwing *Turdus iliacus*, Fieldfare *T. pilaris*, Pied Flycatcher *Ficedula hypoleuca*, Linnet *Carduelis cannabina* and White Wagtail *Motacilla alba*.

Geographical data suggest, therefore, that, for the occupation of an urban area, local abundance of species in their natural habitats is essential, assuring the existence of surplus individuals which may frequently intrude into the cities until successful breeding status is achieved. L.T.

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URETER: see EXCRETORY SYSTEM.

URIC ACID: see ENERGETICS (Existence energy); EXCRETORY SYSTEM; METABOLISM.

URINARY SYSTEM: see EXCRETORY SYSTEM.

URINE: see DROPPINGS; EXCRETORY SYSTEM.

URODAEUM: see EXCRETORY SYSTEM.

UROPYGIUM: the rump (see TOPOGRAPHY); for uropygial gland see OIL GLAND.

UTERUS or SHELL-GLAND: part of the oviduct (see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM).

UTILIZATION BY MAN: human exploitation of wild birds as one of the world's natural resources; for other than wild birds see DOMESTICATION. Wild birds and their eggs have been taken for human food from the earliest times. While they represent important sources of food for some small human groups, they form only a tiny and decreasing proportion of world food consumption. Much the commonest bird in the world is the domestic fowl, which does provide a not insignificant proportion of the human food supply. Its greater productivity, accessibility and standardized taste has led the domestic fowl steadily to replace wild birds for the table. The manipulation and 'farming' of wild or near-wild colonies of large species for human food have increasingly become curiosities, as with the surviving medieval swannery of Mute Swans *Cygnus olor* at Abbotsbury, Dorset, and the sizeable number of ancient dovecotes, now mostly empty, in which feral doves *Columba livia* were induced to nest so that the surplus of their young (squabs) and eggs might be removed, the birds themselves flying free to live off the grain of farmers for km around. Much of the utilization of wild birds is of scant economic but immense anthropological or sociological significance for the societies engaged in it. This applies particularly to shooting for sport and the continued use of feathers for ornamentation. The 'take' by man is of very uneven significance for avian populations and species survival.

The use of bird droppings as agricultural fertilizer has been significant since the 19th century (see CAVE, GUANO; GUANO).

Flesh. The flesh of a majority of species of birds is probably palatable, even highly palatable, to man (see PALATABILITY OF BIRDS AND EGGS). Wild species are still killed for food in many parts of the world. D.L. Serventy's estimate is that approximately 500,000 Short-tailed Shearwaters ('mutton birds') *Puffinus tenuirostris* are taken annually in Australia. In other developed countries the taking of birds for food, other than incidentally in sport as discussed below, was widely practised in the past. By recent centuries, however, larger species of notable palatability were reserved as game birds and it was small passerine species that were being trapped or lured as food, e.g. Wheatear *Oenanthe oenanthe* and Skylark *Alauda arvensis*, and then mainly as delicacies. This use persists in the western world only in certain countries, Italy being a notable example. House Sparrows *Passer domesticus* were taken in clap-nets at roosts in Britain into the 20th century, and Rooks *Corvus frugilegus* were shot as young about to fly, in both instances partly for food, partly as a form of pest control. The taking of wild birds for food in the less-developed countries varies with the opportunity cost of the activity—the alternative value of the time if spent in farming or other directly productive employments. No estimate of the total numbers killed is available. The practice thus depends on a complex of the species present and the levels of economic and cultural development. Modern weapons have not much increased the 'take' for the market and the pot, since trapping birds *en masse* remains more effective and cheaper than cartridges.

The taking of birds on a large scale requires that they be concentrated, either as colonial nesters or in large flocks on passage. Seafowl colonies are a prime example of the first category. Such colonies furnished mariners during the era of sailing ships with regular ships' provisions, on the spot or smoke-dried or salted, as well as acting as emergency stores. The Great Auk *Pinguinus impennis* of Funk Island was routinely driven on board ships over spread sails, to be killed and preserved. More generally, seabirds were netted on their nesting grounds and in much lesser degree while flying low over these grounds. Young were taken while still flightless. Similar catching equipment was in use in north-west Greenland, the Scottish islands and Faroes, the Aleutians, Japan and the Pelew islands.

Gregarious migratory species, especially when fat and numerous in the late summer and autumn, are both rewarding and comparatively easy to catch. Tired and less wary after long flights, they have often been netted or trapped in abundance. The Heligoland trap employed to capture migrants for scientific ringing originated from a device used by fowlers for catching thrushes *Turdus* spp. and other birds. Japanese mist-nets also used for research TRAPPING were originally employed to trap for the table. The netting of Quails *Coturnix coturnix* has long been carried on in the Mediterranean basin. Nearly 2,000,000 were exported from Egypt alone in 1913 but this trade has now been curtailed. Bird-lime smeared on twigs is another means used to catch small perching birds. Artificially-shaped ponds with netted pipes and traps (see DECOY) were also used historically to take ducks (Anatidae) for the market on a large scale. Flight nets were employed in some places.

The effects of hunting for the pot on the reduction and extinction of species are unavoidably hard to disentangle from the influences of hunting for sport, habitat destruction, the introduction of predators, and natural extinctions. Hunting extinctions since the beginning of the 17th century are however thought to include the Broad-billed Mauritian Parrot *Lophopsittacus mauritanus*, Great Elephant Bird *Aepyornis maximus* of Madagascar, Dodo *Raphus cucullatus* of Mauritius, Flightless Blue Rail *Aphanapteryx leguati* of Rodriguez, Spectacled Cormorant *Phalacrocorax perspicillatus* of Bering Island, Labrador Duck *Camptorynchus labradorius* of eastern North America, and the Wake Island Rail *Gallirallus wakensis*, this last having probably been hunted to extinction as food for the Japanese garrison as recently as 1945 (see EXTINCT BIRDS).

Eggs. The use of the eggs of wild birds for human food was systematically reviewed by Cott (1953–1954). More recent work in this detail is not available, but in the interim the importance of the food source has been diminished by the depletion of some species, the protection of others, and the substitution of agricultural foods. At that time as well as today the species providing large supplies of eggs for human consumption were usually in the orders Charadriiformes, Sphenisciformes, Procellariiformes, and Anseriformes. The Sooty Tern *Sterna fuscata* then yielded probably over 1,000,000 eggs annually. A further 11 species each yielded probably over 100,000 eggs annually. It is noteworthy that these 12 high yielders tended to be exploited in islands of the Southern Hemisphere and in the North Atlantic-North-western European region. Only the Moorhen *Gallinula chloropus* and Junglefowl *Gallus gallus* were extensively exploited for their eggs in Asia where the largest and densest low income human populations are to be found. The significance of commercial egging is greatest for marginal island populations with access to colonial nests of large species with highly palatable eggs. Jealously-guarded property rights in the sites of nesting colonies have ensured the 'farming' only of eggs inessential to the replacement of populations, as opposed to opportunistic gathering.

Sport. Firearm development since the 16th century has evolved 'shooting flying' instead of shooting birds when perched or on the ground, and has been employed to devise highly stylized sports. These occur over much of the world, often introduced to outlying parts of the former British empire. The species typically shot are to be found mostly among the pheasants and partridges, ducks and geese, plovers (Charadriidae), woodcock and snipe (Scolopacidae), sandgrouse and pigeons. Such species tend to be especially palatable and relatively large but not easy targets. It is in Britain that the ritualized, seasonal, socially-exclusive killing of pheasants, partridges and grouse has become most intensive. These shoots require expensive equipment, staff, the abridgement or alteration of farming activities, and they are run as profit-making, or at any rate loss-minimizing, businesses. Sporting rights may locally be a considerable element in land values. Since game species are often artificially protected, fed and reared, the effect of sporting uses has been to sustain or increase their numbers. Adverse effects on ornithological variety have come about through the extermination of their predators and the futile killing of species that are scarcely predators on game birds at all, such as owls. There is an even greater slaughter of non-game species in countries where access to land is more open and mass participants in hunting do not restrict themselves to conventional 'game' bird categories. The damaging side-effects of shooting are hard to eradicate in that legal systems do not adequately recognize or enforce public property rights in wild birds. Shooting geese and ducks is less conventionalized and in developed countries is nowadays organized in co-operation with conservation bodies or managed by government agencies so as to yield a wild surplus for sport.

An alternative sport involving wild birds even more intimately is falconry. Various raptorial species are taken from the wild and trained to hunt other birds on the wing and also some ground mammals. In Europe Great Grey Shrikes *Lanius excubitor* are kept as sentinels since they remark the presence and direction of hawks at great distances. Falconry is surrounded by medieval ritual and terminology; in the middle ages gifts of hawks and falcons, notably white specimens of the Greenland Falcon *Falco rusticolus candicans*, were important in diplomatic exchanges (see FALCONRY).

Feathers. Ornamental uses have been found for feathers of many species, especially those with plumes or bright colours. Such feathers were for a long time trade items, notably those of kingfishers, while feathers of the OSTRICH *Struthio camelus* were sufficiently valuable for the species to be farmed instead of merely being hunted. Demand for plumes for women's hats gave rise to a destructive trade during the late 19th and 20th century, the peak of western man's direct impact on wild birds, as opposed to the impact through habitat destruction. Opposition to this trade in turn inspired the early conservation movement (see CONSERVATION; ORNAMENTATION, BIRDS IN HUMAN). Some species remain threatened by the feather (and egg) trades, e.g. Andean Flamingo *Phoenicoparrus andinus*. Feathers were also used for several purposes—to stuff mattresses, quills for writing, to trim the flight of arrows and shuttlecocks, for making the artificial 'flies' used by anglers—for which substitute materials or feathers from domesticated varieties are now mostly available. A significant continuing use is of the down plucked from their bodies by certain ducks as nest-lining for filling duvets and quilted clothing. Colonies of Eider *Somateria mollissima* in Iceland are still exploited for that purpose.

Captivity. Wild birds of diverse species are kept in captivity for aesthetic, educational, utilitarian and scientific purposes (see AVICULTURE; CAGE BIRDS). European seamen of the Age of Discovery were astonished at the number of pet birds kept in warm latitudes, such as the West Indies. They imported many species to Europe, such as the Canary *Serinus canaria*. Finches (Fringillidae) native to Europe were also made captive as cage birds and singing contests are still covertly held in public houses in dockland areas of London. Zoological gardens continue to keep and breed a great variety of species. In addition there is a sizeable and very destructive smuggling trade in ornamental rarities from Asia and Australia, said to pass through south-east Asian entrepôts *en route* to the New York market. Dead specimens of shot or trapped wild species form the collections on which taxonomic work is based (see TAXONOMY). Stuffed specimens in collections made for ornamental or status reasons enjoyed a great vogue, especially in the 19th century, as did collections of blown eggshells. Making private collections undoubtedly endangered the populations of several species in return for a vanishingly small scientific contribution (see OOLOGY).

More utilitarian purposes have been served by captive birds. Oriental fishermen keep Cormorants *Phalacrocorax* spp. and retain a portion of the birds' catch (see CORMORANT). This usage also occurred in 17th century Britain. Wild birds have often been cited as navigational indicators. Frigatebirds *Fregata* spp. have been used to carry messages between Pacific islands. Canaries *Serinus canaria* have been used to test the oxygen available in mines and wells. The Sacred Ibis *Threskiornis aethiopica* was reared in captivity in ancient Egypt and sold for the purpose of mummification in pots placed next to burial chambers. While debatably utilitarian, this was a trade for the suppliers of specimens; and, according to Gooders (1975), many pots excavated were 'adulterated' with bones of other species.

Biological control. Man has manipulated the populations of several species (e.g. Swallow *Hirundo rustica* and Purple Martin *Progne subis*) in the hope of controlling pests, by providing artificial nest sites about farmsteads where there are cattle bothered by insects. Certain species (e.g. Cattle Egret *Bubulcus ibis* and Common Mynah *Acridotheres tristis*) have been introduced well away from their indigenous range in attempts to control insect pests of field crops. Several such introductions have in turn become, or been accused of becoming, pests themselves (Long 1981).

Miscellaneous. Minor uses of wild species are scarcely classifiable. Birds have been used in augury (see OMENS, BIRDS AS). The gelatinous salival nests of the Edible-nest Swiftlet *Aerodramus fuciphaga* have long been a luxury food and trade item in east Asia. The first and successive repeat nests are knocked down with long bamboo poles (see EDIBLE NESTS). The sealing industry in the southern oceans routinely burned the dried carcasses of penguins as fuel on treeless islands, to 'try' out the oil from seal blubber. E.L.J.

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V

VACUUM ACTIVITY: see OVERFLOW ACTIVITY.

VAGRANT: a wanderer outside the normal migration range of the species or subspecies, so far as that can be judged.

VAGUS: the tenth cranial nerve on each side (see NERVOUS SYSTEM).

VALIDITY: for that of scientific names, see NOMENCLATURE.

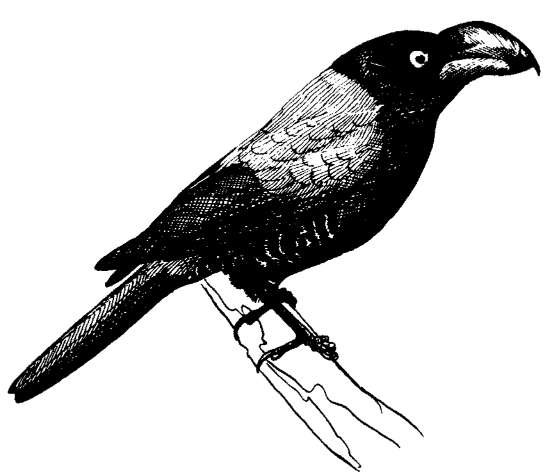
VANE: alternatively 'vexillum', the more or less coherent series of barbs on each side of the rachis of a typical feather (see FEATHER).

VANGA: the name used for 14 species in 11 genera, perhaps forming a single family, the Vangidae (order Passeriformes, suborder Oscines).

Excepting the occurrence of *Cyanolanius madagascarinus* in the Comoros, the family is endemic to Madagascar. In the scutellation of the tarsus, certain genera resemble the helmet-shrikes Prionopidae, of Africa. Maybe the Vangidae have resulted from a single invasion of Madagascar by a prionopid ancestor. If so, then the degree of radiation within a single land mass has been remarkable.

Characteristics. Vangas vary from 12.5–30 cm in length. They are boldly patterned in black and white, or blue and white, or with blacks, rufous browns and greys. Some are sexually dimorphic. The bill is usually heavy, often hooked; the feet moderately strong; the wings rather long, the tail moderately so. In the hand, some species recall bush-shrikes Malaconotinae (see SHRIKE) or even wood-swallows Artamidae. The White-headed Vanga *Leptopterus viridis* has a white head and underparts, and a glossy black back; Chabert's Vanga *L. chabert* is glossy black above, white below; the Blue Vanga *Cyanolanius madagascarinus* is blue above, white below (it has colonized Moheli, in the Comoros); the Rufous Vanga *Schetba rufa* has the whole head black in the male, with rufous back and white underparts; Bernier's Vanga *Oriolia bernieri* is usually black in the male, rufous in the female; and the Hook-billed Vanga *Vanga curvirostris* mainly black above, white below. The 3 species of *Xenopirostris* have the bill high and laterally compressed, the head black, back grey and underparts white. They provide a good example of a superspecies. The Helmetbird *Euryceros prevostii* has a long, much inflated bill, and plumage black and rufous. The Sicklebill *Falculea palliata* has a long, curved bill (for probing holes), with head and underparts white, and black back. The Tylas-vanga *Tylas eduardi*, formerly placed in the bulbuls (Pycnonotidae), lives alongside *Xenopirostris polleni* in the humid east, and is strikingly similar in colour, but with a much finer bill. The 2 smallest species are the Red-tailed Vanga *Calicalicus madagascariensis* and the Coral-billed Nuthatch-vanga *Hypositta corallirostris*. The former has a short bill, and rufous, grey and white plumage, the male with a black throat-patch. The latter was formerly placed in its own special family, but may be a specialized vanga, with (for climbing) elongated feet and claws, particularly the hindclaw. The male is wholly dull blue, the female brownish below.

Habitat and distribution. All the species are arboreal, habitat preferences linked with geographical distribution. *Oriolia bernieri*, *Xenopirostris polleni*, *Euryceros prevostii* and *Hypositta corallirostris* are confined to evergreen forest in the humid east. *Cyanolanius madagascarinus*, *Schetba rufa*, *Vanga curvirostris*, *Calicalicus madagascariensis* and (very rarely) *Tylas eduardi* also extend into more thickly wooded areas in the western savanna. The 2 *Leptopterus* spp. are even more adaptable, occurring also in the sub-desert scrub of the south-west. *Falculea palliata* is essentially only a western savanna form (in well-wooded areas), found but rarely in the sub-desert. *Xenopirostris damii* is similar in habitat, but is replaced in the sub-desert by *X. xenopirostris*. Some species are very restricted. *Xenopirostris damii* is known only from two localities in the north-west, *Euryceros prevostii* only from the north of the humid east.



Helmetbird *Euryceros prevostii*. (*C.E.T.K.*).

Populations. *Xenopirostris damii* and *polleni* are considered endangered, due to habitat destruction. Little is known about the status of *Oriolia bernieri*, but for the same reason it too could be endangered. Indeed, the numbers of all 14 species are probably everywhere dwindling.

Movement. All forms are probably strictly sedentary.

Food. All are insectivorous, but *Vanga curvirostris* and *Euryceros prevostii* may also regularly take tree frogs and small arboricolous reptiles. Most glean food while moving in loose flocks. However, *Xenopirostris xenopirostris* can raise bark with its strong bill to prey on underlying larvae. Furthermore, *Hypositta corallirostris* would appear to be the local ecological equivalent of creepers (Certhiidae) or nuthatches (Sittidae); while *Falculea palliata* is the only true hole-prober in Madagascar, the equivalent of wood-hoopoes (Phoeniculidae) in Africa.

Behaviour. Most species are strongly gregarious (as are Prionopidae). Thus *F. palliata* occurs in flocks of 25 or more. Most also occur in mixed parties with various passerines.

Voice. Some are noisy, giving whistling or chattering notes. One of the calls of *F. palliata* sounds like the cry of a child at play: hence the local name 'voronzaza' (bird baby').

Breeding. What little is known (the nests of only 8 of the species have been found) indicates the nest as a cup of twigs in a tree; the clutch-size as 3 or 4, the eggs whitish or greenish, spotted with brown and lilac. Possibly in all species, both parents share duties at every stage. In *Leptopterus chabert* the parents may be assisted by other individuals of the species, as in Prionopidae. (A.L.R.) C.W.B.

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VANGIDAE: a family of PASSERIFORMES, suborder Oscines; VANGA.

VANISHING BIRDS: see ENDANGERED SPECIES.

VARIABLE: a statistical term for any attribute in respect of which individual birds (eggs, nest, etc.) may differ, e.g. weight, wing length, sex, colour (see BIOSTATISTICS).

VARIANCE: see BIOSTATISTICS (Measures of dispersion).

VARIATION: see EVOLUTION; GENETICS; NATURAL SELECTION; PLUMAGE; POLYMORPHISM; SPECIATION; SUBSPECIES.

VARIATION, COEFFICIENT OF: see BIOSTATISTICS (Measures of dispersion).

VARIETY: a variant form within a population that is in the main homogeneous; used also for a breed under DOMESTICATION. 'Varietas' was the lowest of the taxonomic categories of Linnaeus, but the modern recognition of the polytypic nature of many species has rendered it obsolete in his sense; see also under SPECIES; SUBSPECIES; and POLYMORPHISM.

VASCULAR SYSTEM:

Arteries

Vessels of lungs. Intrapulmonary branches of the pulmonary arteries (see HEART) yield the interparabronchial aa. that provide the microvascular network for the parabronchi, the tubules which make up the exchange tissue of the lungs. The pulmonary capillary bed is drained by the interparabronchial vv., tributaries of the pulmonary veins that conduct blood back to the left heart. The terminal trachea, syrinx, and the larger bronchi are served by branches of the common carotid aa.

Ascending aorta. The definitive avian aorta is derived from the foetal right dorsal aorta (the left in mammals). The coronary aa. arise near the aortic valve; both brachiocephalic aa. spring from the left side of the ascending aorta (Fig. 1). In strong flyers (e.g. pigeons) each brachiocephalic a. is greater in diameter than the aortic arch; in poor flyers such as *Gallus* the brachiocephalic a. is half the diameter of the arch. These differences reflect the enormous demand for blood by the pectoral muscles in the birds adapted for sustained flight. Each brachiocephalic a. divides into common carotid and subclavian aa., carrying blood to the head and thoracic limb.

Arteries of neck (Fig. 2). Each short common carotid divides in the thoracic inlet into its terminal branches: internal carotid a., vagus a. and vertebral a. The ascending branch of the vertebral courses headward through transverse foramina of the neck vertebrae, supplying vertebral muscles and spinal cord. The internal carotids ascend the neck side-by-side in an osseomuscular canal ventral to the vertebral column. This adaptation allows extremes of neck movements without stretching the carotids. The bicarotid condition is the most prevalent. In unicarotid birds, the left carotid usually persists (e.g. passerines); in some birds the single carotid represents fused left and right carotids. Cranially the internal carotids diverge and give off the external carotids, continuing into the skull as the cerebral carotid aa. (Fig. 2).

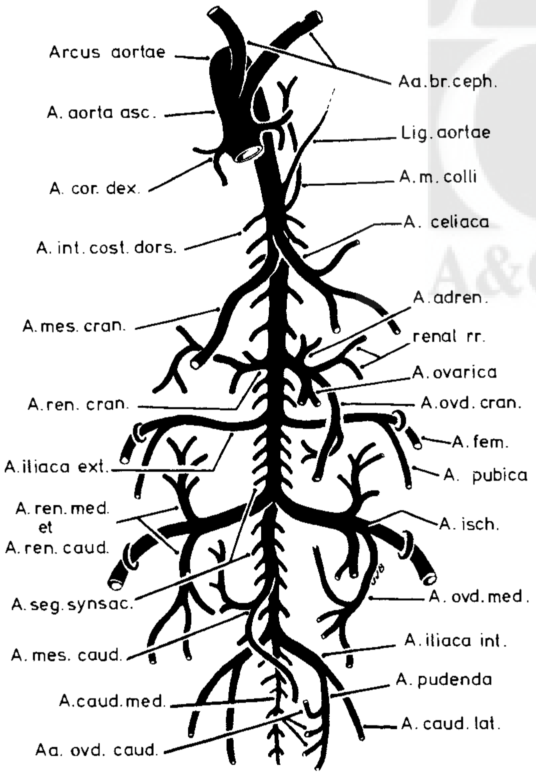


Fig. 1. Main branches of aorta; *Gallus*, female. Ventral view. Note on left side of specimen the prominent unilateral ovarian and oviductal arteries.

Abbreviations: adren. = adrenalis; asc. = ascendens; br. ceph. = brachiocephalicae; caud. = caudalis; cor. = coronary; cran. = cranialis; dex. = dextra; fem. = femoralis; intercost. = intercostalis; Lig. = ligamentum; med. = mediana; mes. = mesenterica; m. = musculorum; ovd. = oviductalis; ren. = renalis; r.r. = rami; seg. = segmentalis; synsac. = synsacralis. (From Baumel 1979).

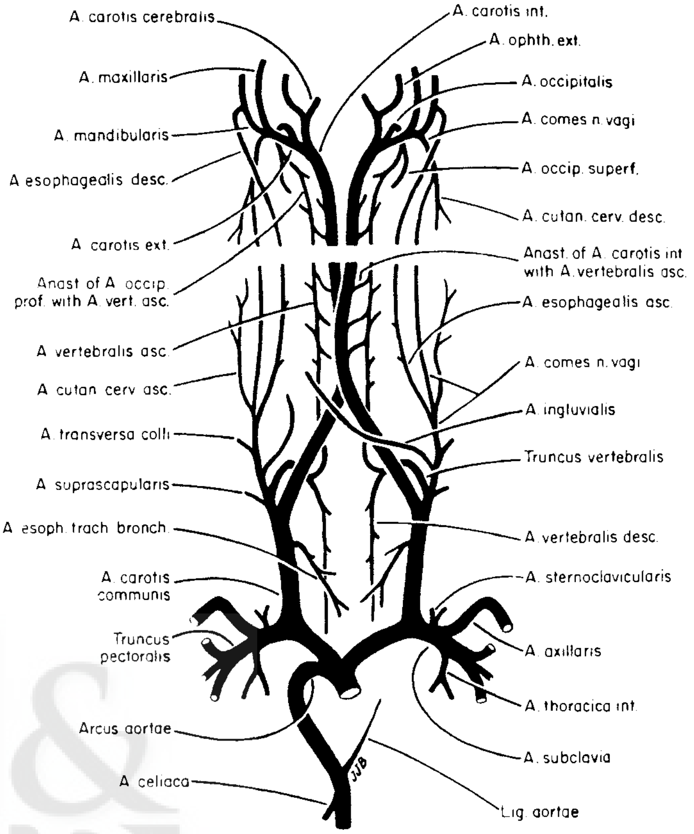


Fig. 2. Main branches of brachiocephalic arteries to head, neck and thoracic limb, *Columba livia*. Ventral view; foreshortening indicated by white transverse band across figure. Note that the common carotid artery consists of a short trunk; its main branch is the internal carotid. The external carotid is a branch of the cranial end of the internal carotid in adult birds. (From Baumel 1979).

Abbreviations: A.c.n. X. = A. comes nervi vagi; Anast. = anastomosis; asc. = ascendens; ax. = axillaris; car. = carotis; cerv. = cervicalis; comm. = communis; crb. = cerebralis; cutan. = cutanea; desc. = descendens; esoph. = esophagealis; esoph.trach. bronch. = esophagotracheobronchialia; ingluv. = ingluvialis; mand. = mandibularis; max. = maxillaris; occip. = occipitalis; oph. = ophthalmica; pect. = pectoralis, sup. scap. = suprascapularis; transv. = transversa; vert. = vertebralis.

Intracranial arteries. The cerebral carotid aa. are the primary sources of blood to the brain and meninges; the vertebral aa. contribute little or none. The external ophthalmic aa. (Fig. 2) may furnish blood to the brain in birds such as pelicans via communications with the cerebral carotids. Near the hypophyseal fossa the two cerebral carotid aa. of most birds anastomose with one another (exceptions: passerines of the suborder Tyranni). The intercarotid anastomosis is functionally equivalent to the cerebral arterial circle (of Willis) of mammals. In the cranial cavity each cerebral carotid releases middle, rostral, and caudal cerebral aa. The caudal cerebral a. in many birds is asymmetrical; the artery of one side supplies both telencephalic hemispheres and/or both sides of the cerebellum. The unpaired a. is formed by fusion of the two caudal rami of the carotids in certain birds, in others by the caudal ramus of one side only.

Extracranial arteries. The definitive external carotid a. (vagus a. is the foetal external carotid) arises from the internal carotid near the caudal end of the mandible. Its descending branches (Fig. 2) pass to the upper cervical viscera, muscles, and integument. Its ascending branches serve the jaws, jaw muscles, tongue, nasal cavity, and palate. The mucous membrane of the nasal, oral, and pharyngeal cavities and the unfeathered skin of the head contain rich microvascular networks, concerned in part with thermoregulation, e.g. gular flutter, panting (see HEAT REGULATION). The external ophthalmic (stapedial) a. leaves the internal carotid and passes through its own canal over the tympanic cavity. In the orbit it breaks up into small plexiform arteries that mesh with a similar venous plexus, the Rete mirabile ophthalmicum, which probably functions as a countercurrent heat exchanger. The external ophthalmic supplies the eye and orbit.

Descending aorta (Fig. 1). The paired segmental branches of the aorta supply the body wall (e.g. intercostal aa.) as well as the vertebral column, spinal cord, pelvic limb, tail, cloaca and vent. Paired visceral branches of the aorta supply the urinary and genital organs. Unpaired visceral branches are distributed to parts of the alimentary canal.

Arteries of digestive organs. The first of the three unpaired visceral branches is the coeliac a., branches of which supply the glandular and muscular parts of the stomach, duodenum, pancreas, liver, and spleen. The hepatic aa. accompany branches of the hepatic portal vv. in the liver. The cranial mesenteric a. serves the postduodenal small intestine as far distally as the ileorectal junction. A chain of anastomoses (marginal intestinal a.) connects rami of the cranial mesenteric a. with those of the coeliac and caudal mesenteric aa. The caudal mesenteric a. arises from the reduced segment of the aorta (median sacral a.) just distal to origins of the ischiadic aa. The branches of the caudal mesenteric a. run near the rectum with the huge caudal mesenteric vein. Its caudal branch extends to the terminal rectum, cloacal bursa, and the cloaca.

Arteries of urogenital organs (Fig. 1). The kidneys receive blood from several sources. The versatile cranial renal aa. arise from the aorta near the cranial mesenteric a. and supply the cranial divisions of the kidneys and adrenal glands. Cranial oviductal and ovarian arteries stem from the left cranial renal a. only; in the male each cranial renal a. yields testicular aa. The caudal renal aa. arise from the ischiadic aa. and serve the middle and caudal divisions of the kidneys. The usually single (left) oviduct is supplied by three arteries of the left side: cranial, middle, and caudal oviductal aa. from the left cranial renal, ischiadic and pudendal aa. Ovarian and oviductal aa. become hypertrophied in laying birds. The cloaca and, in the male, its parts specialized for copulation are supplied by the pudendal a.

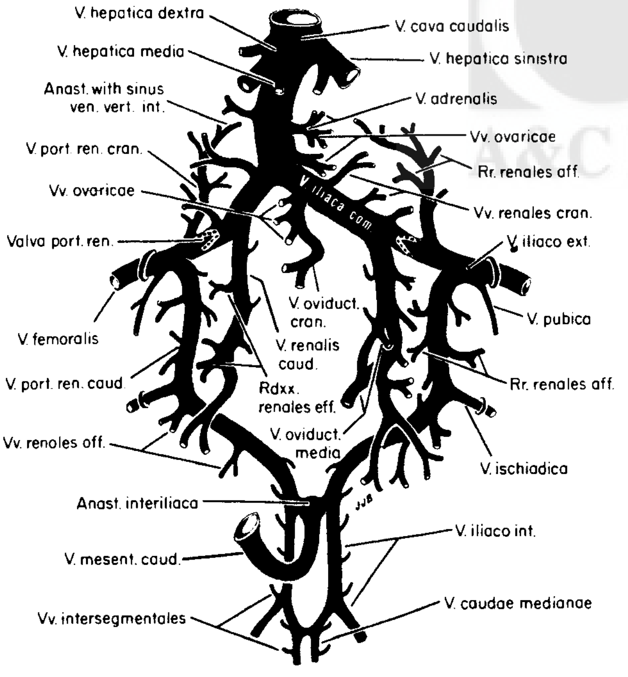


Fig. 3. Caudal vena cava and renal portal system of veins; *Gallus*. Ventral view. (From Baumel 1979).

Abbreviations: aff. = afferentes; caud. = caudalis; cran. = cranialis; dex. = dextra; eff. = efferentes; ext. = externa; fem. = femoralis; hep. = hepatica; int. = interna; med. = media or medianae; mes. = mesenterica; ovd. = oviductalis(es); port. = portalis; ren. = renalis(es); seg. = segmentales; sin. = sinistra.

Arteries of pelvic limb. In most birds the major pelvic limb artery is the ischiadic a.; however, in some species of Tyranni the femoral a. is dominant; the ischiadic is reduced in the Sphenisci; and in the cuculid *Centropus* sp. the ischiadic is completely absent. The Rete tibiotarsale is a vascular network of collateral branches of the distal part of the cranial tibial a. intermingled with satellite veins. The contact between the warm core arterial blood and the cooler venous blood from the periphery, conserves heat loss from the exposed feet (see HEAT REGULATION).

Terminal aorta (Fig. 1). The paired internal iliac aa. arise from the median sacral a. near the caudal mesenteric a. The internal iliacs divide into the pudendal a. and the lateral caudal a. (to muscles and integument of the tail region). The lateral caudal a. contributes to the incubation (brood) patch which is mainly served by the pectoral a. The median caudal a., the slender prolongation of the aorta, supplies the dorsal tail, bulb of the tail feathers, and uropygial gland.

Veins. Among the features of the avian venous system are the presence of: (1) a functional renal portal system; (2) bilateral hepatic portal veins; (3) usual dominance of the right jugular vein; (4) interjugular anastomosis near base of the skull; (5) interiliac anastomosis near the base of the tail (Fig. 3); (6) extensive communication between visceral and somatic veins via the caudal mesenteric (coccygeomesenteric) vein; and (7) the internal vertebral sinus which carries toward the heart much of the drainage from segmental veins. On account of their more dense innervation, avian veins are believed to be more active in distribution of blood and in venous return than veins of mammals.

Cranial vena cava. Each cranial caval v. receives blood from head and neck and the thoracic limb via the two jugular vv. and the internal vertebral sinus. The veins of the brain empty into sinuses which leave the skull through the foramen magnum, flowing into the caudal cerebral vv. and the internal vertebral sinus. Most extracranial veins are tributaries of the rostral cerebral vv. The jugular v. is formed by confluence of the rostral and caudal cephalic vv. The interjugular anastomosis connects the two jugular systems just dorsal to the pharynx. The jugulars receive veins from the skin and viscera of the neck; near their terminations the jugulars are joined by the vertebral vv. and communicating veins from the internal vertebral sinus. Generally, the right jugular is larger than the left. The left jugular is atrophied and nonfunctional in several passerine species.

Internal vertebral venous sinus. The vertebral sinus which is situated within the vertebral canal communicates directly with the intracranial dural sinuses. Segmental veins of the neck and trunk flow *into* the anterior segment of the vertebral sinus, then toward the base of the neck where the sinus empties into the jugulars. Blood in the posterior segment of the sinus flows *away* from the sinus into the internal iliac vv.

Caudal vena cava (Fig. 3). This largest vein in the body drains blood from the body wall posterior to the lungs, the pelvic limb, tail region, the liver and urogenital organs. In laying females the enormous ovary displaces the vein to the right. The caudal caval v. is partially embedded in the liver; it does not directly receive intercostal or other segmental body wall veins (see *Internal vertebral sinus*). Its main tributaries are the common iliac and hepatic vv.

Hepatic portal system. Venous blood from the alimentary tract and other organs served by the coeliac and mesenteric arteries is collected by the large right and smaller left hepatic portal vv. which enter the liver, ultimately dividing into a network of sinusoids between sheets of liver cells. The sinusoids, where exchange of substances occur between liver cells and blood, also receive arterial blood from rami of the hepatic arteries. The sinusoids re-form into radicles of the hepatic vv. that empty into the terminal part of the caudal vena cava.

Genital veins (Fig. 3). The ovarian and oviductal veins are hypertrophied in laying birds; therefore the veins of the left side are conspicuously larger than on the right. Testicular and ovarian vv. drain into the caudal caval v. The three groups of oviductal vv. empty into the left common iliac v., left caudal renal v., and further caudally, into the left pudendal v.

Renal portal system (Fig. 3). Birds possess another functional portal system other than that of the liver. Part of the venous blood from the pelvic limb and tail region may be diverted into the kidney via the renal portal vv. where it mixes with arterial blood in the peritubular network of capillary sinuses, then back into the caudal caval v. for delivery to the heart. The interiliac anastomosis unites the two internal iliac vv. near the caudal poles of the kidneys. The rear end of the caudal mesenteric v. communicates with the anastomosis, thus this vein can conduct blood from the gut into or away from the renal portal system. The renal portal valve is in the common iliac v.; when the valve is open blood from the external iliac and renal portal vv. can progress directly into the caudal caval system. When the valve is closed, blood from the limb passes through the kidney circulation, then back to the caval system via the renal vv. Or the blood may merely flow through the portal veins, by-passing the intrarenal circulation, draining either into the caudal mesenteric v. or into the internal vertebral sinus.

Veins of pelvic limb. In most birds an oblique ischiadic–femoral anastomosis shunts most of the blood from the distal part of the ischiadic v. to the femoral v. in front of the hip joint. The femoral v. becomes the principal vein of the limb. The reduced ischiadic v. continues into the pelvis with its artery and nerve, terminating in the caudal renal portal v. (E.T.B.F.) J.J.B.

For references see HEART.

VAS DEFERENS: (plural 'vasa deferentia')—see ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM.

VECTOR: an animal that is a carrier of parasites or infections to another species; sometimes the vector species is an intermediate host in which the parasite necessarily accomplishes a part of its life-cycle—and in that case is termed a 'biological vector', as contrasted with a 'mechanical' one (see DISEASE; ECTOPARASITE; ENDOPARASITE).

VEERY: *Catharus* (*'Hylocichla'*) *fuscescens* (see THRUSH).

VEGETATION: see HABITAT.

VEINS: see HEART; VASCULAR SYSTEM.

VELVETBREAST: *Lafresnaya lafresnayi* (for family see HUMMINGBIRD).

VENA CAVA: see HEART; VASCULAR SYSTEM.

VENOUS SYSTEM: see HEART; VASCULAR SYSTEM.

VENT: the CLOACA.

VENTRAL: pertaining to the abdominal aspect or, more generally, the lower surface of the body; opposite of DORSAL.

VENTRICLE: a hollow space within an organ, especially the heart or the forebrain (see HEART; NERVOUS SYSTEM).

VENTRICULUS: the gizzard (see ALIMENTARY SYSTEM).

VERDIN: *Auriparus flaviceps* (see PENDULINE TIT).

VERMICULATED: covered with a dense pattern of fine wavy lines.

VERNACULAR NAME: see NAME, VERNACULAR.

VERTEBRAL COLUMN: the backbone (see SKELETON, POSTCRANIAL).

VERTEBRATES: see ANIMAL KINGDOM.

VERTICAL CLASSIFICATION: see HORIZONTAL AND VERTICAL CLASSIFICATION.

VESTIBULE: anatomically, a cavity leading into another; used especially of the cavity of the ear-labyrinth (see HEARING AND BALANCE).

VEXILLUM: the vane of a feather (see FEATHER; VANE).

VIBRISSA: a modified feather, like a bristle (see PLUMAGE).

VICE-COUNTY: a biogeographical subdivision of an administrative county, in Britain, used—primarily by botanists—as a unit area in distributional studies.

VIDUIDAE: a family of PASSERIFORMES, suborder Oscines; WHYDAH (1).

VILLI: (plural of 'villus'), internal processes of the ileum and caeca (see ALIMENTARY SYSTEM).

VINACEOUS or **VINOUS:** wine coloured.

VINCULUM: a fibrous band such as sometimes unites two or more tendons (see under MUSCULATURE).

VIOLETEAR: substantive name of *Colibri* spp. (for family see HUMMINGBIRD).

VIREO: substantive name (from the Latin *virere* 'to be green') for 25 species of *Vireo*, which with 13 species of *Hylophilus* (greenlets) constitute the subfamily Vireoninae and in turn make up the greater part of the New World family Vireonidae (Passeriformes, suborder Oscines). For the other constituent subfamilies, see PEPPER-SHRIKE, SHRIKE-VIREO. Vireos are thought to be of New World origin, but recent biochemical evidence indicates that they have affinities with a predominantly Old World group including crows, cuckoo-shrikes, drongos, monarch flycatchers and shrikes. Thus, vireos may not be closely related to New World nine-primaried oscines.

Characteristics. Vireos are from 10–17 cm long and weigh from 9 g (Black-capped Vireo *Vireo atricapillus*) to 24 g (Black-whiskered Vireo *V. altiloquus grandior*). The beak, characteristically notched near the tip of the maxilla, is heavier than that of New World warblers (Parulidae). Plumage is grey, greenish or brown dorsally and whitish or yellowish ventrally. Three subgenera distinguished both by appearance and behaviour are recognized: *Vireosylva* (e.g., *V. altiloquus*) has a pale superciliary stripe and lacks wing bars; *Lanivireo* (e.g., Solitary Vireo *V. solitarius*) and *Vireo* (e.g., *V. atricapillus*) have pale lores and eye rings and one or two wing bars. Plumage dimorphism is found only in *V. atricapillus* in which the crown is black in males and grey in females. Vireos lack pronounced seasonal differences in plumage.

Habitat. Vireos inhabit broad-leaved or mixed coniferous/broad-leaved scrub and forest. Sympatric species are separated ecologically either by foraging in different strata or by favouring different positions along a gradient of vegetation density or composition, e.g., in mixed forest of western North America, Solitary Vireos *V. solitarius* predominantly use conifers and Warbling Vireos *V. gilvus* occur mainly in broad-leaved riparian growth. North American migratory species winter in habitat resembling that of the breeding grounds.

Distribution. In summer, races of the widespread vireosylvid *V. olivaceus* occur from 65°N in Canada to 34°S in Argentina. The only other vireo breeding in South America is another vireosylvid, *V. gilvus*, which is restricted to the mountains of the northwest. Vireos have successfully colonized Bermuda (White-eyed Vireo *V. griseus*) and the West Indies, where 6 vocally distinct and sedentary species of the scrub-dwelling *V. 'griseus'* complex occur eastward to Puerto Rico. The vireosylvid *V. altiloquus*, often sympatric with West Indian scrub vireos throughout their island range, is even more widespread than the latter in the West Indian region, occupying coastal Florida, the Bahamas and the Greater and Lesser Antilles. On Grand Cayman Island only, *V. altiloquus* is replaced by a race of the closely related Yucatan Vireo *V. magister*. On Jamaica a third species, the Blue Mountain Vireo *V. osburni*, occurs in the mountains. On the mainland the sedentary Yellow-winged Vireo *V. carmioli* (*Lanivireo*), of the mountains of western Panama and the Mangrove Vireo *V. pallens* (*Vireo*), reaching north-western Costa Rica, are the southernmost representatives of their subgenera which in summer have breeding species southward from 62°N in Canada and 47°N in the United States respectively. The highest breeding diversity, 7 summering species, is found in the Conchos River Valley in west Texas.

Populations. Most species of vireos are common to abundant throughout their range, with the Red-eyed Vireo *Vireo olivaceus* regarded as the commonest native forest-dwelling passerine in eastern North America. Only the Slaty Vireo *V. brevipennis* of central Mexico and *V. osburni* of Jamaica are truly rare, the latter occurring in a 1:10 ratio with *V. altiloquus* in montane forest. Numbers of *V. atricapillus* and Bell's Vireo

V. bellii are declining in the south-western United States and north-western Mexico in part because of habitat destruction and cowbird (*Molothrus* spp.) nest parasitism.

Movements. Ten of the 11 species of vireos breeding in North America or the West Indies are migratory. Only the Hutton Vireo *V. huttoni* ranging from British Columbia to Guatemala is sedentary. The Yellow-green Vireo *V. olivaceus flavoviridis* is one of 2 New World passerines that is an intra-tropical migrant—breeding in Mexico and Central America and wintering in the Amazon Basin. Migration distances vary from *c.* 4,800 (northern population of *V. olivaceus* migrating to Amazonia) to 160 km (southern breeding population of the Grey Vireo *V. vicinior* in west Texas).

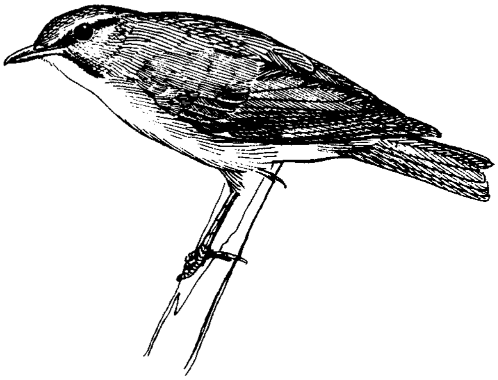
Food. Vireos are to varying degrees insectivorous and frugivorous depending in part on the season. In late summer, primarily insectivorous temperate zone vireos become increasingly frugivorous as migration (late August to October) approaches. Migratory races of *V. altiloquus* and *V. olivaceus* are exclusively frugivorous on the Amazonian wintering grounds and fruit comprises up to 50% of the diet of resident, tropical species. Vireos forage at a more deliberate pace than parulid warblers, taking prey while hopping among foliage and branches or, less often, while hovering at leaf clusters. All vireos also catch some prey by flycatching. Only *V. vicinior* forages regularly on the ground (*c.* 5% of all feeding bouts) but it is not exclusively insectivorous.

Behaviour. Vireos use song to defend territories ranging from 0.2–0.9 ha (*V. bellii*) to *c.* 20 ha (*V. vicinior*). Aggressive displays encompass head forward threat, and ruffling of body and crown feathers. Adults of the migratory species generally remain for a time on territory after breeding is concluded, but defence then is minimal. Prior to migration, young wander in family groups or in mixed flocks with other small birds. Winter territoriality occurs in *V. vicinior* and is suspected in *V. solitarius*, the Yellow-throated Vireo *V. flavifrons* and *V. griseus*. In winter the non-migratory *V. huttoni* forms small flocks or joins mixed flocks of other small species. Tropical vireos generally remain on territories all year.

Voice. Vireos utter tonally pure or frequency modulated notes organized in loud, persistent song of two basic kinds: (1) a 'chattering' repetition (2–30 times) of a single note constituting a single bout of song that in turn may be repeated up to 100 times before switching to a song comprising a different single note; (2) repeated bouts of song that involve 2–20 different notes in each bout. Species with monosyllabic 'chatter' song are mainly subtropical to tropical in distribution (e.g., Cozumel Vireo *Vireo bairdi*). The 'song' of *V. osburni* is unusual in consisting of trills (each *c.* 1.5–2 sec. long and comprising 10–25 notes) given from 1 to 10 times. In addition to song, trills resembling that of *V. osburni* are uttered by *V. vicinior*, *V. solitarius*, *V. flavifrons* and the Philadelphia Vireo *V. philadelphicus*. All vireos have 5 (*V. osburni*) to 15 (*V. gilvus*) calls varying from a simple *tic* to a structurally complex *myaah* given in breeding, aggressive and general maintenance contexts. Song of most scrub dwelling species is somewhat ventriloquial.

Breeding. Vireos breed from mid-April (or mid-November south of the Equator) to early August (early March) throughout their range. Males (arriving a few days in advance of females in migratory species) establish all-purpose territories by fighting and song. Males court females using several ritualized displays, including swaying of the body and/or wing and tail movements. Courting and copulation accompany nest-building (completed 5–15 days) which is shared by the sexes (except that only females build in most *Vireosylva*). Egg-laying follows within 1–2 days of nest-completion and incubation, performed only by females in *V. olivaceus*, *V. magister* and *V. altiloquus*, begins with the second egg and lasts from 11–13 days. Males of most species sing while on the nest. In all species both parents contribute to the care of the young both during the nestling period, which averages 12 days, and after fledging for an additional 20–30 days.

Nests are pensile, suspended from a small forked branch in vegetation from 0.5 m (*V. bellii*) to 25 m (*V. flavifrons*) above the ground. Clutch-size varies from 2 to 5, decreasing southward to the tropics. Eggs are white, ranging from immaculate in *V. atricapillus* to heavily spotted in the Thick-billed Vireo *V. crassirostris*.



Black-whiskered Vireo *Vireo altiloquus*. (*C.E.T.K.*).

Greenlets. Greenlets occur from southern Mexico to northern Argentina but only 3 out of 13 species (Grey-headed *Hylophilus decurtatus*, Tawny-crowned *H. ochraceiceps* and Scrub *H. flavipes* Greenlets) are found north of Panama. Greenlets are uniform in size and appearance and they lack the notch at the tip of the maxilla typical of *Vireo* spp. Song varies among species, from 'chatter' (*H. flavipes*) to songs resembling *Vireo* species (e.g., *H. decurtatus* sounds like *V. philadelphicus*) to distinctive whistled songs (*H. ochraceiceps*).

Greenlets are forest (e.g., *H. decurtatus*) or scrub dwellers (*H. flavipes*), mainly taking arthropods from near ground level (*H. ochraceiceps*, which follows ant swarms) to high in rainforest trees (*H. decurtatus*).

Breeding occurs between January and September in the species of greenlets in which it has been seen (*H. decurtatus*, Ashy-headed Greenlet *H. pectoralis*, *H. ochraceiceps*). Nests are pensile, suspended by the rim from a small fork in a tree or shrub 2–6 m up (in *H. ochraceiceps*), and are built by both sexes. Clutch-size is 2 in these 3 species and the eggs are whitish with small blackish spots. Both sexes incubate and feed the nestlings. The incubation period is 16 days for eggs of *H. decurtatus*; fledging occurs at 12 days in *H. decurtatus* and 14 days in *H. ochraceiceps*. Males of *H. decurtatus* and *H. pectoralis* sing while sitting on eggs.

J.C.B.

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VIREO, ANT-: see ANTVIREO; ANTBIRD.

VIREONIDAE: a family of the PASSERIFORMES, suborder Oscines, treated here as comprising the Vireoninae—the true vireos, including greenlets (see VIREO); the Vireolaniinae (see SHRIKE-VIREO); and the Cyclarhinae (see PEPPER-SHRIKE). It may be doubted whether it is necessary to recognize 3 subfamilies, the second and third including only 1 genus apiece, but they have in the past been treated even as separate families, and the groups are given separate articles in this work.

VIREOLANIINAE: see VIREO-SHRIKE.

VIROLOGY: see DISEASE.

VIRUS: see DISEASE.

VISCERA: the soft internal parts (entrails).

VISIBLE MIGRATION: the section of the stream of birds passing over an area on MIGRATION which can actually be seen from the ground.

VISION: the dominant sense of almost all birds which, with few exceptions, have extremely well developed and efficient eyes. Birds are completely dependent on their eyes while flying and rely heavily on vision for finding food, for recognizing mates or conspecifics (see PLUMAGE), and for detecting predators. Unlike mammals, birds have remained largely diurnal throughout their evolutionary history, and as a result, the eyes of birds are much more highly developed for vision in daylight.

Size and shape of eyes. The paramount importance of the visual sense is reflected in the relatively enormous eyes characteristic of birds; some hawks and owls, for instance, have eyes as large or larger than those of man. In many birds the two eyes together weigh nearly as much as the entire brain and are often as big as the head can accommodate. If the eyes are particularly lateral in their orientation, they will almost touch one another with only a thin, even translucent, bony septum between them. The large size of the bird eye is generally not apparent on superficial observation of the head because of its unusual shape; the cornea, which is usually small in comparison with the rest of the eye, is the only part of the eye externally visible between the lids. In fact, the bird eye is not spherical, as in mammals, but consists of two hemispheres of different radii of curvature joined at the ora serrata. The concavity at the cornea saves space and weight while at the same time achieving a larger retina and retinal image. Bird eyes apparently do not have the natural structural stability of a sphere, and for this reason a ring of cartilaginous plates, i.e. the scleral ossicles, is located at the ora serrata around the base of the cornea to support the eye and provide a firm origin for the intraocular muscles (Figs 1 and 4).

Eye movement. The large eyes of most birds are so tightly enclosed in their orbits that there is little room for the well-developed extraocular muscles found in most mammals. The aspheric shape of the eye may also make large eye movements difficult for structural reasons. In general, eye movements are relatively limited in birds, but there is considerable variation in the range of eye movements in different species. With the exception of many owls, all birds seem capable of some convergence of the eyes toward the beak with amplitudes of 10° to 25°. In the absence of binocular stimulation, the movements of the two eyes are independent. When the head is tilted, birds also show small counter-rotations of the eyes to compensate for the head movement. A few species of birds are reported to have large, easily observable eye movements. Although most of these birds are marine species, including gulls, penguins and cormorants, a recent quantitative study suggests that the domestic chicken also has large eye movements of 50° or more. Eye movements in most birds, however, are small and limited to the horizontal direction. This restricted range of eye movement in birds is compensated for by an extremely flexible neck; even casual observation of birds reveals a heavy dependence on head movements while foraging for food or keeping watch for predators. In owls and in many other species, the head can be turned nearly 180° in either direction.

Nictitating membrane. Like many other vertebrates, birds have a nictitating membrane or third lid which lies under the lids on the nasal side. In diurnal birds this is usually somewhat transparent and can be drawn horizontally across the cornea to clean or moisten it without completely shutting out the light. The nictitating membrane may also be used to protect the eye from physical injury during visually guided behaviour. For example, while foraging for food on the ground, granivorous birds such as the Woodpigeon *Columba palumbus* will often close their nictitating membranes during each peck just as the head nears the ground. The extent to which the nictitating membrane interferes with a bird's vision is unknown. Birds are reported to blink or draw their nictitating membrane across their eyes more frequently while moving their heads than when they are still, possibly in order to block out the blurred images that result from rapid head movements. Alternatively, the nictitating membrane is used to clean and moisten the cornea when normal vision is prevented or impaired by such head movements. Some diving birds that use their eyes underwater, e.g. diving ducks, divers, and auks, have an especially clear central window in their nictitating membranes which would facilitate their vision through the membrane. Contrary to earlier suggestions, however, the membrane in these birds has the same refractive index as the cornea and will not compensate for the loss of corneal refraction underwater.

General structure of the eye. The basic structure of the avian eye follows the general pattern of all vertebrate eyes (Fig. 1). This consists roughly of an optical system made up of the cornea, lens, and vitreous body, which casts an inverted image of external objects on the light-sensitive retina (for connection with the brain, see under NERVOUS SYSTEM). Birds' eyes fall roughly into three groups, of which examples are shown in Fig. 2. The first, from the Mute Swan *Cygnus olor*, is relatively flat and characteristic of most diurnal birds; the second, from the Golden Eagle *Aquila chrysaetos*, is more globose and typical of diurnal birds with especially good vision; and the third, from the Eagle Owl *Bubo bubo*, is a somewhat tubular eye adapted for useful nocturnal vision.

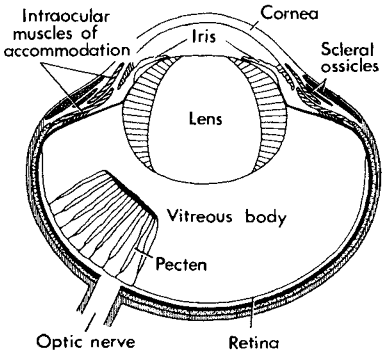

Fig. 1. Diagram of the avian eye. (After Duke-Elder).

Pupil reactions. The amount of light entering the eye depends on the reactions of the pupil. This is the aperture in the centre of the iris, a circular pigmented tissue situated over the anterior surface of the lens (Fig. 1) and giving colour to the eye (see IRIS COLORATION). The iris contains both radial and circular muscles which regulate the size of the pupil. In most vertebrates, these are smooth muscles under involuntary nervous control but, in birds as well as reptiles, both sets of muscles are striated. The fact that the iris muscles are striated suggested to some authorities that the pupil is under voluntary control in birds, but there is no evidence to support this view. Changes in pupil diameter are strikingly rapid and extensive in birds; the pupil of the pigeon, for example, is capable of about a ninefold reduction in area. The striated muscles may simply facilitate more rapid constrictions of the pupil; in some birds the pupil reacts at least twice as fast as the human pupil in response to an increase in illumination. The accommodation reflex that causes the human pupil to constrict for near vision has not yet been conclusively demonstrated in birds. The pupil in most birds is approximately round when fully dilated but may become somewhat more elliptical when constricted. As compared with humans, many diurnal birds have large pupils relative to the size of the eye; for the same illumination, the amount of light striking the retina will be correspondingly greater. It is unclear how the bird's retina withstands these higher light intensities but, under bright light conditions, the black epithelial pigment underlying the retina is reported to move forward to protect the highly sensitive receptor cells, particularly the rods. The sensitivity of the pupillary response appears to vary in different species, but only the pigeon has been studied. In general, the pupils of diving and nocturnal birds are considered more responsive to light; vision underwater requires a higher light sensitivity, and in many diving species the retina approaches the nocturnal type. Such a retina, adapted for low light levels, presumably needs extra protection in full daylight. In some animals, when only one eye is exposed to bright light, the pupils of both eyes will constrict. This consensual pupillary reflex is common in mammals but apparently does not occur in birds, with the possible exception of the owls. Occasional reports of such a reflex are probably due to the fact that the two eyes nearly touch in the heads of many birds; light may pass through the back of one eye and hit the retina of the other eye.

Pecten. One striking feature peculiar to the avian eye is the pecten. This is a pigmented, highly vascularized structure, usually pleated but sometimes with vanes, attached to the optic nerve along its base and standing up in the posterior chamber of the eye supported by the highly viscous vitreous body. When light enters the eye through the pupil, the pecten's shadow falls on its own base, the optic disc, which is a blind spot in the retina. The pecten is composed almost entirely of blood vessels and extravascular pigmented stromal (i.e. connective) cells enclosed in a thin membrane; no muscular or nervous tissue is present. Comparative studies indicate that the size of the pecten and the number of its pleats both increase with the importance of vision in a bird's behaviour but not necessarily with the size of the eye. Thus, the pecten is smallest in nocturnal birds, larger in seed-eating species, larger still in insectivores and largest of all in the diurnal predators such as hawks and eagles. Many theories about the visual function of the pecten have been proposed.

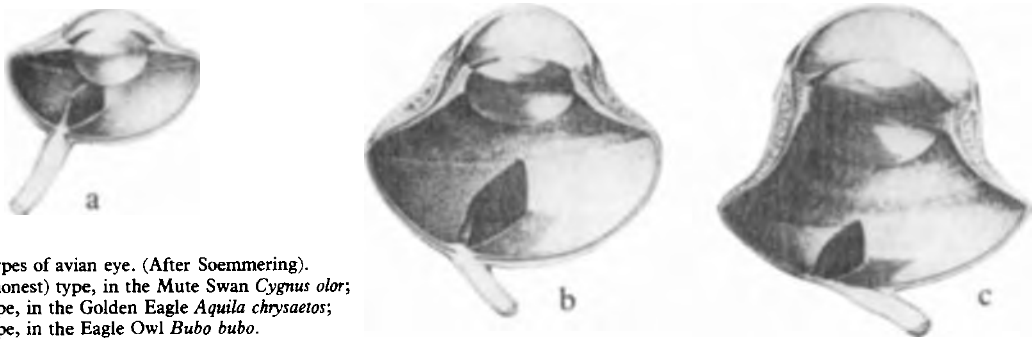

Fig. 2. Three types of avian eye. (After Soemmering).
(a) 'Flat' (commonest) type, in the Mute Swan *Cygnus olor*;
(b) 'Globose' type, in the Golden Eagle *Aquila chrysaetos*;
(c) 'Tubular' type, in the Eagle Owl *Bubo bubo*.

They include suggestions that the pecten acts as an intraocular visor against the sun's glare, that the flicker of an image across its pleats enhances movement sensitivity, or that the pecten's shadow has a sextant-like function in navigation. However, current evidence indicates that the pecten, by means of its enormous vascular surface, supplies nutrients and oxygen to the retina through osmosis and may be involved in the regulation of intraocular pressure. Neither birds nor reptiles have any blood vessels in the retina, although as in all vertebrates there is a blood supply through the choroid beneath the photoreceptors. Retinal blood vessels are believed to interfere with vision and, in primates, are displaced from the fovea, the region with highest acuity. Perhaps the pecten represents a similar adaptation for achieving higher visual acuity throughout the retina in birds.

Retinal structure. The avian retina is unusually thick and well developed, especially in diurnal birds, with many complex interconnections. The actual visual receptors of birds, as of all vertebrates, are of two kinds: rods and cones. The former are generally associated with good sensitivity to low illumination, relatively poor acuity, and imperfect or no colour vision. Nocturnal birds have a great preponderance of rods in their retinae. Cones are associated with good visual acuity at high light levels and with colour vision, but with a low light sensitivity—in other words, with poor dark adaptation. Diurnal birds have retinae in which cones account for up to 80% of the photoreceptors; in different species larger or smaller areas contain only cones, according to their visual requirements. In contrast to mammals, all cones contain a coloured oil droplet through which light must pass before reaching the sensitive outer segment. Moreover, at least two morphologically distinct classes of cone have been identified in the bird retina: single cones and double cones. The double cone consists of a normal cone that partially surrounds an 'accessory' cone, which often lacks an oil droplet. The nervous impulses from the light-stimulated photoreceptors pass through several layers of nerve cells and are eventually transmitted to the visual centres of the brain along the optic nerve. Although the density of photoreceptors in the bird eye remains relatively uniform compared to that in the human eye, the numbers of cells in each of the other neural layers vary considerably across the retina, especially in the inner nuclear layer. In fact, the cell density in the inner nuclear layer is disproportionately high in most birds, suggesting that correspondingly more complex levels of sensory processing occur in the avian retina. In all vertebrate eyes, particularly thick retinal regions, called areas, contain the highest density of cells and are believed to be the sites of best visual acuity. Mammals, as well as birds and reptiles, usually have one such area near the centre of each eye, but in most birds, which have more laterally oriented eyes, the retina also contains a second visual area for looking forward. These two areas are sometimes joined by a ribbon-like area, or 'visual streak', that runs along the horizontal axis of the eye.

Refraction and accommodation. In the avian eye, as in the eyes of all other terrestrial vertebrates, the major structure of refraction is the cornea; the greatest change in index of refraction occurs at the cornea as light passes from the air into the eye. The lens plays a much smaller role in refraction but serves as the primary means for changing the refractive state of the eye during accommodation. Earlier reports suggested that birds with laterally directed eyes were farsighted in the central visual field on either side of the head and nearsighted in the frontal field. More recent studies on the refractive state of the eye in several species (e.g. pigeon, chicken, ducks, owls) have demonstrated that the bird eye is in fact emmetropic, i.e., shows no refractive error, in either the central or frontal horizontal visual fields. In the pigeon, as in the lateral-eyed rabbit, the eye shows both no refractive error and substantial correction for astigmatism for more than 90° along the horizontal axis of the visual field. Such remarkable wide-field corrections are consistent with the idea that lateral eyes represent an adaptation for acute panoramic vision, which is used to watch the horizon for predators. Myopia in the frontal horizontal field would be an obvious disadvantage when flying, but some evidence has been found for nearsightedness in the pigeon's 'pecking field', which is located in front of the head but at least 30° below the beak; this lower part of the frontal visual field corresponds to a second visual area in the pigeon retina, i.e., the 'Red Area', which has an especially high density of photoreceptors.

All fast-flying birds would need an efficient means of quickly altering the focus of the eye, but the power and range of accommodation in birds appears to have been overestimated by early workers; the eyes of pigeons and some ducks, for instance, are only capable of the maximum accommodation of an adult human (5–8 Diopters), not two to three times this range as originally claimed. The ability of pigeons and other birds to examine objects from very short distances may result from the built-in nearsightedness of the frontal field rather than particularly high powers of accommodation. As in other vertebrates, this accommodation is achieved by direct effects of the ciliary muscle on the shape of the lens. In human accommodation, however, the normal sideways pull on the lens is released so that it can take its natural, more highly curved shape, whereas in birds the lens is apparently squeezed into a more convex form (see also MUSCULATURE). Birds' lenses are softer than human ones, and the intraocular muscles concerned with accommodation are more highly developed. These muscles are attached to the ring of scleral ossicles, which support the eye and keep it rigid against their pull.

Adaptations to aquatic habitat. In the air a large part of the refractive power of the eye is produced by the curved surface of the cornea, and the effect of this is lost underwater. The eye may be an efficient organ in the air and virtually useless underwater, and this seems to be true of such plunging birds as terns or pelicans which spot their fish from above, dive blind, and often miss. On the other hand, many birds—penguins, cormorants, diving ducks, divers and auks—have truly amphibious vision. Adaptations for aquatic vision vary in different species. In the Adélie Penguin *Pygoscelis adeliae*, the refractive effect of moving from air into water is minimized by the existence of a relatively flat cornea. Cormorants, dippers, and diving ducks compensate for the refractive loss of the cornea by means of a very large accommodative ability (at least 50 Diopters). Apparently the lens in these species is especially soft, and the contraction of the ciliary muscle pushes the malleable lens through the constricted iris disc (Fig. 4); the central anterior surface of the lens actually bulges through the pupil, resulting in a marked increase in its curvature (and refractive power).

Visual acuity. Visual acuity (the ability to distinguish fine details) should not be confused with visual sensitivity, which is the ability to distinguish small quantities of light as such and is highly developed in all nocturnal birds. The two faculties require rather differently constructed eyes and retinae, and it is rare for an eye to have both well developed. Visual acuity is a property first of the optical apparatus of the eye and secondly of the retinal structure. These can be usefully compared to the lens and film of a camera, the former determining the accuracy of the image and the 'grain' of the latter the fidelity with which the image can be

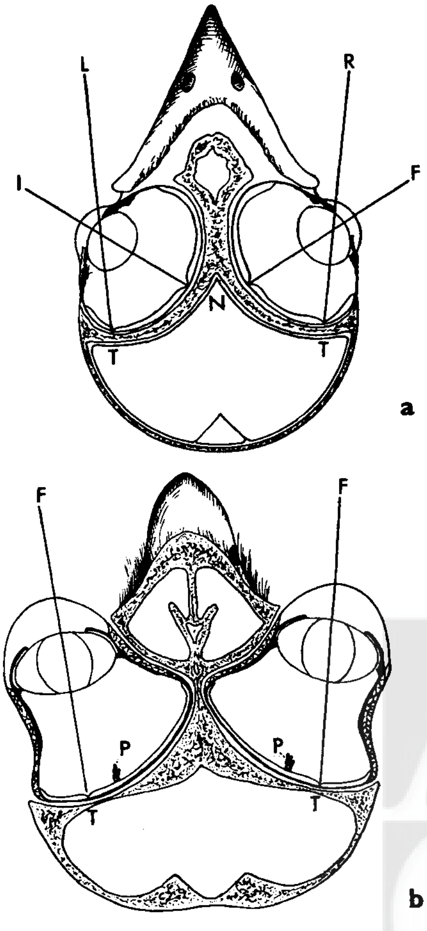

Fig. 3. Bird foveae.
(a) Two foveae of the Tree Swallow *Tachycineta bicolor*; NI and NF visual axes of the central foveae, used for monocular vision: TL and TR visual axes of the lateral foveae, used for frontal or binocular vision.
(b) Single lateral foveae of the Great Horned Owl *Bubo virginianus*, used for binocular vision. (After Slonaker).

reproduced. In birds the optical system is very well developed indeed; those birds needing a high resolution at great distances (wing-feeding insectivorous forms, predators in general, and such birds as crows) have eyes as large as possible and a somewhat flattened lens at a greater distance from the retina (Fig. 2b). This arrangement provides a larger image on the retina, while the highly curved cornea and large pupil ensure that plenty of light will enter the eye. At the same time, the retinal structure is specially well adapted for acute vision. All diurnal birds have a predominance of cones over the whole retina, and all have a central visual area from which rods are entirely absent. In addition, most have a small sharply defined pit in the central retina known as the fovea. Although they are not found in the lower mammals, appearing only in the primates and man, foveas are a common feature of the eyes of such sharp-sighted animals as lizards and some teleost fishes. However, the avian fovea is the most highly developed of all, with the possible exception of the lizards, and only a very few species (e.g. domestic chicken) do not appear to have one. At the fovea the retina contains many extremely fine, tightly packed cones; the correspondingly high density of ganglion cells (whose axons form the optic nerve) around the fovea suggests that each cone may be connected, via the overlying retinal nerve cells, to its own fibre of the optic nerve. Such an organization of connections is well designed for acute vision, since each cone can send an independent message to the brain, so making possible the appreciation of very fine detail within the retinal image. Some authorities think that the actual shape of the pit produces a slight magnification of the image in this region, thus further increasing visual acuity; others believe that it aids in the perception of moving objects. Most likely, the foveal pit results from the need to remove the especially thick overlying layers of retina that would otherwise degrade the optical quality of the image at the photoreceptors. Most birds have their eyes placed laterally in the head. Because the fovea is located near the centre of the retina, this lateral orientation of the eye (and the small range of eye movements in many birds) means that the most acute vision is usually to the sides; the two foveas can not be used for looking straight ahead. However, many birds—hawks, eagles, hummingbirds, bitterns, kingfishers and various passerine species including swallows—that are especially well equipped visually, and particularly those that hunt on the wing and need a good distance judgement, have a second fovea placed in a posterior temporal visual area; this can apparently be used in conjunction with the other eye for binocular vision (Fig. 3).

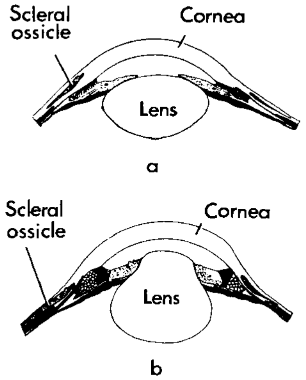

Fig. 4. Accommodation in the Cormorant *Phalacrocorax carbo*.
(a) Unaccommodated;
(b) Accommodated. Note the change in shape of the lens. (After von Hess).

Some birds have, in addition to a central fovea, a ribbon-like central area running across the retina in a roughly horizontal direction. Careful studies of 5 species (Lapwing *Vanellus vanellus*, Oystercatcher *Haematopus ostralegus*, Coot *Fulica atra*, Snipe *Gallinago gallinago*, and Herring Gull *Larus argentatus*) have shown that although the orientation of the bill is very variable between these species when the head is carried in its normal position, this central retinal area, as well as one of the semicircular canals in the ear labyrinth, is always horizontal. The ribbon-like area (known as a 'visual streak' in mammals) consists of an especially high density of photoreceptors and other cells and presumably is designed to improve the acuity of panoramic vision; possibly this retinal structure also gives a plane of reference in relation to the horizon. Such a ribbon-like area has never been found in forest-dwelling species or in birds of prey, but mainly in birds of the open spaces, such as seabirds.

Even casual observation of birds in their natural environment strongly suggests that many granivorous birds as well as predatory species have exceptionally high visual acuity. Indeed, physiological optics studies have revealed that the visual acuity of hawks and falcons could be as much as three times higher than man's, a prediction recently confirmed by behavioural measurements of visual acuity in the American Kestrel *Falco sparverius*. On the other hand, many behavioural studies indicate that the visual acuity of granivorous birds, such as the pigeons, may even be lower than that of man. This evidence has led some workers to take issue with the generally held belief that the visual acuity of birds is very much greater than that of other animals, but it is important to remember that laboratory tests do not necessarily yield an accurate assessment of an animal's best visual capabilities. Biological constraints on learning, specifically those concerned with the location of stimuli in the visual field, may be involved rather than visual acuity *per se*. However, maximum visual acuity is at least partly limited by the absolute size of the eye, so perhaps some smaller birds will turn out to have lower acuities than primates such as man with considerably larger eyes. The other constraint on acuity is the density of photoreceptors (especially cones) and other retinal cells, and many birds appear to have compensated for their smaller eyes by having exceptionally high cell densities. That these densities remain high throughout a larger part of the retina than is true in most mammals has led to the suggestion that visual acuity in birds is greater over a larger part of the visual field; perhaps this facilitates a more rapid assimilation of detail in the visual world.

Adaptations to nocturnal habitat. The majority of birds are predominantly diurnal and become inactive at night. There are, however, great variations in the apparent ability of different species to see at low illuminations; some roost much earlier in the evening than others, which go hunting well into dusk. The retina of a bird active both by day and night, the Manx Shearwater *Puffinus puffinus*, has been compared with that of a purely diurnal petrel, the Fulmar *Fulmarus glacialis*, and has been found, not unexpectedly, to have an increased number of rods. Even such diurnal birds as the pigeon and domestic fowl have powers of dark adaptation about as good as man, although the process is slow, taking nearly an hour or more to manifest itself in the pigeon as opposed to 10 minutes in man. In the Starling *Sturnus vulgaris*, Buzzard *Buteo buteo*, and Kestrel *Falco tinnunculus* the process is slower still, but when it is complete, these birds appear to have useful night vision. In all these species, however, the relatively low density of rods in the retina means that their acuity at dim light levels will be poor.

The birds that have made the most successful visual adaptation to nocturnal living are, of course, the owls. In these the whole eye has become elongated (Fig. 2c) by the development of an enormously enlarged cornea, pupil and lens. By this means the amount of light entering the eye is increased so that a brighter image falls on the retina. Such an optical arrangement entails a relative decrease in the size of the retinal image, but the large absolute size of the eye helps to minimize this disadvantage. In addition, the frontal position of the eyes, which provides better and more extensive binocular vision than is usual in birds, not only provides the basis for good perception of distance but probably also improves sensitivity through binocular summation of the light coming from the environment. (Frontal eyes are often present in nocturnal animals and in abyssal fishes.) Such owls as have been examined have a great predominance of rods in their retinae, and the outer segments are especially long. These retinal features increase both the owls' visual acuity at low light levels and their sensitivity to light. Not surprisingly, all owls have excellent powers of dark adaptation. Although some owls (e.g. Tawny Owl *Strix aluco*) are seldom seen during the day, others such as the Pygmy Owl *Glaucidium brasilianum* and the Burrowing Owl *Athene cunicularia* can hunt quite successfully in the daylight. Still other species (e.g. Hawk Owl *Surnia ulula*) are largely diurnal but also will hunt on the wing at night; they have silent flight and very good hearing and may rely more on this sense than on vision.

Retinal pigments and oil droplets. The outer segments of the photoreceptors (rods and cones) contain the visual pigments that are responsible for the absorption of light incident upon the retina. With the development of microspectrophotometry, it has recently become possible to determine with precision the absorbance spectrum of the visual pigment in a single isolated photoreceptor cell. From studies on a number of species—e.g. chicken, pigeon, Rook *Corvus frugilegus*, Laughing Gull *Larus atricilla* and Tawny Owl—one rod and three classes of cone visual pigments have been identified in birds. The three cone pigments, which are sensitive to red, green and blue light respectively, provide the basis for trichromatic colour vision similar to that in man and other primates. Behavioural evidence in the pigeon, however, further implies the existence of a fourth cone visual pigment that is sensitive to near ultraviolet light, suggesting that birds may in fact be tetrachromatic.

Brightly coloured oil droplets, contained within most cones but not within rods, are a striking feature of the retina of diurnal birds. High concentrations of carotenoids are responsible for the colour of these oil droplets, which are situated just above the outer segment of the cone. Depending on the specific types and amounts of different carotenoids in the oil droplet, only light above a particular 'cut-off' wavelength is able to reach the visual pigment in the outer segment. Oil droplets in birds are highly variable in colour, size and location within the retina. Using microspectrophotometry, at least 5 types of oil droplets, characterized by the cut-off wavelength, have been found. Different combinations of visual pigments and oil droplets will obviously result in many cone types, which are distinguishable by their spectral sensitivities. In many birds, the distribution of different oil droplets, and therefore cone types, is not uniform. The dorsal temporal part of the pigeon retina, for instance, is dominated by single cones with red and orange droplets; this 'Red Area' is clearly distinct from the remainder of the retina, i.e. the 'Yellow Field', which contains mostly double cones with yellow oil droplets. The visual functions of oil droplets are believed to include the reduction of chromatic aberration, a role normally played by the lens in other vertebrates, and the fine-tuning of colour vision by the selective filtering out of shorter wavelengths. Behavioural studies of the pigeon have shown that the Red and Yellow areas of the retina have significantly different spectral, i.e. colour, sensitivities. Such differences in colour vision are probably related to the visual tasks performed by these two retinal areas, which view different regions of the visual field.

Colour vision. All diurnal birds appear to possess colour vision, although it is thought that most nocturnal ones do not. This is reflected in the gaudy plumage of many diurnal species and the drab appearance and lack of colour in the plumage of many nocturnal birds. In view of the many different types of visual pigment and coloured oil droplets found in the retina, the colour vision of diurnal birds may well be more complex than in all other vertebrates, including man. Numerous behavioural studies have demonstrated that pigeons and chickens, at least, have colour vision; that is, these birds are able to distinguish stimuli on the basis of their wavelength content. Although early evidence indicated that a bird's ability to distinguish one hue from another was similar to that in man, more recent work using electrophysiological as well as behavioural techniques strongly suggests that colour vision in birds may be based on as many as four or five primary colours rather than the three found in man. The potential for such complexity lies in the different combinations of four visual pigments and five coloured oil droplets; at least six types of cone have been identified on the basis of their spectral sensitivity. Another important consideration is that the pure 'colours' perceived by the pigeon, and presumably by other diurnal birds, do not necessarily coincide in terms of wavelength with the basic colours visible to the human eye. For example, two of the peak wavelength sensitivities in the pigeon correspond to colour mixtures, i.e. blue-green and greenish-yellow, in the human spectrum. Moreover, depending on the relative frequencies of various cone types in different areas of the retina, colour vision is correspondingly altered for different parts of the visual field. In fact, the predominance of certain oil droplet colours in the eyes of various species of birds has been correlated with the background colour of the environment or the need to make difficult discriminations between similarly coloured food types. The greater complexity and sensitivity of avian colour vision suggests that the birds' view of the world may be considerably different from our own.

Ultraviolet and polarized light. Human colour vision is limited to a narrower range of the wavelength spectrum (400–750 nanometers) than the total range available for vision (300–800 nanometers). Limits on spectral sensitivity are determined by both the visual pigments and the parts of the eye and retina through which incident light must pass before reaching the pigments. Although in man the yellowish lens filters out near ultraviolet (UV) and violet light to reduce chromatic aberration, the lens in birds is transparent to these same wavelengths; the coloured oil droplets apparently serve to minimize chromatic aberration at the retinal level. Behavioural studies have confirmed that the pigeon and several species of hummingbirds do indeed see UV light (325–360 nanometers). Other evidence also suggests that there is a fourth UV-sensitive pigment in the avian retina; cones with this pigment possess a clear oil droplet that presumably allows UV light to reach the pigment. The adaptive significance of this sensitivity to UV light is unknown. Many flowers and leaves are known to have UV-specific colour patterns; although clearly relevant to hummingbirds, the advantage of UV colour vision is less obvious in other birds.

Very recently, sensitivity to polarized light has also been demonstrated in the pigeon. Apparently this ability not only involves the detection of changing axes of polarization but also the discrimination of (and orientation to) a fixed axis of polarization. The pattern of polarization in the sky varies during the day strictly in accordance with the position of the sun, and many migrating birds, as well as homing pigeons, are known to use the sun's position as a compass in navigation. Perhaps the ability to detect polarized light eliminates the need directly to visualize the sun when determining its location in the sky. Interestingly, pigeons can only discriminate the axis of polarized light when the lighted area is large and located in the upper visual field, which normally contains the sky. The inferior Yellow Field of the pigeon retina views this part of the field and is dominated by double cones, suggesting a role for this special type of receptor in polarized light vision.

Visual fields, binocular vision, and stereopsis. Birds (including even the owls) have eyes that to a greater or lesser extent are laterally oriented in the head (Fig. 3). Yet the obvious need to see straight ahead while flying appears to have resulted in at least some overlap between the visual fields of the two eyes in all species. The size of this binocular field is very small in most granivorous birds (10°–30°), larger in insectivores, hawks

Short-eared Owl *Asio flammeus* showing binocular vision. (*Photo: E.J. Hosking*)

and other predatory birds (35°–50°) and, of course, most extensive in the owls (60°–70°). The lateral orientation of the eyes and the limited range of eye movements necessarily means that the avian central fovea is restricted to a monocular view of the world. Even birds-of-prey are primarily monocular in terms of the relative sizes of their monocular and binocular visual fields; in fact, recent behavioural tests of visual acuity in the American Kestrel suggested that these birds usually turn their head to one side and use one central fovea, rather than both temporal (i.e. binocular) foveas, when making a difficult discrimination. Although the two temporal foveas found in the eyes of some insectivores and predatory birds are probably used for binocular vision, the second visual area in the eyes of other birds is not necessarily used in the same way. For example, the region of the Red Area of the pigeon that contains the highest density of cells views an inferior portion of the visual field that lies as much as 30° to the side (i.e. outside the binocular field); the Red Area is thus well adapted for examining the ground for food when the head is held in its normal position.

Birds must be capable of precise judgements of distance when flying and landing. While this is especially true for birds-of-prey that dive at high speeds for prey on the ground, judging distance may also be important for granivorous birds when pecking for food. In man the most accurate method of judging distance and solidity is by means of stereoscopic vision. This depends on the simultaneous appreciation of the slightly, but not too widely, dissimilar images from corresponding points on the two retinas. For this to be possible, it is obviously essential to have binocular vision, i.e. the faculty of viewing an object with both eyes simultaneously. Stereopsis, the perception of the two somewhat disparate retinal images as a single 'fused' image, involves the integration of the binocular inputs by visual centres in the brain. Unlike many mammals, the two optic nerves of birds are completely crossed at the chiasm; each side of the brain receives inputs from only one eye. Recent anatomical studies of the Burrowing Owl *Athene cunicularia*, however, have revealed that binocular integration of visual inputs from the two eyes does occur at a still higher level of the brain in a telencephalic structure called the visual Wulst. The organization of the Wulst appears to be very similar to that of the striate cortex, which mediates stereo vision in mammals. Electrophysiological studies of the Barn Owl *Tyto alba* have identified in the Wulst a large population of neurons selective for binocular disparity, a necessary prerequisite for stereopsis, and stereoscopic depth perception has recently been demonstrated behaviourally in the American Kestrel. Although found in the brain of all birds, the Wulst varies considerably in size. Indeed, comparative studies indicate that the relative size of the visual Wulst is directly proportional to the extent of the binocular visual field. The fact that binocular neurons are also present in the smaller Wulst of the pigeon strongly suggests that even birds with a small binocular field are capable of some degree of stereoscopic depth perception. Preliminary behavioural evidence that pigeons use binocular cues in judging distance has been reported.

The variation in size of the binocular field appears to correlate with the need for better and more extensive stereopsis. Yet the more common lateral orientation of the eyes in birds indicates that there is a countervailing selection pressure for maximizing the total extent of the visual field in the absence of head or eye movements. Presumably the resulting panoramic view of the world facilitates the detection of predators while foraging for food; aerodynamic constraints on the shape and size of the head may also play a role in determining the orientation as well as the general structure of bird eyes.

For birds that have limited binocular vision and appear to be very dependent on monocular information, a number of monocular cues are available for judging distances—such as size, overlapping contours, and parallax. Moreover, other animals, such as chameleons and toads, are known to determine the distance to an object of interest monocularly by using the precise accommodative efforts required to bring its image into focus; camera lenses or rangefinders use exactly the same principle. The extent to which birds use any or all of these cues is unknown. Some workers have pointed out that the conspicuous head bobbing, shown by many birds when they walk, may provide the basis for a kind of monocular 'stereopsis'. Whereas in binocular stereopsis two slightly different images are received by the brain simultaneously, the two disparate views seen by the same eye before and after a head bob might be integrated sequentially to yield a fused image of an object. Much work on avian vision remains to be done, however, before we have an adequate understanding of the bird's eye view of the world.

Visual behaviour. A thorough knowledge of the vision of a particular animal often makes possible a more complete understanding of its behaviour. Moreover, a detailed comparison of visual systems in a variety of species may provide insights into specific behavioural differences between groups of animals.

Head-bobbing is a striking behaviour of many birds. When walking, pigeons, chickens and numerous other common birds thrust the head forward in a rapid movement, hold it stationary while the body catches up and then thrust it forward again. The head appears to 'bob' because it moves backward and forward with respect to the body, but in reality, it moves only forward in the environment. Contrary to earlier suggestions that head bobbing is mechanically driven by the stepping movements of the legs and may aid balance, more recent work has demonstrated that this peculiar behaviour is totally under visual control. Movement of the visual world alone will cause the bird to bob its head.

When a man walks forward, the frontal placement of his eyes ensures that the visual world remains relatively still. Most birds, however, have laterally oriented eyes, so as they walk forward, much of the visual world moves backwards. Experimental evidence suggests that the stationary phase of the head 'bob' is an adaptation to allow a motionless view (with the central fovea) of the bird's surroundings; the forward thrust is especially rapid in order to maximize the duration of this fixed view. While flying, birds presumably use their frontal vision, which will operate similarly to man's and/or take advantage of the fact that the visual world will move more slowly because it is more distant.

Another curious but characteristic behaviour of many birds is called 'rapid peering', i.e. the side-to-side motion of the head while viewing an object or foraging for food. In many mammals, each eye sends information to both sides of the brain, whereas in birds, each eye projects only to half of the brain. Indeed, behavioural studies indicate that when a pigeon is trained to make a visual discrimination with one eye only and then forced to use the other eye, the bird often behaves as if it has never 'seen' the problem before. Perhaps rapid peering simply results from the need for a bird to see an object with each eye so as to store the necessary information in both halves of its brain.

See photo NOCTURNAL HABITS. (K.T.) J.T.E.

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VISITOR: alternatively 'visitant', meaning present in the area under reference only at certain times of year, the term being applied to a species, subspecies, population, or individual bird as the context requires. Thus, there are 'summer visitors', 'winter visitors', 'visitors on migration' (='transients'), and 'occasional visitors'; but these terms indicate merely local status and are meaningless except in relation to a stated area, a summer visitor in one place being necessarily a winter visitor somewhere else (see MIGRATION; also VAGRANT).

VISORBEARER: substantive name of *Augastes* spp. (for family see HUMMINGBIRD).

VITAMIN REQUIREMENTS: see NUTRITION.

VITELLUS: the egg-yolk (see EGG).

VITREOUS BODY: part of the eye (see VISION).

VOCALIZATION: sound produced by the special vocal apparatus, which in birds is the SYRINX. Vocalizations are traditionally divided into calls and songs, and although there are considerable difficulties in exactly defining the two terms, the distinction still remains in common use. Generally, calls are short, simple and produced by both sexes at any time, whereas songs are long, complex and produced only by males in the breeding season. There is also a phylogenetic trend, in that songs are more common and complex amongst the most recently evolved group of birds, the passerines, and in one sub-group in particular, the Oscine songbirds. The scientific study of vocalizations has been revolutionized by the advent of light, portable tape recorders used in conjunction with parabolic reflectors or sensitive gun microphones. A major breakthrough in analytical techniques was the application of the sonagraph pioneered by W.H. Thorpe. By plotting frequency (in kiloHertz) against time (in seconds) a clear picture of an individual sound could be displayed as a sonagram (Fig. 1). Sonagrams have since become the standard method of both analyzing and illustrating vocalizations in scientific ornithology. The sonagraph has to a certain extent been replaced by a new generation of more modern frequency spectrum analysers, which display sonagrams instantaneously on a Visual Display Unit screen before printing out on a hard copier. The tremendous saving in time means that hundreds of songs can be quickly examined, or whole populations screened for particular song types.

Calls and their functions. Calls are often given in quite specific contexts, such as fighting or courtship, which makes their functional interpretation relatively easy. The call itself may affect the behaviour of the receiving individual, again throwing some light upon its probable function. Calls can be thought of as expressing a tendency to behave in a certain way, and transmitting that information to other individuals who may modify their own behaviour accordingly. By studying different calls in relation to behaviour it is possible to build up a vocabulary of calls for a species. Passerines seem to have a vocabulary of up to 20 different calls, whereas gulls have about half that. There are calls for threat, courtship, flight, alarm, begging and so on, to cover most aspects of social behaviour.

Some species have calls which serve more specialized or unusual functions. Cave-dwelling birds such as the Oilbird *Steatornis caripensis* and the Cave Swiftlet *Aerodramus vanikorensis* produce a series of clicks when flying in the dark. These are special echolocating calls and the birds have developed a form of sonar similar to that possessed by bats. Unlike bats, the bird calls are not ultrasonic, but produced at normal frequencies and so can be clearly heard by humans. Another very special call is that produced by the African Honeyguide *Indicator indicator*. The calling birds lead larger animals to nests of wild honeybees. The nests are broken open by the large animal, and the honeyguides can then feed on any small pieces of honeycomb left. This symbiotic relationship appears to have developed originally between the birds and honey-eating Ratels *Mellivora capensis*. African tribesmen later learned that the persistent calling birds would lead them to honey (see HONEYGUIDE).

A more widespread kind of call which has been the subject of considerable study is the alarm call given by many passerines when a predator such as a hawk flies over. It was Marler (1981) who noticed that calls given by many different species shared the same basic design (Fig. 1). He reasoned that although it may be advantageous for a bird to warn his mate or offspring of impending danger, it was also dangerous for the calling bird to give away his position. The conflict has been resolved by the evolution of special flying predator calls which can be clearly heard, but which transmit a minimum of directional information and are difficult to locate. Birds and humans are thought to locate sounds by binaural comparisons of phase, intensity and time differences. Phase differences are more effective at low frequencies, as the information becomes ambiguous when wavelength is less than twice the distance between the two receiving ears. Conversely, intensity differences are more effective at high frequencies, because the sound shadow formed by the head of the listening bird only operates when the head dimension exceeds sound wavelength. Time differences are effective throughout the frequency range, but are enhanced by interruption, repetition and modulation. The further apart the ears of the listening bird, the more obvious time differences will become. Rough calculations suggest that for a medium-sized bird of prey, a call pitched at about 7 kHz would be too high for detectable phase differences, and too low for an appreciable sound shadow intensity effect. As Fig. 1 shows, this is just the frequency range of the special alarm calls many passerines produce when a real or experimental hawk flies over. Any possibility of binaural time differences are minimized by the almost imperceptible gradual start and finish, modulations are minimal and the calls are not repeated close together. Although these calls are theoretically extremely difficult to locate, recent research has shown that at least some birds of prey can orientate towards their source under experimental conditions (see Lewis and Cole 1980).

Although calls are relatively short and simple, there is now considerable evidence from a number of species that they contain enough information to transmit the identity of a particular individual. Many observers have noted the apparent ease with which parents returning to a densely packed seabird colony manage to locate their own young. Thorpe

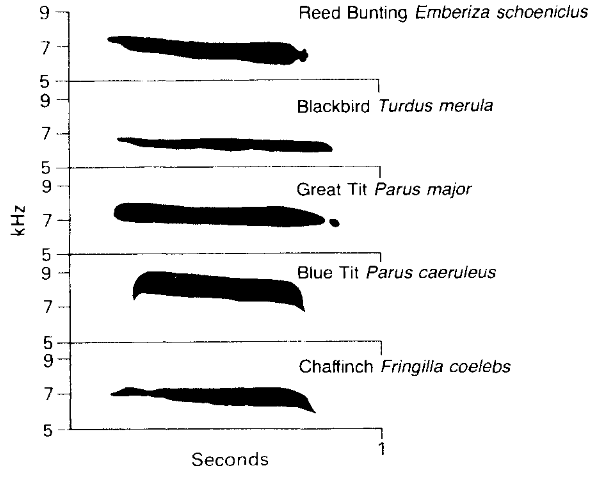

Fig. 1. Calls given by 5 different species when a hawk flies over.

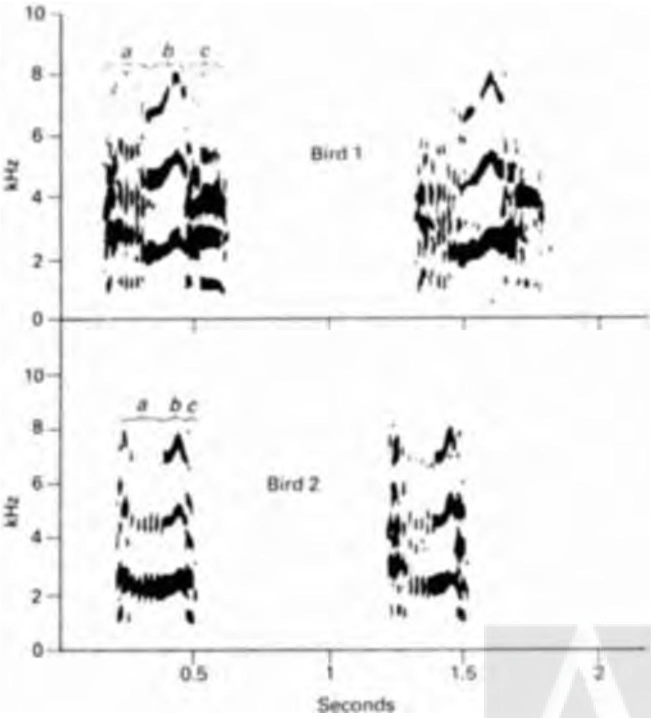

Fig. 2. Individual distinctiveness in successive calls from 2 Sandwich Terns *Sterna sandvicensis.*

and his fellow workers found that in species such as the Sandwich Tern *Sterna sandvicensis* each bird had its own distinctive version of a call. The calls can be divided into three separate segments (a, b and c) which vary consistently in frequency and duration between individuals (Fig. 2). In playback experiments, the young in the nest only reacted to their own parents' call. Similar results were obtained in recognition experiments with mated pairs of Gannets *Sula bassana* and several other species of colonial seabird.

Songs and their functions. The additional length and complexity of songs provides even more potential for information transfer between individual birds. The most obvious function is that of species recognition. Ornithologists use songs to identify a species and it would be surprising if the birds themselves were incapable of similar powers of discrimination. Many experimental studies have confirmed that whilst songs do act as specific signals, the cues which listening birds use for recognition are not necessarily the same as we use. J.-C. Brémond studied species recognition in the European Robin *Erithacus rubecula* by playing back tapes of modified Robin songs to territorial males. Males reacted strongly to normal control songs by approaching the speaker. Normal Robin songs are extremely complex and composed of alternating high and low phrases. Brémond constructed artificial songs consisting of either all high or all low phrases (Fig. 3), and obtained a much weaker response. Even a completely synthetic song constructed of high and low phrases produced from a sound generator achieved a good response. Clearly the basic syntactical rule of high-low-high-low is more important than the actual structure of the notes or syllables themselves. But other species seem to have quite different cues to which they respond. In Bonelli's Warbler *Phylloscopus bonelli*, the actual structure of the syllables themselves is more important, and any tampering with their fine structure renders an experimental song very ineffective. In the Indigo Bunting *Passerina cyanea* the very opposite applies, and individual syllables in songs can be completely reversed without any effect at all. In this species timing seems to be the most important factor, and if intervals between the syllables are lengthened or shortened, a very weak response is obtained during playback. It seems quite clear that there are no general rules of song structure for species recognition, but instead considerable variation from species to species.

Just as each species has a distinctive song, in many cases there is considerable intraspecific variation. For example each male Yellowhammer *Emberiza citrinella* has at least one version of the species song which appears to be individually distinct (Fig. 4). There is some evidence from playback experiments that territorial males learn both the identity and positions of their neighbours from their individual songs and respond very quickly to a strange new bird or a neighbour shifting his territory boundary.

Assuming that male songs carry both specific and individual information, there is still the question of what function or functions the songs may serve. One clue comes from the normal context in which song production occurs, by the unmated male in territory. This suggests the possibility that song has a dual function, as a territorial proclamation directed at other males, and as a sexual attractant directed at females. Much debate concerning the functions of song has centred upon the relative importance of these two aspects in individual species. Considerable evidence for a territorial function comes from a variety of experimental studies. One method is to trap territorial males and mute them by operation, thus stopping normal song production when the males are released back in their territories. In Red-winged Blackbirds *Agelaius phoeniceus* this resulted in the territories of mute males being constantly invaded by their rivals. Another more difficult method is to remove territorial males completely, and replace them with a system of

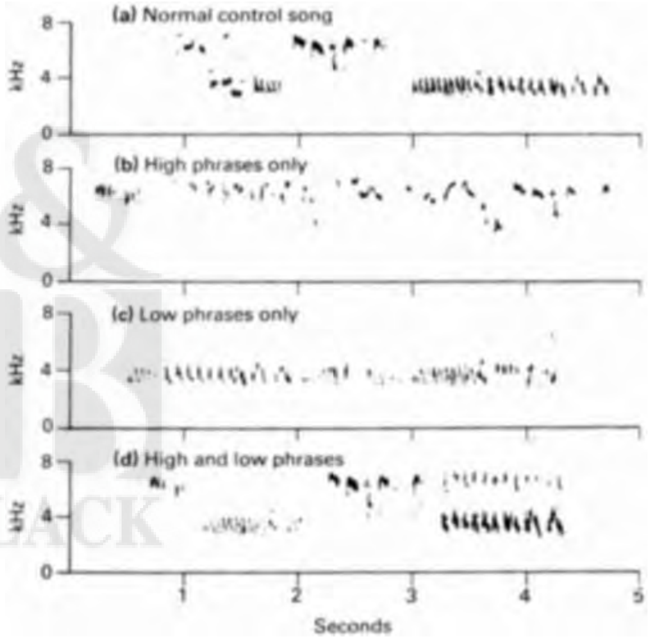

Fig. 3. Normal and artificial Robin *Erithacus rubecula* songs.

Robin *Erithacus rubecula* singing. (*Photo: J.B. & S. Bottomley*).

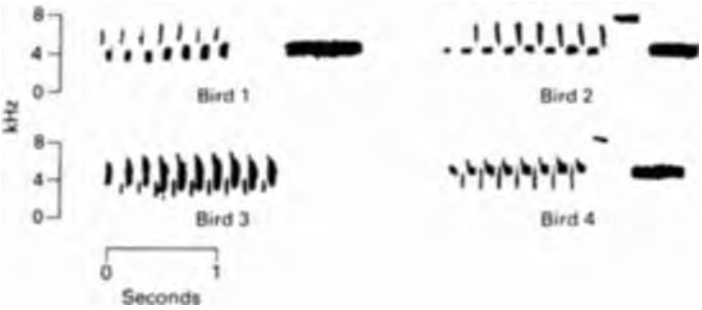

Fig. 4. Individually distinct songs of 4 male Yellowhammers *Emberiza citrinella*.

speakers which broadcast songs or control noises. In the Great Tit *Parus major*, prospecting males re-occupied the control areas several hours before the areas with broadcast song. Both these experiments suggest that song is an important first line of defence and does have some aversive effect upon rival males searching for a territory. But Great Tits like many species have more than one version of the species song, a repertoire of different song types. Each song type is repeated several times before switching to another, and so on. J.R. Krebs has suggested that Great Tits may be practising a subtle form of deceit; by singing in this way the impression is created that there are many more males present in a given area. Listening prospecting males may well decide to try their luck in a less crowded area. Krebs has tested his Beau Geste theory by using a similar speaker replacement technique as before. This time he broadcast a repertoire of song types in one area, and found that it was re-occupied later than an area broadcasting just one song type. It does seem that a repertoire is a more effective territorial proclamation, but there may be a variety of reasons. Switching song types may just prevent habituation, which has also been shown in the Great Tit. Having a large repertoire of song types may permit a resident to match the song of an intruder, indicating to the latter that his challenge is being answered.

Evidence that sexual attraction is the main function of song has been more difficult to obtain. Female songbirds seem to be far too elusive and reticent for field experiments. Much of the evidence is of an indirect nature such as the effect of females upon song production in the male. After the attraction of a female, song production decreases or in rare cases, such as the Sedge Warbler *Acrocephalus schoenobaenus*, ceases altogether. Normal territorial behaviour is continued by visual threat displays and fighting, but the male never sings again. The song structure of the Sedge Warbler also provides a clue in that it is unusually long and complicated. Songs can be up to a minute long and are composed of a variety of syllable types (Fig. 5). Instead of one or several song types, no two songs are alike, each being composed from a repertoire of up to 50 syllable types. C.K. Catchpole has suggested that such complexity is the acoustic equivalent of the Peacock's train, an extravagance whose only possible function could be to influence female choice. This was tested in the field by recording all the males in a population and estimating their repertoire size. It was found that the males with the most complicated songs obtained females before their rivals with less complicated songs. Similar results were obtained for another species well known for its song complexity, the Mockingbird *Mimus polyglottus*. There is also some evidence that more complicated songs of male Canaries *Serinus canaria* are more effective in stimulating the reproductive physiology and behaviour of females.

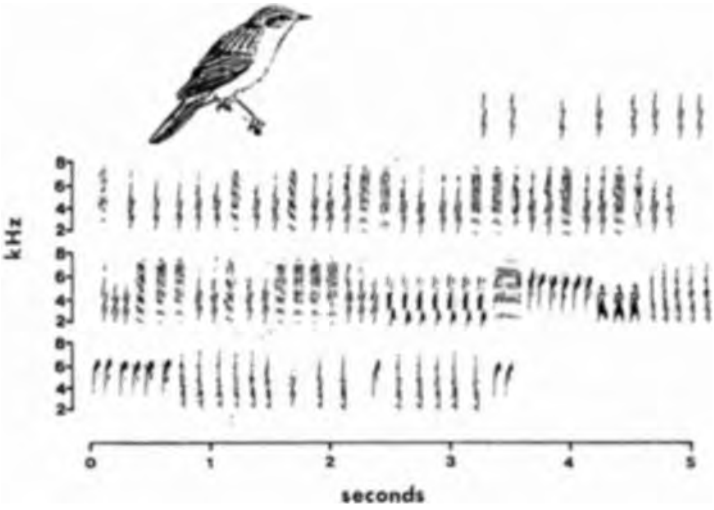

Fig. 5. The complex structure of one male Sedge Warbler *Acrocephalus schoenobaenus* song.

Grasshopper Warbler *Locustella naevia* singing on exposed perch. (*Photo: K. Carlson*).

An important point is that sexual and territorial functions are not mutually exclusive, and for many species a duality of function may well be built into their song structure. However, clues to function are more likely to be found either in species at one extreme of the functional spectrum, or by comparative studies on closely related species with differing song structures. The Sedge Warbler is a case in point, where the long, complex song and its use in sexual attraction seem linked. Catchpole then investigated song structures in other *Acrocephalus* species, and found major differences. The 4 monogamous species (including the Sedge Warbler) all have long complex songs for mate attraction, as females appear to select their mates directly on aspects of male quality including song complexity. The 2 polygynous species defend much larger territories, and as the female is likely to be left feeding the young alone, she selects her mate indirectly through territory quality. As a result the polygynous species have developed songs for territorial defence, and they are much shorter and simpler. One of these 2 species, the Great Reed Warbler *Acrocephalus arundinaceus*, is a partial polygynist, and this is also reflected in song structure. The unmated male has a longer version of his song which he uses to attract females. When he is paired, he detaches this longer and more elaborate section, and is left with a short, simple song which playback experiments have confirmed is more aversive to rival males. How far these findings can be related to other groups is not yet clear, but it does seem that long complex and variable songs are more likely to function in sexual attraction, and short, simple and stereotyped songs are more likely to have a territorial function.

Duetting. Duetting seems to be another case where the complexity of a song is increased by including contributions from two individuals, usually a mated pair. The songs produced are generally quite stereotyped and the two contributions so well co-ordinated that to the listener it seems to be produced by only one bird. Duetting has been found particularly in groups of tropical birds such as African shrikes of the genus *Laniarius*. In some species such as *L. erythrogaster*, the male produces one syllable and the female adds another in a simple alternating system called antiphonal song. In other cases, such as *L. funebris*, syllables are combined in a more complex sequence as shown in Fig. 6. The precise timing of the different contributions to within hundredths of a second is a striking feature of duetting between mated pairs. The functions of duetting remain obscure, but there are a number of clues

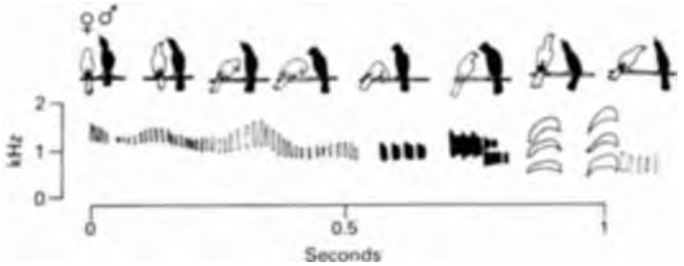

Fig. 6. Duet produced by a pair of African shrikes *Laniarius*.

from the distribution, ecology and behaviour of duetting birds. They are often tropical birds who live in dense vegetation and have high mate and territory fidelity. Perhaps duetting has developed to maintain contact between the mated pair under such conditions. However, in some species the mated pair sit close together and direct their loud duets as territorial proclamations to other neighbouring pairs.

Song development. It was Thorpe (1961) who pioneered the scientific study of song development in his classic work on the Chaffinch *Fringilla coelebs*. Until then, it had often been assumed that birds inherited their complex song structures. Thorpe was able to show the importance of early learning by raising nestlings in sound-proof chambers where they were deprived of external auditory feedback. The simple isolated song the birds eventually produced was nothing like the complex structure of normal adult song. How Chaffinches normally develop their song structure was also studied with captive birds. After fledging, a rather loose, rambling kind of quiet song, called early subsong, appears (Fig. 7a). It ceases in winter, but reappears in spring as a more complex version called late subsong (Fig. 7b). When the young male takes up territory and is exposed to the songs of nearby males the song structure becomes more recognizable as a Chaffinch song divided into three distinct phrases with a terminal flourish. At this stage it may still be changed and is called plastic song (Fig. 7c). When changes no longer occur and the structure becomes quite stereotyped it is called full song (Fig. 7d). In the Chaffinch and many other species the song will now remain unaltered for life.

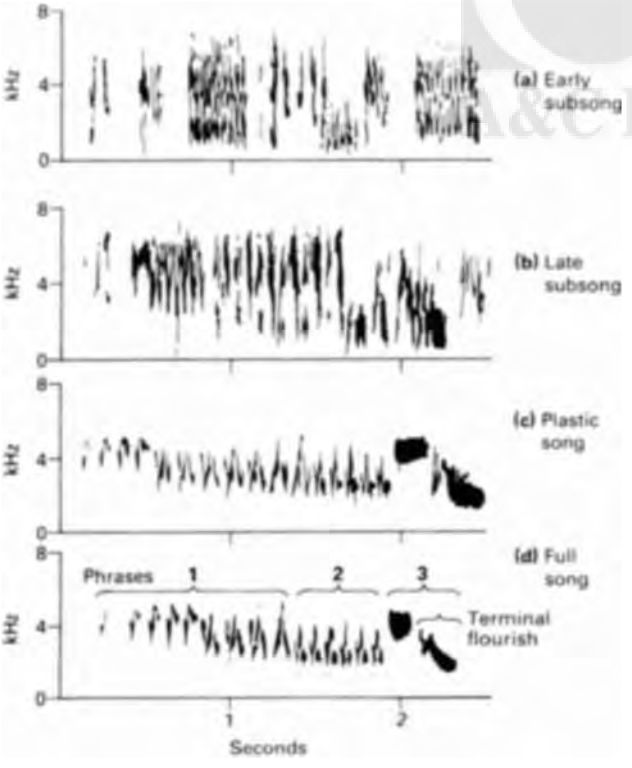

Fig. 7. Normal song development in the Chaffinch *Fringilla coelebs*.

By isolating his birds, Thorpe had prevented them from learning any detailed structure from other birds throughout this important first year. When he raised nestlings in groups, they tended to develop slightly more complex songs as they were able to copy a few more elements from each other's impoverished songs. Young males taken from the wild in autumn and then isolated subsequently developed almost normal songs in the spring, suggesting that learning starts at a very early stage. Later work established that just hearing playback of recorded songs at this early sensitive stage is enough to enable later development of full song. Another interesting point is that the bird is capable of storing some sort of model of full song structure as a neural template for several months before starting to sing in the following spring. The importance of auditory feedback was confirmed when F. Nottebohm carried out deafening experiments on Chaffinches at various stages. The difference is that this particular technique removes any auditory feedback the bird receives from his own songs, however inadequate they may be. Nestlings deafened at an early stage produced noises less structured than Thorpe's isolated but intact birds. When adult birds were deafened, however, they were able to retain their full song structure for several years. The basic concept of an early sensitive period of song learning in the first year, and then no further significant changes is now well established, but there are some exceptions. It is claimed, for example, that Canaries and Red-winged Blackbirds are both capable of adding to their repertoire in later years. There is obviously considerable interspecific variation in the length of the sensitive period for early learning. Even in the Chaffinch, the end of the sensitive period may not be just age-dependent. If a juvenile male is castrated before coming into song, then the ending of the sensitive period is delayed for another year as it is largely under hormonal control. When and where a young bird actually learns its song may be controlled by a number of factors which confer considerable flexibility in the final composition of a song type repertoire. For example, species or individuals which hatch early and are relatively sedentary will end up with songs learned from parents or neighbours in the natal area. Those which hatch late may be too late to hear local songs, and if they disperse to other areas will inevitably copy the songs of their new neighbours.

Hazel Grouse *Bonasa bonasia* male on song perch. Note feathered legs. (*Photo: A. V. Andreev*).

Finally, there remains the question of constraints and selectivity in song learning. If birds merely learned any acoustic stimulus then there would be no such thing as a species song. Most species have therefore evolved song-learning mechanisms which have built-in constraints imposing some control upon what can and cannot be learned. This selective learning was also revealed by Thorpe during his Chaffinch experiments. Having used recordings to tutor young birds during the critical period with normal Chaffinch song, he also tried using a number of artificial and alien songs as well. However, these were only successful if their characteristics were similar to those in Chaffinch song. For example, the Tree Pipit *Anthus trivialis* has a song which sometimes resembles that of the Chaffinch and young birds tutored on this eventually produced quite a reasonable imitation. Real Chaffinch songs re-articulated so that the terminal flourish appeared in the middle instead of the end were also used, and the young birds were able to learn these extremely well.

Marler (1981) and his group have investigated in some detail the basis of selective learning in Song *Zonotrichia melodia* and the Swamp Sparrows *Z. georgiana*. The songs of the 2 species differ particularly in temporal organization. Swamp Sparrows have a fairly regular, slow trill, whereas Song Sparrows have a more complex pattern of different fast and slow sections. Marler anticipated that these differences in temporal patterning might form the basis for any selective learning and to test the hypothesis constructed a series of artificial songs with which to tutor young Swamp Sparrows. These included Swamp Sparrow-like patterns, which were sequences of identical elements at a steady rate, and Song Sparrow-like patterns which had the more complicated structure of at least two different fast and slow parts. The young males were tutored with the various songs twice a day between the 20th and 50th day after hatching, within the critical period for this species. When they eventually came into song several months later, only Swamp Sparrow songs had been learned. The young Swamp Sparrows had rejected Song Sparrow elements even when presented in Swamp Sparrow-like patterns, and the selective learning was clearly based upon the specific structure of the elements, not their temporal patterning as first thought. By fostering Swamp Sparrow eggs into Canary nests, Marler also demonstrated that this early disposition for selective learning occurred without the possibility of earlier auditory experience. The experiments were repeated with these more thorough isolates who had no opportunity to hear their species song even as embryos. A similar pattern of results confirmed what appears to be an inherited basis for selective learning in this species.

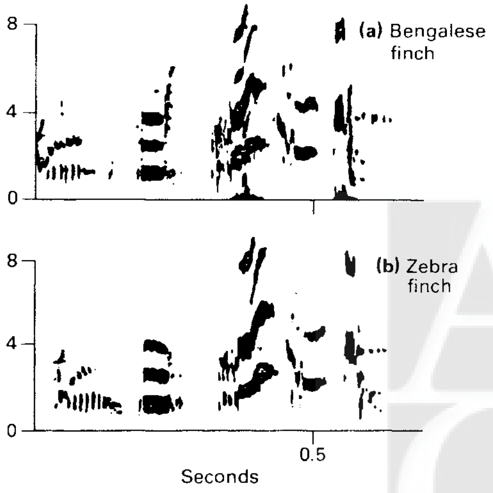

Fig. 8. Song of a Bengalese Finch *Lonchura striata* foster father and the young Zebra Finch *Poephila guttata* it raised.

However, not all species are subject to the same type of constraints, as shown by K. Immelmann in his work on tropical grassfinches such as the Zebra Finch *Poephila guttata*. The advantage of working with Zebra Finches is that in captivity they can be readily fostered upon other closely related species such as the Bengalese Finch *Lonchura striata*. Single eggs of one species were added to the clutch of another species and the brood reared in a sound-proof cage. At various stages the fostered young were then isolated in other sound-proof cages until their song developed. Young males separated after 80 days invariably developed the song of their foster-father even though he was a quite different species. Just how complete and accurate the copying is can be seen from the song of a young Zebra Finch raised with a Bengalese Finch foster father (Fig. 8). Such individuals can then be housed with fellow Zebra Finches singing normal songs, but they still persist in singing Bengalese Finch songs. Even though the critical period is shorter and the song of another species learned, once the process is complete it appears to be irreversible, as with other species. Why Zebra Finches are not so selective in the types of songs they will learn may be explicable in terms of their ecology and breeding behaviour. Unlike passerines in temperate latitudes they sing and breed throughout the year, often in colonial conditions and frequently near other species of grassfinch too. Under these conditions, the best strategy for song development might well be to learn the species song quickly from the father before going off to feed in mixed-species flocks where the risk of contamination would be high. The constraints here are applied through social bonding and a quick end to the critical period, rather than through an inherited preference for learning a specific song as in most other passerines.

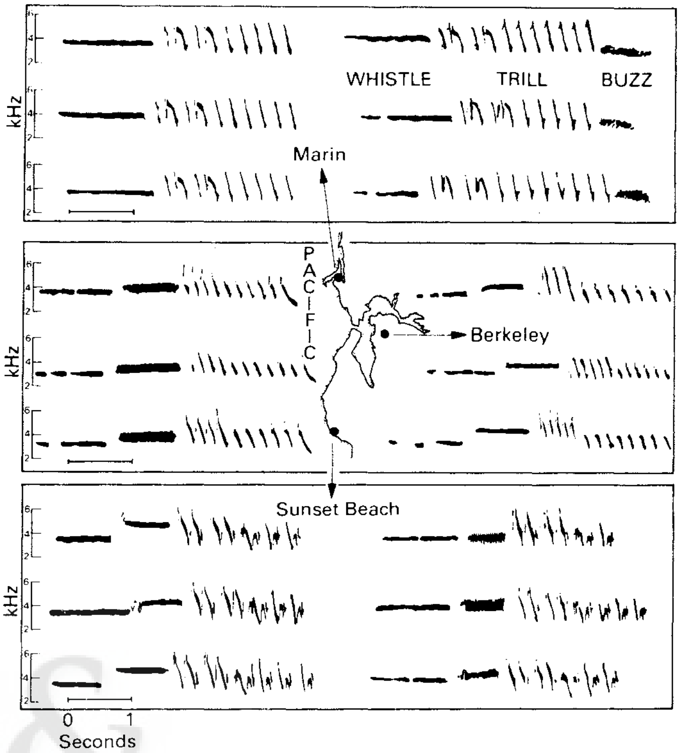

Fig. 9. Three different dialects shown by White-crowned Sparrows *Zonotrichia leucophrys* around San Francisco Bay.

Song dialects. Local dialects occur when the songs within one population share certain structural characteristics which are different from other populations nearby. It is usual to separate such microgeographical variation from geographical variation which occurs over much longer distances. Although local variations have been reported for many species, the most studied is the White-crowned Sparrow *Zonotrichia leucophrys*. Originally working around the San Francisco Bay area Marler and his group obtained sonagraphic evidence of clear dialects based upon variations in the pattern of introductory whistles, the fine structure of the trill, and the position of the buzz (Fig. 9). The population at Berkeley, for example, has three or more ascending introductory whistles, that at Marin has one or two with a terminal buzz, and that at Sunset Beach has two ascending or two followed by a buzz. There are other consistent differences in the fine structure of the trill which make this an excellent example of how individuals within each population conform to the dialect for their particular area. The question arises as to how this conformity comes about, and the answer lies in what is already known about the development of song. Marler took nestlings as well as young birds from the wild at up to 100 days old and raised both groups in acoustic isolation. The nestlings eventually produced abnormal songs which bore no relation to their home dialect, whereas the older wild trapped birds produced good copies of their dialect. This suggests that the special features of dialects are not inherited but learned with the general features of the species song. Marler confirmed this by tutoring young birds during the critical period and showed that they could learn their own or even a 'foreign' dialect at this time. Whilst the neural template rejects the songs of closely related species as a model, it is clearly flexible enough to accept different varieties of the species song. With the critical period in the White-crowned Sparrow ending as soon as 50 days, it seems highly likely that the model will be either the song of the father, or a neighbouring

Curlew *Numenius arquata* calling in flight. (*Photo: J.B. & S. Bottomley*).

male, and thus the local dialect is preserved and passed on by a form of cultural transmission.

The question which remains to be answered is, are dialects merely a functionless by-product of song learning, or do they have some additional role to play in communication? There are many theories concerning the significance of dialects, but perhaps the most interesting to emerge is that they may be involved in reducing gene flow between populations. Dialects are sometimes associated with different habitats and it has been suggested that dialects might attract only those females which are best adapted to breed in local conditions. Several predictions follow from such a theory: local populations are genetically different, there is reduced gene flow between populations, and females select males which sing their own dialect. In the White-crowned Sparrow there is some evidence from playback experiments that both males and females show a stronger response to their own dialect. Electrophoretic analysis of proteins from presumptive genetic loci demonstrate that there are greater genetic differences between populations of White-crowned Sparrows which also have dialects, and that gene flow appears to be reduced between them. However, when females were taken from mated pairs in the wild, and injected with testosterone to make them sing, most produced songs of a different dialect to their mate. It seems that some females disperse and select a mate from a different dialect area to their own. Clearly, more research is needed before the significance of dialects is fully understood.

That dialects are the result of song learning confers a degree of flexibility in the evolution of song structures. Cultural transmission may be an efficient way of passing on complex structures, but it is also prone to errors. Chaffinches normally copy their songs extremely accurately from other birds or tape recordings, but occasionally an element may be missed out or one added on. Such changes may be passed on through learning and can spread rapidly through wild populations in only a few years. After 10 or 20 years, the songs in a population may have changed beyond all recognition. This enormous potential for generating new variety is one of the reasons why bird songs are so remarkably complex and diverse in their structure. C.K.C.

Nightingale *Luscinia megarhynchos* singing in daylight. (*Photo: P. Munsterman*).

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VOCAL ORGANS: see SYRINX.

VOICE: see VOCALIZATION.

VOLANT: unusual word, meaning in the act of flying or capable of flight; also a heraldic term for a bird flying or with wings stretched.

VOLTERRA-GAUSE PRINCIPLE: see GAUSE'S RULE.

VOMER: see PALATE.

VULTURE (1): the Old World vultures are a group of specialized carnivorous birds, which are usually classified in the family Accipitridae (order Accipitriformes). They are the most distinct group within the order and, although their relationship to other members is not clear, they may be related to the fish eagles *Haliaeetus* and snake eagles *Circaetus*. They have a long fossil history dating to the Lower Miocene, over 20 million years ago. Fossil species of these vultures have been recorded in both the New and the Old World, but the group is now extinct in the Americas, where their role has been replaced by the more recent cathartid vultures (see VULTURE 2). The 15 modern species of Old World vultures are now confined to Africa, Asia and southern Europe.

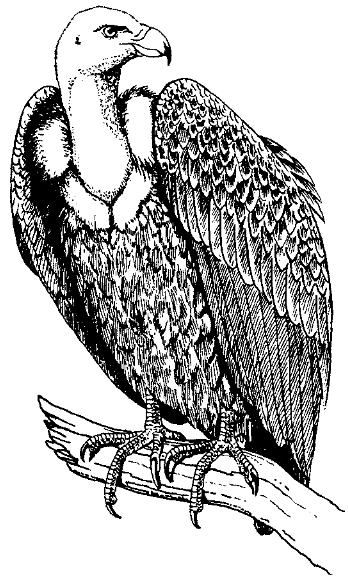
Characteristics. These birds (lengths varying from 40–100 cm) have a number of features which distinguish them from the other members of the Accipitridae (see HAWK). Most species of vulture feed almost exclusively by scavenging and they rarely or never kill their prey, but rely on finding dead animals. They depend on soaring flight to a greater extent than most other birds of prey, and the larger species are incapable of sustaining a flapping flight for more than a few seconds. The birds are, therefore, dependent on finding rising air in order to gain altitude. In flat country they use thermal upcurrents, and vultures cannot fly early in the morning until the heat of the sun has started to generate thermals. But in hilly or mountainous regions the birds chiefly fly by slope soaring, and can then be airborne at first light. Most species show no sexual dimorphism, so that the sexes of all the species are indistinguishable in the field; exceptions are the White-headed *Trigonoceps* and possibly the Indian Black *Sarcogyps*. The density at which some species of vultures can occur, in areas with a suitable food supply, is far greater than that of any other kind of carnivorous bird. Some species can congregate in groups of several hundred individuals at a food site. Like all birds of prey, the vultures have powerful bills with hooked tips, but their feet and claws are alleged to be comparatively weak (a fact which is not always apparent to those who have handled them). Most species have bare areas of skin on the head and neck, and these patches are most extensive in the larger species: they may reduce the fouling of the plumage when the birds are feeding, and may also be important in heat regulation because these areas are heavily supplied with blood vessels. Many of these features of the Old World vultures are shared by the New World vultures (Cathartiformes). But the 2 groups of vultures are not at all closely related and their superficial similarities are due to convergent evolution.

Habitat and distribution. The distribution of the Old World vultures is confined to more of less open country, and they are widespread in savanna, grassland and desert areas. None of the species are found in areas of dense forest. They are often associated with tropical climates, but they can also be found in cool regions, such as the Tibetan plateau, and until a few hundred years ago there were several species which were found commonly in Europe as far north as central Germany. Their distribution is governed as much by suitable food supplies as by climatic conditions: most species feed chiefly from the carcasses of antelope or other large grazing mammals, and they are generally abundant in areas which have large herds of grassland ungulates, and are notably absent from regions where such mammals do not occur such as Australia, Madagascar or Sri Lanka.

Griffon vultures. The 7 species of griffon vultures, belonging to the genus *Gyps*, feed almost exclusively from the carcasses of large mammals, and these species are usually the most numerous type of vulture in any region. They include the largest species of vulture, the Himalayan Griffon *Gyps himalayensis*, perhaps weighing up to 12 kg with a wing span of about 2.8 m. All members of the genus have long and flexible necks which enable them to penetrate far into carcasses to remove muscles and viscera. The bill has sharp edges for slicing through meat, and the tongue is serrated so that they can swallow their slippery food rapidly. They can be delicate in their feeding, and can detach virtually all soft tissues from even complicated bones. Most species have capacious crops, which can store about a quarter of the bird's body weight in food. Vultures are clean birds who will usually bathe and preen thoroughly when they have finished feeding. Griffon vultures can collect in groups of up to several hundred individuals at a large supply of food. When present in such numbers they are extremely efficient in their feeding, and can remove all the soft tissues from a large antelope in about half-an-hour. The birds are aggressive in their feeding, and all the species have developed a complex and ritualized series of threat displays and calls which are used to intimidate their colleagues (although vultures have few other displays or vocalizations). The various species have separate distributions and, although there is some overlap, the 2 smaller white-backed species, *Gyps africanus* and *Gyps bengalensis* (formerly in the genus *Pseudogyps*) are largely confined to flat savannas, while the larger species occupy mountainous or hilly terrain. Griffon vultures feed chiefly by locating animals which die from disease, starvation or accidents. They regularly travel great distances in their food searching, and may be partial migrants in many parts of their range. They do not search in groups, but they do depend heavily on watching the activities of their neighbours in order to locate food. Griffon vultures have no sense of smell—like all the Old World vulture species (and unlike some of the New World vultures). Birds sometimes forage at comparatively high altitudes (up to 1,500 m) and each individual is usually within sight of several other searching birds. When one bird sees a carcass it starts to descend rapidly. Other birds who see this descent will then drop to the ground, to be followed in turn by still more distant individuals, and so a chain reaction quickly radiates out from a source of food. Birds can congregate in this way from a radius of 50 km or more. The bigger griffon species sometimes roost in large numbers, and also nest colonially on cliff ledges. Some colonies contain only a few nests, but colonies may contain several thousand pairs. The smaller white-backed griffons are tree nesters and may congregate in loose colonies or nest solitarily.

Nest construction varies greatly between individuals, as well as between species. Some cliff-nesting birds lay on a ledge containing only a few twigs, while other individuals may have a nest site which has been in use for many years and which contains a construction of twigs a metre or more in depth and width. Most individuals line the nest with a few green branches before egg-laying. All species are probably monogamous, lay a single egg (as do most other vulture species) and have an incubation period of about 55 days. Both sexes share in the nesting duties and the birds have comparatively long fledging periods of up to 150 days.

Other vultures. The Lappet-faced Vulture *Torgos tracheliotus* (mass 7–8 kg, wing span 2.5 m) and the European Black Vulture *Aegypius monachus* (mass 7–10 kg, wing span 2.5–3 m) are very closely related and should perhaps be considered congeneric. They congregate at large ungulate carcasses, together with griffon vultures, although usually there are only 2 or 3 individuals at each feeding group. They are aggressive in their feeding, have intimidating threat displays and can usually drive off a group of griffon vultures. The birds chiefly take skin, tendons and other coarse pieces of tissue which they tear off with their powerful bills, and they do not usually eat large amounts of muscle tissue. They do not forage widely, but probably remain in a fixed feeding range throughout most of the year. When ungulate carcasses are not freely available the birds also feed on much smaller food items, such as hares, young antelope or game birds. It is very likely that they kill some of these animals.



Griffon Vulture *Gyps fulvus*. (*K.J.W.*).

The Indian Black Vulture *Sarcogyps calvus* (mass 4.5 kg, wing span 2 m) and the African White-headed Vulture *Trigonoceps occipitalis* (mass 4–4.5 kg, wing span 2.2 m) are probably closely related. Despite some accounts in the literature, they are quite unlike other large vultures. They do not usually feed in mixed groups. Both species are timid and retiring in their behaviour and, if they do come to a large carcass, they often confine their activities to isolated bones at the outside of the main feeding groups of griffon vultures. It is unusual to see more than 2 or 3 individuals at a feeding site and they appear to occupy fixed territories in which a pair and their young remain throughout the year. They probably feed chiefly from small carcasses which the other species do not locate, and they probably kill a proportion of their food.

The Hooded Vulture *Necrosyrtes monachus* and the Egyptian Vulture *Neophron percnopterus* are very similar in their feeding habits, but they are probably not closely related (the Egyptian Vulture shares a number of characteristics with the Lammergeier *Gypaetus barbatus*). Both are small species (mass 1.5–2 kg, wing span 1.5–2 m) with catholic feeding habits. They can collect in considerable numbers at the carcasses of large mammals, and peck at small scraps of meat dropped by the larger birds. But they also feed on insects, small reptiles, birds' eggs, young nestlings and even the dung of carnivores. The Egyptian Vulture is one of the few birds which uses tools while feeding (see TOOLS, USE OF). It regularly feeds on birds' eggs. Small eggs are picked up in the bill and dropped on to the ground to break them open, but to crack larger eggs the birds pick up stones which are then hurled on to the shell.

The Lammergeier (mass 5 kg, wing span 2–2.5 m) is a solitary and uncommon bird over most of its range, although feeding groups are commonly seen in Ethiopia. It is confined to precipitous mountain regions, where it feeds from the carcasses of large mammals such as sheep and goats. It carries large bones and tortoises high into the air and drops them on to rocks to break them open, and then sweeps down to feed on the contents.

The least typical of this group of birds is the Palm-nut Vulture *Gypohierax angolensis* (mass 1.5 kg), which rather resembles a sea eagle. It feeds on stranded fish and carrion, but its main food is the fruit of the oil palm and its distribution closely matches that of the palm plantations.

Most of this group of vultures are specialized for feeding on the carcasses of large ungulates and, because of their gliding flight, can travel great distances each day in search of food. They can therefore exploit the food supply which is available for scavenging animals far more successfully than any mammalian scavengers, and the total food consumption by the various vulture species makes them important members of many tropical communities. D.C.H.

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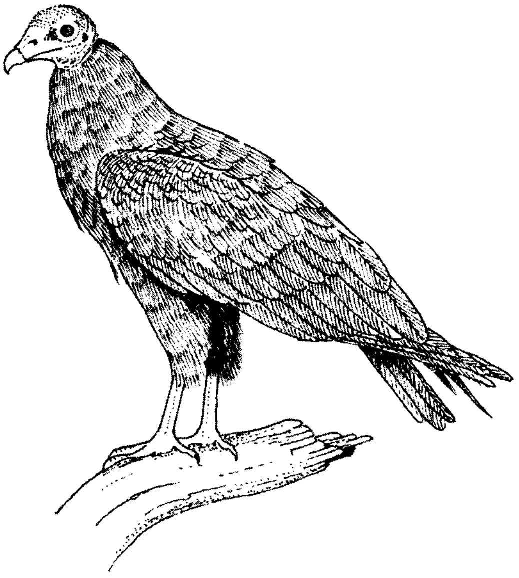
VULTURE (2): substantive name for 5 of the 7 species of Cathartidae (Cathartiformes). The remaining 2 species, differentiated by their larger size, are known as condors. These 7 species are collectively known as 'New World vultures', but perhaps are better described as cathartid vultures, since the fossil record for the group includes 'Old World' forms.

Characteristics. The cathartid vultures are large (60–100 cm long), soaring birds, generally black or dark brown in colour with patches of white or greyish white on the wings. The one exception is the King Vulture *Sarcorhamphus papa* which has a white plumage with black on the tail, rump and wings. The condors possess a feathered ruff around the neck, consisting of white down on the Andean Condor *Vultur gryphus* and black, lance-shaped feathers on the California Condor *Gymnogyps californianus*. All species have essentially unfeathered heads and necks and, with the exception of the Black Vulture *Coragyps atratus*, the bare skin is principally red, orange or yellow. In size, they range from the relatively small Black Vulture with a 1.5 m wing span to the immense Andean Condor with a span up to 3.2 m. Sexes are similar in size and colour except for a tendency for male condors to be slightly larger, and the presence of a large, comb-like caruncle on the head of the male Andean Condor. Cathartid vultures differ from Old World vultures primarily on anatomical characters, most notably by their perforated nostrils.

Distribution and habitat. Cathartid vultures range from southern Canada to the southern tip of South America, with the greatest number of species and abundance of individuals in tropical and subtropical regions between Mexico and northern Argentina. Two species, the Andean Condor and Greater Yellow-headed Vulture *Cathartes melambrotus* occur only in South America, while the severely endangered California Condor is restricted to approximately 5 million ha in southern California; only an estimated 30 birds remained by 1980. The Turkey Vulture *Cathartes aura* and Black Vulture are the 2 most widespread and conspicuous species in most regions, and have correspondingly broad habitat tolerances. Greater Yellow-headed and King Vultures are often associated with forested regions, while the Lesser Yellow-headed Vulture *Cathartes burrovianus* is a bird of humid savannas and marshes, and the 2 condors occur in rugged, mountainous regions.

Movements. Turkey Vultures from western North America are highly migratory with large flocks passing through Central America into northern South America each fall. The other species are generally non-migratory, although south-bound flocks of Black Vultures have been observed during the fall in Costa Rica and Panama.

Food. Cathartid vultures are carrion feeders, although Black Vultures occasionally, and Turkey Vultures rarely, kill new-born or defenceless animals. Black Vultures also congregate in large numbers at garbage dumps, primarily at the edges of tropical towns. Vultures may routinely soar tens of kilometres from roosting or nesting sites when searching for food. Apparently most species locate food by sight or by keying in on other vultures already feeding, but Turkey Vultures also locate food by smell.


Turkey Vulture *Cathartes aura*. (*K.J.W.*).

Behaviour and breeding. Most vultures and condors are colonial in the formation of roosts, and various numbers may congregate at a carcass. The Black Vulture is the most colonial, and is the only one that may also nest in loose colonies. The exception is the King Vulture which is usually seen singly or in pairs. No species constructs a nest. Condors lay a single egg on an overhung ledge or in a small cave on a rocky cliff. Pairs of condors may remain mated for several years, and apparently do not breed annually, presumably due to the prolonged nesting cycle and period of dependence by the fledged chick. The King Vulture lays a single egg, and the Black and Turkey Vultures lay 2-egg clutches. Vultures nest in a variety of locations, including a patch of bare ground in a dense tangle of vegetation, in an upright or fallen, hollow log, between jumbles of boulders or in caves. Incubation (32–58 days) and brooding and feeding of nestlings are performed by both adults. A Black Vulture chick may make the first short flight at 10 weeks of age, while a California Condor chick first flies at 22–25 weeks. Cathartid vultures are generally silent except for low hissing or grunting sounds heard from nestlings or adults.

See photo FLIGHT. J.C.O.

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W

WADER: in the plural, general term commonly used in the British Isles for members of the suborder Charadrii of the Charadriiformes. 'Shorebirds' has a similar meaning in North America, where 'waders' tends to be applied to the Ciconiiformes.

WADING: see LEG.

WAGTAIL: substantive name of some species in the family Motacillidae (Passeriformes, suborder Oscines), which also includes the pipits and longclaws, all of which will be covered in this article.

Characteristics. Small (lengths *c.* 14–17 cm), slender-bodied ground birds with long tails that are often wagged up and down. The legs and toes are long and these birds either walk with a rather deliberate gait or run at great speed over the ground. The hind-toe is elongated in most species and may reach 4 cm in length in some longclaws. The bill is slender and pointed. There are 11 species of wagtails (*Motacilla*) all strikingly coloured with black, white, grey, yellow or green plumage. The 35 species of pipits (*Anthus*) are duller and cryptic in coloration, often with heavily streaked brown plumage. Many species look alike and they are often difficult to identify. The longclaws (*Macronyx*), of which there are 8 species, are more robust in build and rather lark-like in appearance; they are often brightly coloured.

Habitat and distribution. All species inhabit open country from rocky shores (Rock Pipit *Anthus spinoletta*) to wet meadows and grasslands (many pipits, e.g. Meadow Pipit *A. pratensis*), arid and sandy regions (Tawny Pipit *A. campestris*), streams (Grey Wagtail *Motacilla cinerea*) and mountain tops (Hodgson's Pipit *A. roseatus*, which occurs up to 4,000 m in the Himalayas). The Pied Wagtail *M. alba* is common on farmland and also near human habitation, often running after insect prey on roads and roof-tops.

The wagtails occur throughout the Old World but they are only rare visitors to Australia. A geographical race of the Yellow Wagtail *M. flava* is the only wagtail to breed in the Western Hemisphere, nesting in the arctic tundra of western Alaska. The pipits are among the most widely distributed song birds in the world; they breed in all continents from the arctic tundra, through the South American pampas and African desert to the antarctic, where one species (*Anthus antarcticus*) breeds on the island of South Georgia. The Rock Pipit *A. spinoletta* has a wide distribution, inhabiting rocky shores in northern Europe, high mountain valleys throughout the Palearctic (where it is known as the Water Pipit) and alpine meadows and tundra in north America. The Tree Pipit *A. trivialis* inhabits open woodland and regularly perches on tall trees. Richard's Pipit *A. novaeseelandiae* extends throughout the Palearctic to Australia where it is the only pipit.

The longclaws are African; the Yellow-throated Longclaw *Macronyx croceus* is extremely similar in appearance to the Meadow Lark *Sturnella neglecta*, a New World ecological equivalent; both these unrelated species have cryptic upperparts and bright yellow underparts with a dark band round the breast, a striking example of plumage convergence, presumably under similar selective pressures on the two continents.

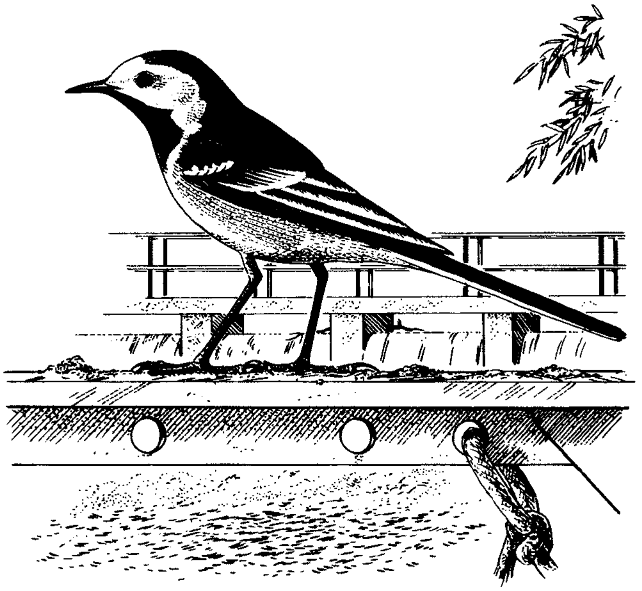
Populations and movements. The Palearctic wagtails and pipits are migratory, many moving to tropical Africa and Asia for the winter. In African winter quarters the Tawny Pipit inhabits dry country, the Tree Pipit open ground where there are well spaced trees and the Red-throated Pipit *Anthus cervinus* open wet country. Populations of the Pied Wagtail that breed in northern Britain migrate to southern Britain in the winter and, if the weather is harsh, they may move further south to France and Spain. The continental race, often referred to as the White Wagtail, migrates to the Middle East and northern tropical Africa. Ringing recoveries have shown that the Icelandic population winters in Senegal. In winter, the White Wagtail may come into competition with the similar African Pied Wagtail *M. aguimp* which some authorities have regarded as conspecific. Both occur round human settlements, especially villages and rice-fields, but most of the White Wagtails probably occur further north than the African Pied.

The Yellow Wagtail *M. flava* is famous for its geographical variation in plumage and there has been considerable argument about the designation of populations as subspecies. As many as 8 subspecies winter in Africa, from the truly yellow *M.f. flavissima* that breeds in Britain to the black-headed *M.f. feldegg* from the Balkans and the Black Sea. Several subspecies join together in winter quarters to feed and roost in large flocks. At the end of the winter the different subspecies leave successively for their breeding grounds, those breeding furthest south migrating first (e.g. *M.f. iberiae*) and the northernmost subspecies departing last of all (e.g. *M.f. flava*).

Food. Mainly insects, both adult and larvae collected by picking from the ground or, in wagtails, also by fly-catching in mid-air. The frequency of fly-catching in the British wagtails is related to tail length, the Grey Wagtail, which has the longest tail, doing the most and the Yellow Wagtail the least, with the Pied Wagtail intermediate. It seems likely that the tail assists in the control of aerial manoeuvres during the capture of flying insects. Adult Diptera (especially Scatophagidae, Tipulidae and Chironomidae) are common in the diet, also grasshoppers, spiders, worms, molluscs and crustaceans. Seeds are occasionally eaten and in winter wagtails often congregate at artificial food sources on rubbish dumps.

In mid-winter, when there may be only 8.5 hours daylight for feeding in southern Britain, both the Pied Wagtail and the Rock Pipit feed for about 90–95% of the time, collecting one prey item every 3 or 4 seconds throughout the day. Rock Pipits that winter on rocky shores may eat *Littorina neritoides* (a small periwinkle) at an average rate of 33 per minute and Chironomid midge larvae at 35 per minute. They also eat isopod crustacea (*Idotea*) and amphipods (Talitridae). In winter, Pied Wagtails regularly feed on small adult insects and their larvae at a rate of 20 per minute. Even with these prodigious rates of feeding, calculations show that both these birds only just manage to find enough food to maintain their energy balance on a winter's day.

Behaviour. In summer, wagtails and pipits space their nests out and defend breeding territories. In favourable habitats there may be up to 5 pairs of Rock Pipits per km of coastline. In winter some species usually feed in flocks (Meadow Pipit, Pied Wagtail), and exploit large patches of abundant food. Pied Wagtails also roost communally in reed beds, low trees and bushes, and near human activity such as sewage farms, factories and greenhouses. In mid-winter the roosts may build up to several hundred or even 2,000 individuals. Extensive colour ringing studies have shown that most birds feed within 12 km of the roost. In the early morning, the flocks leaving the roost depart towards good feeding sites. One advantage of roosting communally, therefore, may be that it allows



Pied Wagtail *Motacilla alba*. (*A.H.*).

information transfer in the population about the location of food. Roosts may also provide warm, sheltered sites safe from predators.

Some species defend territories in winter. Rock Pipits defend stretches of the coast, and some Pied Wagtails also defend winter feeding territories and individuals may return to the same territory in successive winters. Territory boundaries are vigorously defended with displays involving head bobbing and short jumps into the air. Observations in Japan, Israel and Britain have shown that winter territories are often occupied by single birds but sometimes 'winter pairs' form, usually involving a male and a female, or a male and a bird in juvenile plumage. The pair defends the territory together, but the male is the dominant partner and the other bird continually appeases it with special postures. Sometimes, when food is scarce, the male evicts his 'mate' from the territory. These pairs are apparently not related to breeding and seem to be just concerned with winter survival.

The social organization of Pied Wagtails in winter is related to the food supply. Sometimes individuals may be defending territories and, nearby, other conspecifics are feeding in large flocks on locally abundant foods. Social behaviour can be changed experimentally by altering the pattern of food distribution. On small piles of food, individuals will defend territories. If the food in these same piles is then spread out and dispersed evenly, flocks of wagtails will form to exploit the food. This is presumably because it is uneconomical to defend widely scattered food supplies.

Voice. The pipits are well known for their spectacular song flights (e.g. Meadow Pipit, Tree Pipit) in which the song is delivered from high in the air as the bird parachutes slowly back down to the ground or a tree perch. Both the wagtails and the pipits often give flight calls and in the pipits these calls are one of the best ways of identifying species in the field. The Pied Wagtail has a territorial call that is only given by territory owners. The call (*chee-wee*) dissuades intruders from landing on the territory. If tape-recordings of the territorial call are broadcast on an occupied winter territory, the owner reacts violently and flutters within a metre or so of the loudspeaker, as if it thinks there is another owner present!

Breeding. Pipits nest on the ground, amongst grass. Wagtails also nest on the ground (Yellow Wagtail) or in crevices in rocks, walls, under bridges, haystacks etc. (Pied Wagtail). Nests are neatly built of grass and moss and lined with hair. The eggs are white or buff, speckled brown or grey. Incubation, usually by female only, is from 12–16 days. Both parents usually care for the young, which fledge in *c.* 14 days. Pied Wagtails finish breeding during July and then moult, the primary moult taking about 57 days. Almost all the population has finished the moult by the end of September.

See photos LOCOMOTION, TERRESTRIAL; MAMMALS, ASSOCIATION WITH.

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WAGTAIL-TYRANT: substantive name of the 2 tyrant-flycatchers of the genus *Stigmatura* (see FLYCATCHER (2)).

WAGTAIL, WILLY: misnomer applied to the ground-feeding *Rhipidura leucophrys* of the Australasian Region (see FANTAIL).

WALDRAPP: alternative name of the Bald Ibis *Geronticus eremita* (see IBIS).

WALKING: see LEG; LOCOMOTION, TERRESTRIAL (and photo).

WALLACEA: the geographical area east of Wallace's Line (q.v.), which runs up the Sunda Shelf, between Bali and Lombok (only *c.* 30 km apart), Borneo and Sulawesi (*c.* 100 km apart) and south of a line between the Philippines and Sulawesi. At this line a marked faunal change takes place, very many families, genera and species of the Oriental Region penetrating no further east than this line. The eastern boundary of Wallacea is the Sahul Shelf, on which lie New Guinea and Australia (the Australasian Region). A similar marked faunal discontinuity is repeated here between Australia and Timor, the Southwest Islands and Tanimbar and between New Guinea and Kai, Seram and the northern Moluccas. Wallacea is a mosaic of oceanic islands falling outside the continental faunal regions. (*See* C.M.N. White and M.D. Bruce, The Birds of Wallacea. In press 1985, British Ornithologists' Union.)

WALLACE'S LINE: see above and ORIENTAL REGION; also AUSTRALASIAN REGION.

WALLCREEPER: substantive name of the Old World family Tichodromadidae (Passeriformes, suborder Oscines). The Wallcreeper *Tichodroma muraria* is put in a family of its own as its former inclusion with the Certhiidae, later Sittidae, was not based on any firmly established relationship. Only 2 subspecies are recognized.

Characteristics. The Wallcreeper is 135–165 mm long, and its weight at 17–19 g corresponds to that of the Great Tit *Parus major*, but the wings measure 98–116 mm, those of the Great Tit only 70–78 mm. Apart from the red and white marks on the wings, the blue-grey plumage is like that of the Nuthatch *Sitta europaea*. The bill is slender and curved, like the treecreeper's *Certhia*. The feet are noticeably weak. In breeding plumage the male has a black throat and breast; in the female the breast is either whitish-grey or there is a grey or black mark of varying size. After the breeding season, both sexes moult into winter plumage with whitish-grey underparts. In the spring plumage only breast, throat and head are moulted. The wings are often used as an aid in climbing, being constantly flicked, showing the white and red markings. The tail is not used as a support when climbing.

Habitat. The Wallcreeper is found among the rocky areas of mountains where it climbs by hopping from one projection to another. Flowing water, in the form of mountain streams or small waterfalls, is a characteristic feature of most nesting areas. Wallcreepers also nest readily in gorges where there is an alternating pattern of sun and shade.

Distribution. Wallcreepers are found in the highest mountain ranges of Europe and Asia from the Cantabrians and Pyrenees in the west, through the Alps, the Carpathians, Balkan peninsula, Asia Minor, to the Caucasus, Iran and the Himalayas, where they live as high as 5,000 m. In the Alps they breed mostly between 1,000 and 2,500 m; but in Switzerland nesting places are known at only 350 and 550 m.

Wallcreeper *Tichodroma muraria*. (*D.W.*).

Movements. In the autumn Wallcreepers leave the high mountains and move down to lower rocky areas or ruins; there they may defend a winter territory against all others of their kind.

Food. Both in summer and winter the food consists of insects and spiders, which are extracted from their hiding places with the thin bill, or seized directly.

Behaviour. Except in the breeding season, Wallcreepers lead a solitary life and will attack any conspecific from October onwards. In addition to flicking the wings, the male flutters round the female, who may shiver her wings. They bend their heads upwards till their bills are almost upright and crossed.

Voice. Wallcreepers have a few quiet calls which are seldom heard. Both sexes sing short melodious phrases while climbing.

Breeding. The nest, built by the female alone, is situated in a crevice or hole in a wall or rock face, and consists of moss, roots, grass, feathers and wool. The eggs are white, sparsely freckled with fine reddish-brown. The clutch of 3–5 eggs is incubated by the female alone for 18–19 days. She is fed regularly by the male. The young fledge at 28–29 days old.

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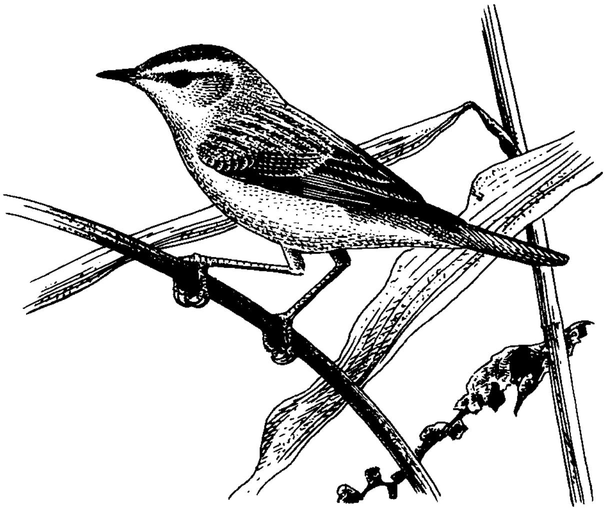
WARBLER (1): substantive name of many species of the family Sylviidae (Passeriformes, sub-order Oscines); in the plural a general term for the family. The Sylviidae are commonly known as Old World warblers, having 10 primaries, as opposed to the New World warblers (Parulidae) of the 9 primaried group (see WARBLER (2)). The family encompasses about 350 species in 63 genera, nearly half of which are monotypic (Morony *et al* 1975). Many warblers are of uncertain affinity. Here the family is taken to include the genera *Chloropeta*, *Hyliota* and *Parisoma* (sometimes regarded as flycatchers Muscicapidae), the longbills (genus *Macrosphenus*, sometimes included with the babblers Timaliidae or the bulbuls Pycnonotidae), the Fernbird (genus *Bowdleria*) and the kinglets (sometimes considered a separate family Regulidae) but not the Australian Maluridae (see WREN (2)) and Acanthizidae (see WARBLER, AUSTRALIAN). With the exception of the gnatcatchers (Polioptilinae, see GNATCATCHER) the warblers form a single subfamily, Sylviinae.

Characteristics. Warblers are typically small or tiny (from 9cm), with fine, narrowly-pointed bills. They are mostly insectivorous, capturing prey mainly by foliage-gleaning, and many are arboreal. Plumage colours are generally unobtrusive, greenish, brownish or grey, although some tropical species are brightly coloured. In most the sexes are alike in plumage although there are exceptions as in *Regulus* and some species of other genera including *Sylvia*, *Apalis* and *Orthotomus*. The juvenile plumage is unspotted, in common with that of the babblers but distinguishing the warblers from 2 other families, the flycatchers and the thrushes (Turdidae), to which they are also closely related.

The variety of warblers. The differences between genera are often more obvious to the field observer, familiar with habitat preferences, voice and behaviour, than to the museum worker since inter-generic distinctions in morphology tend to be vague, involving such characters as relative bill size, size of the first primary, presence and length of rictal bristles and relative tail length and shape. Morphological distinctions between closely-related species may also be slight and identification accordingly can require examination in the hand for small structural differences, as in wing formulae or primary emarginations. Description of so diverse a family is facilitated by dividing it into a number of groups, principally on grounds of broad similarities in ecology and habitat preferences, without necessarily implying taxonomic relatedness.

Reed and bush warblers. Several warbler genera are well represented in marshes, reed-beds, swamps and rank vegetation, although each has members in less humid habitats. The largest genus *Acrocephalus* has some 28 species spread throughout Eurasia, Africa and Australia. The genus is a very successful colonizer of oceanic islands, particularly in the Pacific. They are robustly-built warblers, with prominent bills and large feet, able to clamber about in reeds and other vertically-growing marsh vegetation. Most are a uniform brown colour but the harsh, chattering songs are species-distinctive. The mainly Asian genus *Cettia* consists of secretive, plain-coloured birds with rounded, sometimes long, tails of only 10 rectrices. They inhabit reed-beds, dense forest undergrowth and lush vegetation some, notably the Large Bush Warbler *C. major*, ranging to 4,000 metres in the Himalayas in rhododendron and bamboo thickets. Cetti's Warbler *C. cetti* is a marshland species which extends into southern Europe, from where it has recently expanded northwest as far as southern Britain. Members of this genus have surprisingly loud, melodious voices. The *Bradypterus* warblers of Africa and Asia are similarly brown, skulking birds with distinctive voices. They are known as bush-warblers or scrub-warblers but the 18 species are spread through a variety of habitats from swamps to damp forest undergrowth. The genus *Locustella* is characteristic of dense low vegetation in Eurasia. The whirring songs of some species resemble the stridulations of Orthoptera, hence the familiar name grasshopper warblers. One species, the Taiga Grasshopper Warbler (*L. fasciolata*), has a loud, bell-like song. *Locustella* warblers are morphologically distinctive, with long undertail coverts, very narrow beaks lacking rictal bristles, and large feet. They are chiefly terrestrial, creeping readily on the ground under and through the densest vegetation.



Sedge Warbler *Acrocephalus schoenobaenus*. (*A.H.*).

Scrub and woodland warblers. Many genera are represented in scrub but in Europe the term scrub-warblers refers to the genus *Sylvia*, some 20 species of which breed chiefly in the west Palearctic. They are found in a broad range of vegetation types from very low scrub (e.g. the Desert Warbler *S. nana*) to mature, deciduous woodland (e.g. the Blackcap *S. atricapilla*) but are particularly characteristic of dense evergreen scrub (maquis) in the Mediterranean region. Most are distinctively patterned; black or grey above with contrasting pale or rufous underparts and characteristically the sexes differ in plumage. Another typically Palearctic genus is *Hippolais*. These may be close to *Acrocephalus* and like them have large bills (although relatively wider and flattened) and harsh, varied songs. The tails of *Hippolais* are square-ended, not graduated as in reed warblers, and, although the species are largely plainly coloured, some are bright yellow. The latter include the Icterine Warbler *H. icterina*, a characteristic bird of European parks where the generic tendency to place nests well up in shrubs enables it to survive even in the absence of much ground cover.

Leaf warblers. The monograph by Ticehurst (1938) remains the authoritative guide to the genus *Phylloscopus*, a confusing assemblage of some 40 species of small, short-billed warblers which breed throughout the Palearctic and in the tropical African forests. The various species look remarkably alike, mostly coloured olive or yellowish-green, but have distinctive songs. Most are arboreal in broad-leaved trees, but some also frequent the canopy of coniferous forests (e.g. the Pallas's Leaf Warbler *P. proregulus*). *Phylloscopus* is largely replaced in the tropical Asian forests by the genera *Seicercus* and *Abroscopus*, which have stouter bills and brighter plumage, including rufous or grey head markings. The 2 latter genera are called flycatcher-warblers and indeed they and some species of *Phylloscopus* are active foragers which employ flycatching methods more frequently than most other sylviids.

Grass warblers. The 40 species of *Cisticola* (all but 6 described by Lynes 1930) are characteristic of grassy habitats in Africa from where one species, the Fan-tailed Warbler *C. juncidis*, has spread into Europe and Asia and as far as Japan and Australia. Another species, the Golden Cisticola *C. exilis* of India, south-east Asia and Australia, is the only one unrepresented inside Africa and its continental islands. Within Africa it is evident that evolution has resulted in greater interspecific differences in voice and habitat specialization than in morphological distinctions. *Cisticola* warblers range through a variety of lowland and montane grassy habitats including marshes (e.g. the Great Black-backed Cisticola *C. galactotes*) and woodland clearings (e.g. the Rattling Cisticola *C. chiniana*). Most are tiny, short-tailed birds, with the morphological distinctions in many species of having longer tails during than outside the breeding season, a double annual moult and strong size dimorphism between the sexes, the males being larger than the females. Many warblers of low vegetation have aerial displays but those of some *Cisticola* warblers are especially noteworthy, the cloudscrapers (e.g. the Crackling Cloud Cisticola *C. ayresii*) having particularly dramatic performances with wing-snapping and song delivered from a great height. The wren-warblers *Prinia* are typical of African and Asian grasslands and scrubby habitats. They are dull-coloured birds with long, graduated tails. They are partly terrestrial, foraging through low vegetation, and are often found in small parties. Grassy habitats also house a number of very large distinctive warblers among which may be mentioned the canegrass warblers *Megalurus* of south-east Asia and Australia, the Broad-tailed Warbler *Schoenicola platyura* which has separate populations in Africa and southern India and the Large Grass Warbler *Graminicola bengalensis* of India and south-east Asia. Three large warblers in the genus *Sphenoeacus* (each formerly in a monotypic genus) form a superspecies of the African grasslands although one species, the Damara Rockjumper *S. pycnopygius*, is associated with rocky areas.

African tree warblers. The genus *Apalis* is typical of the evergreen forest canopy, although the Yellow-breasted Apalis (*A. flavida*) occurs in a wide variety of bushy habitats, from light forest to acacia steppe. Conspicuous tail movements, which serve to emphasize the tail pattern in some species, may be important in species-recognition. Some (e.g. the Masked Apalis *A. binotata*) have well differentiated montane and lowland forms and the status of these as subspecies or species is problematical. The Bar-breasted Apalis *A. thoracica* has 16 well-marked geographical races (Hall and Moreau 1970) and provides a striking example of geographical differentiation in the African avifauna. Some of its subspecies are isolated in montane forests and others have clearly been isolated in the past but have since come together and intergrade. Some of the genus (e.g. the White-winged Apalis *A. chariessa*) are brightly coloured and have striking patterns. The genus *Eremomela* includes principally arboreal warblers inhabiting dry scrub and woodlands and secondary forest. Different species tend to be segregated by habitat and this has also been claimed for some species of *Camaroptera*, *Sylvietta* and *Apalis*. The *Eremomela* warblers are greyish or green above, some with contrasting head markings. The crombecs *Sylvietta* are short-tailed, typically-arboreal warblers, soberly-coloured in buff, green or grey. They frequent various habitats from arid scrub to evergreen forest. Some, notably the Crombec *S. brachyura*, forage on tree trunks and branches, probing in crevices with their long bills, a habit which has earned them the name nuthatch-warblers. The genus *Camaroptera* inhabits dense undergrowth, scrub and lowland evergreen forest. They are an inconspicuous green or brownish in colour but some have distinctive calls. On this account *C. brachyura* is frequently known as the Bleating Bush Warbler. Some species sew leaves together when nest-building, suggesting a taxonomic relationship with the tailorbirds *Orthotomus*, to which they also show some resemblance in voice and morphology. The Cinnamon-breasted Warbler *Euryptila subcinnamomea* is believed to be allied to *Camaroptera* on morphological grounds but is distinct ecologically, frequenting boulder-strewn hillsides in south-west Africa. The longbills or bush-creepers *Macrosphenus* are aberrant warblers, having long bills sharply hooked at the tip, and long, loose feathers on the flanks which are used by at least one species (Kemp's Longbill *M. kempi*) in display. They occur in dense undergrowth, typically in evergreen forest.

Tailorbirds. The tailorbirds *Orthotomus* are so called for their habit of sewing a large leaf or several leaves together to form a cone in which the nest proper is built, using plant wool. The leaf-stitching involves passing vegetable fibres or cobwebs through holes punctured in the margins with the bills. Tailorbirds are familiar inhabitants of gardens in India and south-east Asia, otherwise occurring in forest and scrub. One montane forest species occurs outside Asia, the African Tailorbird *O. metopias*. Tailorbirds have long, decurved bills, short wings and graduated tails, the latter held characteristically cocked-upwards. Males have longer tails than females and more striking, frequently rufous, head-markings.

Kinglets. The kinglets *Regulus* are tiny birds which typically inhabit the canopy of coniferous forest, although the Firecrest *R. ignicapillus* occurs in European deciduous woodlands also. Two other species occur in the Old World, the Goldcrest *R. regulus*, with various subspecies ranging between the Azores and Europe and Japan, and the Formosan Kinglet *R. goodfellowi* restricted to Taiwan. The Ruby-crowned Kinglet *R. calendula* and the Golden-crowned Kinglet *R. satrapa* occur in North America, the former extending south to northern Mexico. Kinglets resemble some leaf warblers *Phylloscopus* in coloration but have dense, soft plumage and red or orange central crown markings which can be erected in display. The Ruby-crowned Kinglet has a melodious voice but the others have thin, high-pitched songs and calls. Kinglets are active birds, frequently hovering as they forage through the forest canopy, often in flocks with other kinglets and tits (Paridae). The tit-warblers *Leptopoecile* resemble the kinglets in their gregariousness and in having soft, copious plumage but they may not be closely related. They inhabit fir forests and juniper scrub in Central Asia and western China. Both they and the kinglets have formerly been considered aberrant members of the tit family.

Other warblers. The archipelagoes of the Pacific and Indian Oceans, Madagascar and the forests of the African and Asian mainland contain a variety of aberrant warblers, many in monotypic genera. Among these may be mentioned 3 African genera (*Chloropeta*, *Parisoma* and *Hyliota*) which are sometimes regarded as flycatchers. *Chloropeta* may be closely related to *Acrocephalus* and indeed one of the 3 species, the Yellow Swamp Warbler *C. gracilirostris* is a marshland bird, the other 2 frequenting bushy woodland and forest edges. The tit-flycatchers *Parisoma* resemble *Sylvia* warblers in coloration and in nest structure. They frequent acacia savanna, their foraging activities also suggesting that they are warblers. The 3 species of *Hyliota* are dark above and pale below, with white wing patches. They forage in typical warbler fashion in the canopy of woodland or forest. The genus *Tesia* (including *Oligura*) contains several active, tiny, almost tail-less warblers which occur in the forests of south-east Asia. They are called ground-warblers, being largely terrestrial. *Hemitesia* of Africa may be a close relative. The unusual warblers of Madagascar include the 2 species of emu-tails (*Dromaeocercus*). They are secretive birds of swamps or forest undergrowth, unusual in having only 8 rectrices, these consisting of feathers in which the barbs are not all joined together. The tail-feathers of the Fernbird *Bowdleria punctata* are of a similarly unusual structure, the barbs being disconnected so that the rectrices have a spike-like appearance. The Fernbird, an inhabitant of swamps and adjacent undergrowth, is the sole sylviid of New Zealand. The morphological resemblance between the Fernbird and the emu-tails is presumably due to convergence; a similar tail structure also occurs in *Stipiturus* (see WREN (2)).

Habitat. The above accounts make it clear that warblers frequent all types of vegetation, although most are found in dense habitats. Ecological segregation of closely-related species may involve differences in habitat selection. For example, the 3 *Phylloscopus* species nesting in Britain are largely separated there by habitat, the highest densities of the Willow Warbler *P. trochilus* occurring in bushy scrub and open areas with scattered trees, the Chiffchaff *P. collybita* favouring bushy deciduous woodland and the Wood Warbler *P. sibilatrix* occurring in dense deciduous woodland, often beech, with little or no bushy understorey. The warblers also provide examples of different species exhibiting vertical stratification within the same habitat. For example, the Long-billed Crombec *Sylvietta rufescens* and the Red-faced Crombec *S. whytii* are sibling species which are separated by foraging height in the limited area where their ranges overlap in Zimbabwe, the former foraging in the undergrowth and the latter in the canopy.

Distribution. The Sylviidae reach their greatest diversity in tropical and southern Africa, where 160 of the approximately 350 known species breed. By contrast the Asian tropics have a smaller variety (about 84 species). The warblers of tropical Asia and Africa are joined during the northern winter by many of the 106 species which breed in the Palearctic. Mainland Australia has only 8 species, including the endemic genera *Cinclorhamphus* (2 species of song larks) and *Eremiornis* (Spinifex Bird), the family being largely replaced there by the native wren-warblers

(WREN (2)). The ecological equivalents of the Sylviidae in the Americas are the wood warblers (Parulidae, see WARBLER (2)) and in some ways also the vireos (Vireonidae, see VIREO) but the family is represented there by the gnatcatchers, 2 species of kinglets and also the Arctic Warbler *Phylloscopus borealis*. The latter has established breeding populations in western Alaska which nonetheless migrate to south-east Asia, in common with their Palearctic-breeding conspecifics.

Populations. Virtually nothing is known of the actual size of the populations of most species, although it is clear that many of the Palearctic migrant species especially are extremely abundant. The Willow Warbler has an autumn population which has been roughly estimated at 1,000 million birds (Moreau 1972), making it the most numerous of the Palearctic passerines which winter in Africa. Palearctic warblers wintering in the African Sahel zone were badly affected by drought in 1968 and subsequently. The decline of the western populations of the Whitethroat *Sylvia communis* was particularly severe; the British population decreased by over 75%, with only a slow recovery evident a decade later. A few warbler species, especially island endemics, have tiny populations and so are vulnerable to extinction. For example, the Aldabran Brush Warbler *Nesillas aldabranus* was believed to number fewer than 11 individuals in 1983.

Movements. Like many insectivorous birds, most breeding warblers of the cold and temperate zones are strongly migratory. Some western Palearctic species winter in the Mediterranean area where resident warblers, mostly *Sylvia* spp., are joined by large numbers of Blackcaps and Chiffchaffs from central and northern Europe. Other Palearctic warblers winter chiefly in Africa or tropical Asia, some undertaking prodigious journeys. For example both Siberian Willow Warblers and north European Arctic Warblers make journeys of up to 12,000 km twice yearly to and from Africa and south-east Asia respectively. The available evidence is that most warblers of the Ethiopian and Oriental regions are sedentary or perform only local movements. Fidelity to both breeding and winter quarters has been found in a number of species, particularly of *Sylvia*, *Acrocephalus* and *Phylloscopus*, and may be widespread generally.

The requirements of migration have affected the morphology and physiology of migrant species. Such species tend to have long, pointed wings, as opposed to the short, rounded ones of other warblers, including resident congeners. Short-distance migrants (e.g. the Blackcap) may moult before their southward journey, but many warblers moult in winter quarters and others moult only the body plumage before departing in the fall. The Willow Warbler has two complete annual moults; post-breeding and after arrival in Africa. Endogenous rhythms underlying migration have been investigated in a number of species, notably *Sylvia* warblers. In the Garden Warbler *S. borin* endogenous timing processes have been shown to influence the directional changes performed during fall migration.

Food. Most warblers have a varied diet including a broad range of insects and other arthropods. Some take tiny items such as scale insects and insect eggs. Frugivory is common in some species, especially of *Sylvia*. Indeed the Blackcap and the Garden Warbler are among the very few Palearctic passerines that winter commonly in the African evergreen forests, where they eat many fruits (Moreau 1972). Other plant material is occasionally taken; the kinglets in particular seem to consume tiny seeds regularly. Nectarivory has been recorded in some species of *Apalis*, *Sylvietta*, *Eremomela*, *Cisticola* and *Prinia*, at aloes (*Aloe* spp.) in Africa and there are similar observations from Europe where in some localities Blackcaps, Sardinian Warblers *Sylvia melanocephala* and Chiffchaffs regularly take nectar from aloes and other flowers, both native and exotic. Nectarivory may be more widespread in the family than the available records suggest. Detailed comparative investigations of warbler diets are few but seem to suggest that, although large overlaps in diet may occur, different species may specialize on different prey species or sizes.

Behaviour. Most warblers are solitary birds although some (e.g. the kinglets and grass warblers *Prinia* spp.) forage in small parties outside the breeding season or join mixed-species flocks. Temperate zone species are highly territorial on their breeding grounds, the males establishing territories which they advertise by persistent song. In some species (e.g. the Reed Warbler *Acrocephalus scirpaceus*) territories are small and closely packed together in dense cover such as reed beds. They provide the nest site but birds forage widely outside their boundaries. In others (e.g. the Blackcap) large territories, up to a hectare in extent, are established and most of the food requirements of the resident pair and its progeny are obtained there. Some warblers defend territories not only against conspecific intruders but also against members of closely related species. Such interspecific territoriality has been studied in detail in the case of 2 European species-pairs, the Reed Warbler and Sedge Warbler *Acrocephalus schoenobaenus* and the Blackcap and Garden Warbler. In both cases, males react to each other's songs and interspecific fights are frequent. In the case of Blackcaps in Britain responses to song playback experiments with Blackcap song and with Garden Warbler song are equally strong and experiments involving the removal of territorial Blackcaps have shown that the species can prevent the establishment of Garden Warblers in the same area. Such studies show that in certain warblers segregation may be as much by behavioural as by ecological mechanisms.

Voice. The Sylviidae include some distinguished singers, such as the Blackcap and the Chinese Bush Warbler *Cettia diphone*, which are noteworthy for their varied, melodious voices. However, only a minority of warblers actually warble i.e. produce a continuous, gentle, trilling sound, and the range of vocalizations in the family is broad. Song is used to advertise the positions of territories particularly in temperate zone populations where breeding birds occur at high densities. In some (e.g. the Sedge Warbler) song output declines markedly or even ceases once the birds have attracted mates but in others (e.g. the Willow Warbler) song is obvious throughout the breeding season. Some temperate zone species sing in winter quarters and in at least some of these (e.g. the Great Reed Warbler *Acrocephalus arundinaceus*) the behaviour is known to be associated with maintenance of feeding territories.

The songs themselves are often distinctive between genera but considerable variation may occur even within a single genus. For example, in *Sylvia* warblers stereotyped, harsh songs are characteristic of species of dense low scrub (e.g. the Dartford Warbler *S. undata*) whereas those of woodlands (e.g. the Blackcap) have varied songs with a high proportion of pure notes. Habitat acoustics for both *Acrocephalus* and *Sylvia* warblers have been investigated and seem to have played an important part in the evolution of vocalizations intended for long distance communication. Many warblers are vocal when foraging or when disturbed at the nest and their various calls can also be distinctive, especially those of mainly tropical genera such as *Cisticola*.

Some warblers are excellent mimics of the vocalizations of other birds. The Blackcap and Icterine Warbler are good examples but the Marsh Warbler *Acrocephalus palustris* is arguably the outstanding example of avian vocal mimicry. Its song consists entirely of imitations of other species but arranged in a species-characteristic manner. Average repertoires of individual Marsh Warblers comprise imitations of some 80 species, over half of them African birds heard in the warbler's winter quarters.

Breeding. Most warblers are monogamous but occasional instances of polygamy have been reported for a number of species (e.g. Garden Warbler, Sedge Warbler and Chiffchaff). Warblers typically build elaborate, carefully-woven nests, which are spherical or domed structures with an entrance in the top or side. Such nests are characteristic of *Phylloscopus*, *Prinia*, *Cisticola* and *Apalis*, among others. The crombecs build a dangling pouch of soft grass, cobwebs and moss. The stitching of leaves together during nest building is seen not only in the tailorbirds and *Camaroptera* but also in 3 species of *Cisticola*, about 8 of *Prinia* and in the Red-winged Warbler *Heliolais erythroptera*. Open, cup-shaped nests are typical of the Polioptilinae and some Old World genera including *Eremomela*, *Acrocephalus*, *Hippolais* and *Sylvia*. Most nests are placed in low cover, on or near the ground or in bushes. Those of reed warblers are often slung between reed stems. Nest construction may involve the female alone (e.g. Chiffchaff), or more frequently both sexes with the male commencing construction. The eggs are usually darkly spotted or blotched on a pale ground colour. In the tropics clutch sizes are usually 2–4 but in temperate zones 3–7 eggs are usual. Incubation is by both sexes or sometimes the female alone (Chiffchaff). Incubation and fledging periods are approximately 12–14 and 11–15 days respectively, slightly longer in some tropical species. The nestlings have natal down in some genera (including *Phylloscopus*, *Cettia*, *Regulus* and *Locustella*) and are naked in others (including *Acrocephalus*, *Sylvia* and *Hippolais*). They may leave the nest before they can fly and are attended by the parents for some days thereafter.

See photos BROOD-PARASITISM; NEST BUILDING; PARENTAL CARE; VOCALIZATION.

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WARBLER (2): substantive name of most species of Parulidae (Passeriformes, suborder Oscines); in the plural, often in the form 'wood-warblers' or 'American warblers', general term for the family. The wood-warblers belong to the great complex of New World 9-primaried songbirds that includes such groups as the tanagers (Thraupinae), cardinal-grosbeaks (Cardinalinae), buntings (Emberizinae), and troupials (Icteridae). Division of this complex into families and subfamilies is in some instances difficult, and various rearrangements at this level have been proposed in recent years. The honeycreepers, formerly segregated as a family (Coerebidae), are currently considered to be nectarivorous tanagers except for 2 genera, *Coereba* and *Conirostrum*. These 2 are of uncertain affinities. They may be related to the Parulidae, but are here treated as a separate family (see HONEYCREEPER; BANANAQUIT; CONEBILL). A few aberrant species generally placed in the Parulidae may ultimately be found to belong elsewhere.

Characteristics. The wood-warblers are small birds, lengths 10–16 cm, the largest being little larger than a House Sparrow *Passer domesticus*. Many are brightly coloured, with yellow, orange, black, and white among the most frequent colours. A few species have blue or red plumage, while others are greenish, dull brown, olive or grey. Sexual and seasonal colour dimorphism is frequent among northern species, but in many tropical wood-warblers the sexes are equally brightly coloured all the year round.

Habitat. Wood-warblers are widely distributed ecologically, inhabiting coniferous and deciduous woods, tropical rain-forests, swamps and marshes, old fields, shrubbery, and sparse desert vegetation.

Distribution. The family ranges throughout the New World, from Alaska and northern Canada to southern South America. Omitting those here placed in the Coerebidae, there are some 114 species; a number of these form closely related species-pairs or superspecies. There are some 27 genera (including those tentatively assigned to the Parulidae); attempts to reduce this number have not been based on adequate study, and a few of the widely recognized genera may be composites. Most of the genera (18) are predominantly North American or West Indian; 7 are primarily tropical, and 2 (*Parula*, *Geothlypis*) are widely distributed through both American continents.

Movements. Most northern species are highly migratory, and frequently travel in mixed flocks. The great migrating 'waves' of wood-warblers are among the most impressive features of the bird life of eastern North America. Some migratory species merely move to the southern part of the breeding range, but others winter as far south as Argentina.

Food. Most species are insectivorous, but some add berries and other vegetable matter to their diet.

Voice. Wood-warblers have well developed songs, typically of relatively short duration. Many have a complex pattern and are of rather low volume. Those of the more terrestrial species tend to be loud and ringing, often (as in the Ovenbird *Seiurus aurocapillus* and the White-browed Warbler *Basileuterus leucoblepharus*) of an uncomplicated series of notes. The well-studied species in the genera *Dendroica* and *Vermivora* have two distinct songs, used in separate contexts.

Breeding. Northern wood-warblers build their nests in a variety of sites—on the ground, in bushes and vines, or in trees. Two species, the Prothonotary Warbler *Protonotaria citrea* of the south-eastern and Lucy's Warbler *Vermivora luciae* of south-western United States, are hole nesters, the latter sometimes re-using the globular nests of the Verdin *Auriparus flaviceps* (see PENDULINE TIT). Members of the genus *Parula*, which constitute a single superspecies, nest in hanging bunches of 'Spanish moss', beard-lichen, or similar vegetation. Most tropical members of the family nest on the ground, or on ledges and banks. Eggs are usually white, more or less speckled with various colours; a few species lay immaculate white eggs. Clutches among tropical species usually range from 2–4, whereas northern wood-warblers lay 3–5 eggs, exceptionally 6. Incubation and fledging periods are usually 11–12 and 8–10 days, respectively, in North American species and distinctly longer, 13–17 and 12–15 days, in the few tropical species studied.

Distribution and systematic characteristics. The largest genus, with some 27 species, is *Dendroica*, a North American and West Indian group. The most widely distributed species is the Yellow Warbler *D. petechia*, the only member of the genus that breeds south to northern South America and the only wood-warbler in the Galápagos Islands. Predominantly yellow, the males of most races have chestnut streaks on the breast, and some have chestnut caps or hoods. Concealed white tail spots are typical of *Dendroica*; only in *D. petechia* are the spots yellow. The most frugivorous member of the family is the Yellow-rumped Warbler *D. coronata* of North America south in the mountains to Guatemala (with which Audubon's Warbler *D. auduboni* is now considered conspecific). It feeds extensively on berries in autumn and winter. The Cerulean and Black-throated Blue Warblers *D. cerulea* and *D. caerulescens*, also North American, are the only members of the family in which the males are conspicuously blue in colour. The large Kirtland's Warbler *D. kirtlandii* has one of the most restricted breeding ranges among non-insular birds. It nests only in an area of about 100 by 130 km in central Michigan, and within this range only in dense stands of pine about 1–6 m tall. In winter it is confined to the Bahamas and adjacent Turks and Caicos Islands.

Seven species of *Dendroica* are confined to the West Indies. Of these, 3 belong to superspecies with allospecies on continental North America. The other 4 comprise an endemic West Indian superspecies of uncertain affinities within the genus. These are *D. plumbea* of Dominica and Guadeloupe, *D. pharetra* of Jamaica, *D. angelae* of Puerto Rico, and *D. bishopi* of St Vincent (the latter often placed in a monotypic genus *Catharopeza*). The group differs from all other *Dendroica* in lacking sexual dimorphism in colour, but retaining a dull immature plumage for a full year.

Closely related to *Dendroica* are 2 North American species that have evolved morphological and behavioural adaptations to specialized feeding niches, and are placed in their own monotypic genera. The Black-and-white Warbler *Mniotilta varia* has become adapted to a tree-climbing, bark-foraging habit much like that of the treecreepers (Certhiidae), with corresponding development of toes and claws. The American Redstart *Setophaga ruticilla*, which has little in common with the redstarts (*Phoenicurus* spp.) of the Old World, has become adapted for the aerial capture of insects. It is a common and well-known species, breeding in the temperate portions of the United States and Canada and wintering south to northern South America. The male is glossy black with a white belly and patches of orange on tail, wings, and sides, while in the female the black and orange are replaced by grey and yellow. It is unique among the Parulidae in that first-year males, although capable of breeding, wear a female-like plumage.

Several other genera of wood-warblers share the flycatching habit; as is the case in other families in which this habit has evolved, the bills in these genera tend to be wider and flatter and the rictal bristles better developed than in most wood-warblers. About 11 brightly-coloured species of the tropical genus *Myioborus* are also called 'redstarts'; the northern-most, the Painted Redstart *M. pictus*, was formerly placed in *Setophaga* but agrees with *Myioborus* in nesting habits, song, plumage pattern, and lack of sexual dimorphism. Another flycatching group of wood-warblers is the genus *Wilsonia*, consisting of 3 North American species that are predominantly yellow in colour but with various striking black markings on face or head. In pine forests of Middle America live 3 species of flycatching warblers that are partly or predominantly bright red. The Red-faced Warbler *Cardellina rubrifrons* ranges north to the mountains of the south-western United States, whereas the Red Warbler *Ergaticus ruber* is exclusively Mexican and the Pink-headed Warbler *E. versicolor* is confined to Guatemala and adjacent parts of Mexico.

The 11 species currently placed in the genus *Vermivora* fall into three natural groups that may prove to be generically separable, having in common sharply pointed bills. These are a face-patterned group, a plain group, and a tropical group. One of the face-patterned group, Bachman's Warbler *V. bachmani* of south-eastern United States, is at the point of extinction but may persist deep in heavily wooded swamps. The 2 tropical species *V. gutturalis* and *V. superciliosa* show some resemblance to *Parula*.

The largest of the primarily tropical genera is *Basileuterus*, with 21 species ranging from northern Mexico to northern Argentina. Most species are predominantly yellow, some with brown or grey backs. Most have a sharply defined crown-patch or other conspicuous marks about the head. Typical of this group is the Golden-crowned Warbler *B. culicivorus*, a species whose range virtually coincides with that of the entire genus. Sometimes placed in *Basileuterus* are the 2 species of the genus *Phaeothlypis*, dull-coloured birds with no striking markings and more terrestrial in habits than typical *Basileuterus*.

The Wrenthrush *Zeledonia coronata* of the mountains of Costa Rica and Panama was long given its own monotypic family, generally placed adjacent to (or by a few authors included within) the Turdinae. Recent studies of egg-white proteins, syringeal and limb musculature, and general life-history all indicate that *Zeledonia* is a member of the New World 9-primaried group, nearest to the Parulidae and probably best placed in that family. Specifically, it bears strong anatomical and external resemblances to the tropical genus *Basileuterus*, but exhibits some major adaptive modifications, notably long legs and reduced flight mechanisms, for a largely terrestrial existence.

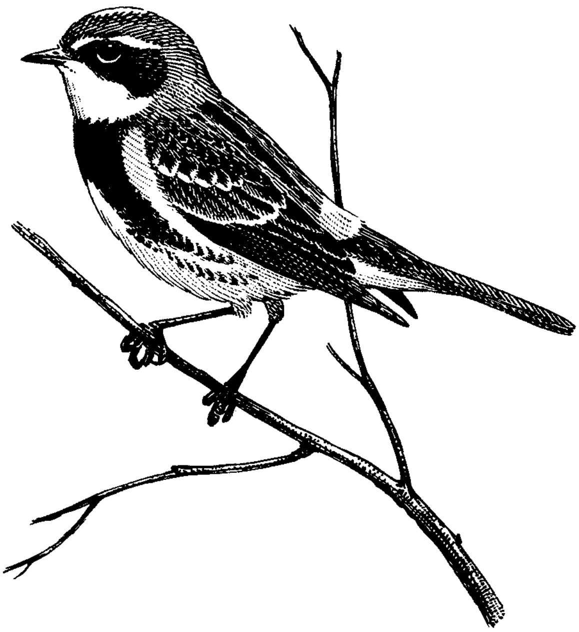
Also notably terrestrial in a predominantly arboreal family are the 3 members of the North American genus *Seiurus*. Best known and most widely distributed is the Ovenbird *S. aurocapillus*. Like its namesakes of the unrelated Neotropical family Furnariidae, the Ovenbird builds a dome-shaped nest, reminiscent of an old-fashioned outdoor oven, on the ground. It shares with the 2 species of waterthrushes *S. motacilla* and *S. noveboracensis* the habit of walking rather than hopping when on the ground. The waterthrushes, however, have a tail-bobbing motion much like that of wagtails (*Motacilla* spp.) and numerous other waterside birds.

The yellowthroats comprise a widespread group of closely related species of the genus *Geothlypis*. These are dwellers in marshes, meadows, and undergrowth, almost throughout the Americas. Most have greenish backs and yellow underparts, and males have a black facial mask of varying degrees of development. Rather similar (and considered congeneric by a few authors) are the 4 North American species comprising the genus *Oporornis*. Two of these, the Mourning Warbler *O. philadelphia* and Macgillivray's Warbler *O. tolmiei*, yellow-green birds with (in males) grey hoods and black throats, may prove to be conspecific.

The West Indies are the home of several somewhat aberrant wood-warblers, including 4 endemic genera. Semper's Warbler *Leucopeza semperi* of St Lucia, an exceedingly rare bird, is a nondescript grey. Two species of the genus *Teretistris*, grey-backed with yellow underparts, divide the island of Cuba between them. Two monotypic genera are found on Hispaniola: the Ground Warbler *Microligea palustris* and the White-winged Warbler *Xenoligea montana*. The latter strongly resembles certain West Indian tanagers (Thraupinae), and may possibly be misplaced as a wood-warbler.

Other species whose allocation to the Parulidae has been questioned include the largest of the wood-warblers, the Yellow-breasted Chat *Icteria virens*, a relatively heavy-bodied, stout-billed, long-tailed species that is coloured much like a yellowthroat (*Geothlypis*), but behaves and sounds more like a member of the unrelated family Mimidae (mocking-thrushes). It is a North American species, breeding south to the tableland of central Mexico. Also called 'chats' but very different in appearance are the 3 species of the genus *Granatellus*, tropical birds that are strongly sexually dimorphic (underparts rosy red in males, buff in females) and somewhat reminiscent of tanagers. Finally, the Olive Warbler *Peucedramus taeniatus*, which extends from south-western United States through Central America, has been thought to be related to *Dendroica*, but there is a substantial body of evidence to suggest that its affinities are closer to the 'Old World insect-eaters' (Muscicapidae in the wide sense) than to the New World 9-primaried group.

The Parulidae are notable for the number of hybrid combinations that have been reported. Hybrids are known between several species-pairs, especially the Blue-winged Warbler *Vermivora pinus* and the Golden-winged Warbler *V. chrysoptera*, which regularly hybridize where their breeding ranges overlap; 2 of the hybrid forms are so distinctive that they were originally described as species and are still known by the English names of 'Brewster's' and 'Lawrence's' Warblers. Few hybrid birds have been so thoroughly studied under field conditions, as the principal zone of interbreeding includes several of the major cities of the eastern United States. Intrageneric hybrids between sympatric species that are not species-pairs are very rare, even though (for example) 6 or more species of *Dendroica* may inhabit the same wood in north-eastern United States. On the other hand, at least 8 intergeneric hybrids of various parentage have been reported. This is not just a function of excessive generic splitting in the Parulidae, as the parent species in these combinations are often very different (see HYBRIDIZATION, ZONE OF SECONDARY). K.C.P.



Yellow-rumped Warbler *Dendroica coronata*. (*R.G.*).

Note: In the Checklist of North American Birds (6th edn) 1984, wood-warblers and troupials are placed as subfamilies (Parulinae and Icterinae) of an expanded family Emberizidae.

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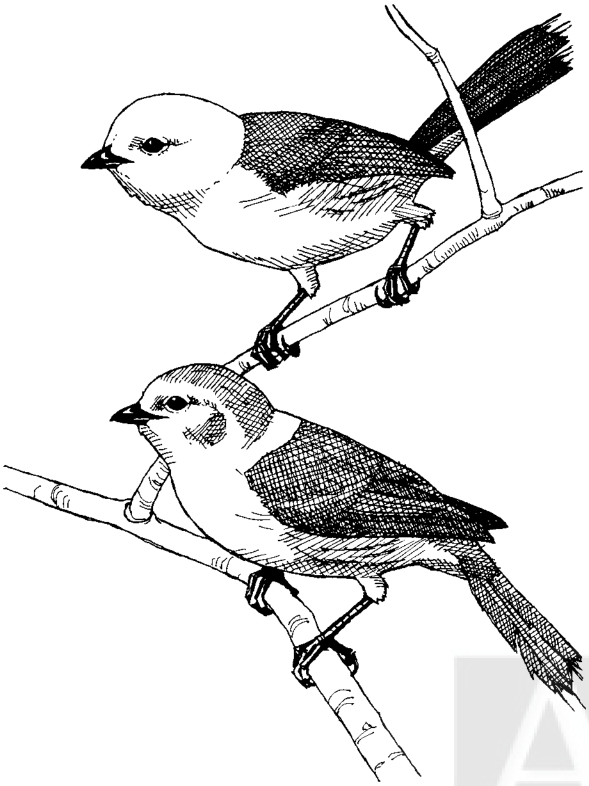
WARBLER (3): substantive name sometimes applied to species of Maluridae (see WREN (2)).

WARBLER, AUSTRALIAN: substantive name for species of Acanthizidae (Passeriformes, suborder Oscines); a family of 14 genera and about 65 species which includes scrubwrens, thornbills and allies. The largest genus, *Gerygone* (19 species) extends from the Malay Peninsula through Indonesia, New Guinea, Australia and New Zealand to the South-west Pacific. *Sericornis* (scrubwrens, 14 spp.) is shared almost equally between New Guinea and Australia. *Acanthiza* (thornbills, 13 spp.) has one species, *A. murina*, in New Guinea, the rest in Australia. The remaining 11 genera have no more than 3 species each and, with the exception of the New Guinean *Crateroscelis*, are confined to Australia. K.H. Voous regards the New Zealand genera *Mohoua* and *Finschia* as constituting a subfamily Mohouinae of the Acanthizidae. Keast (1977, Notornis 14: 50–58) however, has suggested that their affinities lie rather with the pachycephaline flycatchers.

Characteristics. Although recently separated from the Maluridae (see WREN (2)), the family Acanthizidae has yet to be rigorously defined, particularly in anatomical terms. It consists of small (*Smicrornis brevirostris*, Weebill, 9 cm) to medium-sized (*Dasyornis* spp., bristlebirds, 25 cm) songbirds of unexceptional proportions, mostly dull or cryptically coloured, with little or no obvious sexual dimorphism, semi-terrestrial to wholly arboreal and building domed nests. Some species have loud melodious songs. The tails of some species are regularly cocked, hence the name 'wrens'.



Whitehead *Mohoua albicilla*. (*N.W.C.*).

Habitat. Primary rain-forest (*Crateroscelis*, *Oreoscopus*, many *Sericornis* spp., several *Gerygone* spp.), second-growth, monsoon forest and mangroves (some *Sericornis* spp., many *Gerygone* spp.), to lower, dryer, more open habitats such as sclerophyll woodland, mallee-heath and acacia shrubland (many *Acanthiza* spp., *Hylacola*, *Pyrrholaemus*), tussock grassland (*Calamanthus fuliginosus*), and samphire flats (some populations of *Acanthiza iredalei*). The Rock Warbler *Origma solitaria* is remarkable in being restricted to the caves and boulders of sandstone and limestone districts of eastern New South Wales. The bristlebirds *Dasyornis* (3 spp.) inhabit extremely dense thickets in forests and on coastal dunes, in which they are more often heard than seen.

Movements. At least some (possibly most) rain-forest species are strongly sedentary. Woodland and mallee-heath species are generally resident with some local dispersal, whereas several arid-zone species are highly mobile, e.g. Slender-billed Thornbill *Acanthiza iredalei*, Chestnut-breasted Whiteface *Aphelocephala pectoralis*. A few species are known to be migratory; these include the Western Warbler *Gerygone fusca* and the White-throated Warbler *G. olivacea*.

Food. Chiefly small insects and vegetable matter: lacewings, bugs, ants, wasps, flies, beetles, orthopterans, caterpillars, seeds and berries. Whereas *Gerygone* spp. are more or less wholly insectivorous, most other species take a varying proportion of seeds and other plant matter as well as insects; the proportion of seeds is apparently highest in the thick-billed whitefaces *Aphelocephala* spp. Some ground-feeding species (e.g. Scrub Tit *Sericornis magnus*, White-browed Scrubwren *S. frontalis*) also take tiny snails and crustaceans, while a substantial part of the diet of the Pilotbird *Pycnoptilus floccosus* apparently consists of worms and tiny freshwater mussels. The Rufous Bristlebird *Dasyornis broadbenti*, on the other hand, takes in season large quantities of the small fleshy fruits of 'Native Currant' *Leucopogon parviflorus* (Epacridaceae) and a *Rhagodia* sp. (Chenopodiaceae).

Behaviour. Most aspects of behaviour are very poorly known, even for the commonest species. Many species breed in pairs, though co-operative breeding has now been reported for the Buff-rumped, Striated and Yellow-tailed Thornbills *Acanthiza reguloides*, *A. lineata* and *A. chrysorrhoa*, for the White-browed Scrubwren and the Weebill. Outside the breeding season, individuals of some species are mostly found singly (e.g. *Gerygone olivacea*, *G. fusca*), whereas in other species they occur in family parties or small flocks (e.g. *Acanthiza chrysorrhoa*, *Aphelocephala* spp.).

Voice. Many species have a loud, melodious and distinctive voice, and some are exceptionally fine songsters, e.g. *Crateroscelis murina* of New Guinea and *Hylacola pyrrhopygia*, *Calamanthus* spp. and *Pyrrholaemus brunneus* of Australia; *H. pyrrhopygia* and the Speckled Warbler *Chthonicola sagittata* are accomplished mimics. *Gerygone* spp. have high, thin songs, mostly uttered as plaintive repeated rising or falling strophes or staccato bursts of the same pitch. Others, including *Sericornis* and *Acanthiza* spp., utter mainly buzzing, rattling or trilling notes, though some of these species also possess short unobtrusive songs. The furtive, thicket-loving bristlebirds have loud, far-carrying whistling calls, usually the sole indication of their presence.

Breeding. Nests are globular or oval, with a side-entrance; made of pliant plant-material (grass, bark, stems, roots) sometimes decorated with moss, cocoons and spiders' silk and lined with plant down, fur and feathers; the nest of the Fern-wren *Oreoscopus gutturalis* is made almost entirely of moss, whereas that of the Banded Whiteface *Aphelocephala nigricincta* is constructed largely of twigs and, atypically for this family, has a spouted side-entrance. Nests may be supported from below, on or near the ground (e.g. *Dasyornis*, *Pycnoptilus*, *Hylacola*, *Calamanthus*, some *Acanthiza* spp., *Sericornis* except *S. citreogularis*), or be pendent in outer foliage (e.g. *Gerygone*, *Smicrornis*, some *Acanthiza* spp., *Sericornis citreogularis*). The Common Whiteface *Aphelocephala leucopsis* and at least 2 species of *Acanthiza* regularly nest in hollows in trees and fenceposts or under bark. The Rock Warbler suspends its nest by dense spiders' webbing from cave-ceilings and rock-overhangs.

Where details are known, the nest is built by the female or by both sexes; in *Acanthiza chrysorrhoa* both birds build the main nest, after which the male often builds one or more cup-shaped false nests on top of the main one.

The eggs of the scrubwren group (*Sericornis*, *Hylacola*, *Calamanthus*, etc) can be quite striking in coloration, having in most species a dark ground (grey, grey-brown or terra cotta) with or without darker spotting. Those of *Acanthiza* and *Gerygone*, on the other hand, are of a whitish or creamy-pink ground with spots and speckles of reds and lavender greys. The clutch is mainly 2 or 3, less often 4 or 5 (as sometimes in *Acanthiza* and *Aphelocephala*). Many species are favoured hosts to cuckoos.

Details of egg-laying, incubation and nestling periods are poorly known, but according to Courtney and Marchant (1971) some species may lay at intervals of 48 rather than 24 hours. S.A.P.

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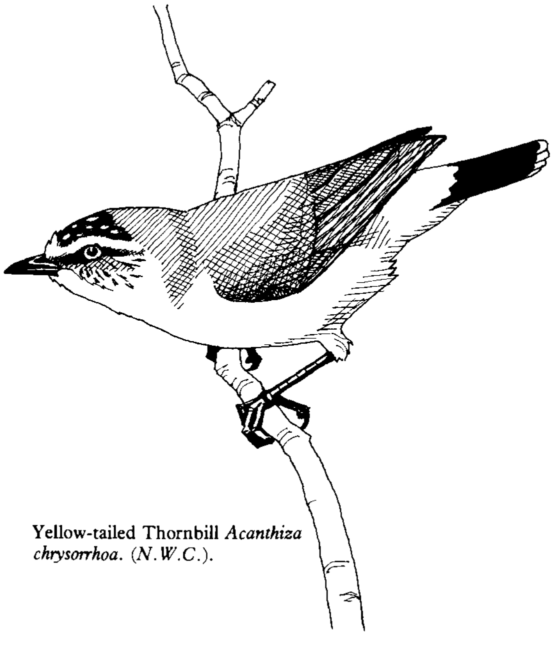

Yellow-tailed Thornbill *Acanthiza chrysorrhoa*. (*N.W.C.*).

WARBLER-FINCH: *Certhidea olivacea*, one of DARWIN'S FINCHES which superficially resembles a warbler and fills the ecological niche of the warblers in the Galapagos.

WARBLING-FINCH: substantive name of the species of *Poospiza*, a genus of South American finches (for family see FINCH).

WARM-BLOODEDNESS: see ENERGETICS; HEAT REGULATION.

WARNING: the approach of a predator may be announced by potential prey species either visually or aurally. Visual signals usually emphasize some striking feature of the plumage; for example, the tail-flirting of the Moorhen *Gallinula chloropus* when the white under tail-coverts are displayed prominently. Audible signals are loud or penetrating calls, sometimes specialized to denote the type of danger, for example, an aerial or a ground predator (see ALARM; VOCALIZATION).

WATERCOCK: *Gallicrex cinerea* (see RAIL).

WATERFOWL: vague term for aquatic (usually fresh-water) birds of wild species, especially of the Anatidae (see DUCK); in Britain applied more particularly to those kept for ornamental purposes, in some degree of captivity, on private lakes or artificial ponds (see AVICULTURE); in North America used in the sense (British) of WILDFOWL.

WATERHEN: alternative name (perhaps obsolescent) in Britain of the Moorhen *Gallinula chloropus*; also used as substantive name of *Amaurornis* spp. (see RAIL).

WATERTHRUSH: substantive name (now commonly written as one word) of 2 *Seiurus* spp. (see WARBLER (2)).

WATER-TYRANT: substantive name of tyrant-flycatchers of the genera *Fluvicola* and *Ochthornis* (see FLYCATCHER (2)).

WATTLE: see INTEGUMENTARY STRUCTURES.

WATTLEBIRD (1): substantive name of *Anthochaera* spp. (see HONEYEATER). This Australian usage is of uncertain priority in relation to the next below.

WATTLEBIRD (2): name introduced by George Forster in 1777 and used in the plural as general term for the Callaeidae (Passeriformes, suborder Oscines), of which all species have different substantive names. The family is restricted to New Zealand and comprises 3 monotypic genera (one extinct). Relationship of the Callaeidae to other families is uncertain; generally placed near the starlings (Sturnidae), they may be closer to the Corcoracidae, or to the bowerbirds and birds-of-paradise. They probably arose by adaptive radiation from a single immigrant stock that developed wattles; the resemblance of *Callaeas* to the Apostlebird *Struthidea* is thus probably in part convergent.

Characteristics. Wattlebirds are medium-sized (25–48 cm) birds of the primitive forest, arboreal but sometimes feeding on the ground. Their most conspicuous common characters are the paired fleshy wattles at the gape. They share certain skeletal characteristics and others such as extremely rounded wings with very long first primaries, long tails, somewhat arched in profile and section, with projecting feather shafts; powerful legs and feet with long hind claws. The wattles (orange except in one form) develop from the fold of skin at the angle of the nestling's gape, remain small in juveniles and are largest in adult males; their function is obscure. In *Callaeas* they are normally held close in to the throat, overlapping in adult males and meeting below the bill, and never pendulous (as often illustrated). The 3 species are the Saddleback *Philesturnus* (*Creadion*) *carunculatus*, the Kokako *Callaeas cinerea* and the extinct Huia *Heteralocha* ('*Neomorpha*') *acutirostris*.

Habitat and distribution. Inhabitants of the forest interior, the wattlebirds are now much localized. Kokako persist only in little modified and extensive remnants of original lowland forest. The Huia was recorded only from the southern part of the North Island. Saddlebacks are now restricted to a dozen islands, free of predatory mammals, off the North Island and Stewart Island, having been transferred to some by the New Zealand Wildlife Service.

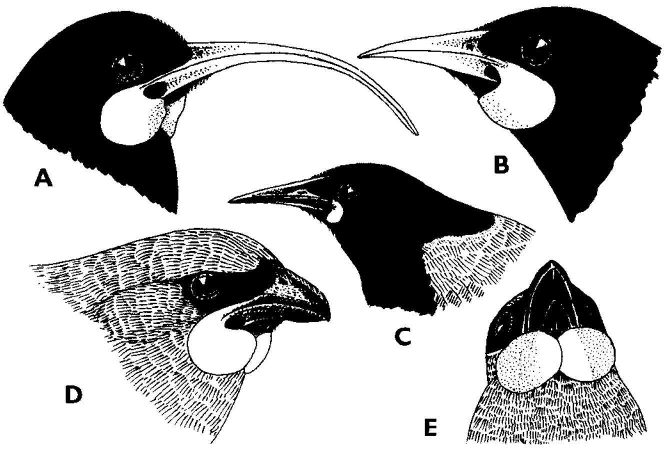

Fig. 1. Bills of New Zealand Callaeidae. **A** and **B**, female (left) and male Huia *Heteralocha acutirostris*; **C** Saddleback *Creadion carunculatus*; **D** and **E** Kokako *Callaeas cinerea*. (*C.F.*).

Food. The Saddleback feeds mainly on insects from decaying wood, bark and the forest floor, but also on fruits; the diet of the Huia was similar but the Kokako feeds mainly on young leaves and fruit, with some invertebrates. Food is occasionally grasped with a foot, parrot-fashion. The Saddleback (and formerly the male Huia) can prize open insect tunnels in wood by a 'gaping' technique, using specially adapted muscles.

Breeding. The nests are shallow, open, loosely built of rootlets, twigs and leaves, lined with moss and fern-scales, generally sheltered from above and placed in a hollow or ledge up to 10 m above ground. The 2–3 (sometimes 4) eggs are grey or brown, with purplish-grey or brown blotches. The incubation period of the Saddleback is 19–21 days; 20 days or more for the Kokako, which fledges in *c.* 27–28 days. Incubation and brooding are by the female only, but both sexes carry food. Nestling faeces are removed (Saddleback) or eaten (Kokako).

The Huia was notable for the extreme sexual differentiation of the bill, each sex using a different technique to obtain beetle larvae ('huhu') and wingless orthoptera ('weta') from decayed wood; the male chiselled out grubs while the female's long pliant bill probed borings; but there is no evidence that they cooperated in feeding. The sexes were otherwise alike, glossy black with a broad white band across the tip of the tail. The Maori wore the prized tail feathers in their hair as a mark of rank and traded them throughout the country. Extinction has been attributed to hunting by the Maori and by collectors during the 19th century (last recorded *c.* 1910).

The Saddlebacks are the best known wattlebirds; sedentary and long-lived, they pair for life and occupy territories that are maintained by the loud male songs of varying 'dialect', culturally transmitted (Jenkins, 1977). When excited, the male's wattles stand out and are curved to lie forward of the gape. Bill-touching, mutual preening and courtship-feeding maintain the pair-bond at all seasons. The display involves bowing to exhibit the chestnut saddle, tail fanning and stretching of the neck, and wing vibration by the female. Saddlebacks rarely undertake sustained flights, although they crossed water gaps of *c.* 200 m between the Chickens Islands.

Kokako resemble Saddlebacks in their sedentary habit, mating for life, maintenance of the pair-bond and displays. They use their strong legs to leap through the forest between the canopy, where they sing and display, and the understorey of shrubs and lianes where they feed. Formerly known as 'wattled crows', they are bluish-grey, with velvety black lores and short, stout, arched bills. The wattles are orange with bluish bases in *Callaeas c. cinerea* (South and Stewart Islands) and bright blue in the North Island *C.c. wilsoni*. The song, mellow and bell-like, has earned the bushman's names of 'organbird' and 'true bellbird'. The South Island subspecies is probably extinct; the North Island race has become a symbol for the conservation movement in New Zealand.

C.A.F.

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WATTLE-EYE: substantive name of *Platysteira* spp. and related forms (for family see FLYCATCHER (1)).

WAVEY: a name in North America for the Snow Goose *Anser caerulescens* (see under DUCK).

WAXBILL: substantive name of various *Estrilda* spp. etc.; in the plural, general term for the family Estrildidae (see ESTRILDID FINCH).

WAX, METABOLISM OF: see HONEYGUIDE.

WAXWING: substantive name of the 3 species of the subfamily Bombycillinae of the family Bombycillidae (Passeriformes, suborder Oscines), used without qualification in Britain for the only European species; in the plural, general term for the subfamily (for related forms, see under HYPOCOLIUS). The English name refers to the red, drop-shaped and wax-like tips of the secondary flight feathers, which are prolongations of the shafts. The phenomenon can be seen to a much lesser degree in the tail. Many individuals of all species lack these appendages, which are not correlated with age, sex or season: their exact function is unknown, but it may be that the decoration of the tail-wing-tip area distracts the attention of a predator.

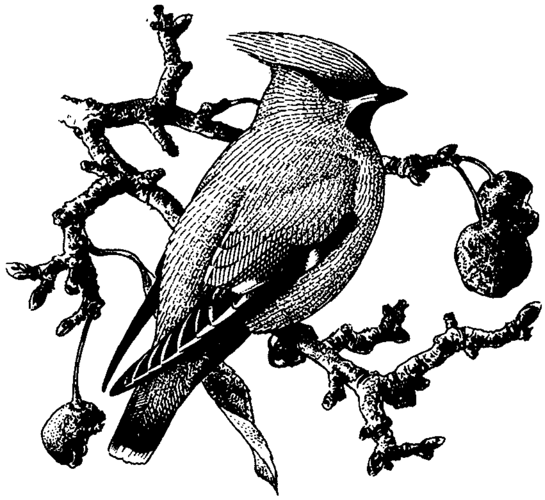
Characteristics. The 3 species are similar in size (*c.* 18 cm long) and colour, with characteristically soft, silky plumage, relatively long, pointed wings and slightly rounded tails. Their heads are crested and the vinaceous brown plumage shades into greyish-brown on the back and grey on the rump. The tails are black, tipped with lemon-yellow or red. The short bill is broad at the gape, slightly hooked and notched; feet and legs are short and stout. The sexes are similar, except that males as a rule have black throats. Juveniles of all species lack a throat patch.

Habitat. Outside the breeding season waxwings may be found wherever acceptable fruits are available, including gardens and even the centres of cities. The breeding habitat is coniferous forest, often near water but also on dry heaths.

Distribution. The one genus consists of the (in American usage) Bohemian Waxwing *Bombycilla garrulus* of Holarctic distribution, the so-called Japanese Waxwing *B. japonica*, native to eastern Siberia, and the Cedar Waxwing *B. cedrorum* of North America.

Movements. Their flight is strong and undulating and flocks make irregular movements in winter from their northern breeding areas to central Europe (in some years to Britain), central China, Japan and as far as Central America (see IRRUPTION).

Food. The highly nomadic waxwings are the only primarily frugivorous bird group in the North Temperate zone. They eat only the flesh of the berries and capture insects in the air during the breeding season.



Waxwing *Bombycilla garrulus*. (*A.H.*).

Display. Aggressiveness in *Bombycilla garrulus* is indicated when one bird perches upright near another, with all its feathers and its crest sleeked down, making it appear tall and thin. In the courtship display, however, the axis of the body is horizontal and the feathers erected rather than sleeked. The male hops towards the female, depresses his tail and erects the feathers of his lower back, rump and upper tail-coverts to form a smooth continuous hump. At the same time he raises the feathers on his belly and under tail-coverts, making him appear much larger and shorter-legged. As he erects his feathers, he pivots a little towards the female, at the same time turning his head slightly away. His crest is erected almost vertically. As he turns his head away, he bends his closed tail laterally towards the female. If she is responsive and shows signs of erecting her feathers in similar fashion, a 'gift-passing' ceremony follows, in which the pair perch near one another and may face in the same or opposite directions. The male has in his bill a small object which may be a morsel of food but may equally well be someting inedible which he has just picked up. He stretches his neck so that he is looking down at the female, who is crouching slightly, and deliberately places the object in her open bill. The two birds then hop apart and relax the plumage a little. They remain motionless, then a second or two later they move together again, take up the same posture, and the ceremony is repeated with the roles reversed. This silent passing backwards and forwards of the 'gift' may continue and has been seen to take place up to 14 times in succession. Copulation may occur after perhaps one display in 10.

Voice. A soft whistle, trill and chatter have been recorded, but no true song.

Breeding. Nests may be found singly or in small groups. They are usually in spruces but sometimes in pines or deciduous trees. They are made of twigs, beard moss, lichens and moss with a soft lining; the male may assist the female in building. Clutches of 3–7 (most commonly 5) eggs are laid late in May but usually in June. The ground colour is pale greyish blue, marked profusely with small black dots and fine irregular lines. Both sexes incubate for 15–18 days, the female being fed on the nest by her mate. The naked young are fed by regurgitation, fledge in from 19–22 days and accompany their parents for 3 weeks. E.P.

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WEATHER AND BIRDS: the state of the atmosphere at a definite time and place with respect to heat or cold, wetness or dryness, calm or storm, clearness or cloudiness, and its bearing on the behaviour and life history of birds. Here, weather is taken to mean short-term, somewhat irregular changes in atmospheric factors within the seasonal climate of a given latitude and longitude.

General considerations. As homeotherms, birds possess a high, constant core body temperature. Weather conditions play a role in determining what proportion of their food birds must convert to heat energy to maintain their body temperature (see ENERGETICS). Within a certain range of ambient temperatures, called the thermoneutral zone, the cost of body temperature maintenance is minimal. In progressively lower air temperatures more energy must be spent in activities such as shivering to keep up body temperature. Conversely, in ambient temperatures above the thermoneutral zone, birds spend energy (and water) to keep down their internal temperatures by evaporative cooling of moist tissues (see HEAT REGULATION). Increasing solar radiation or relative humidity pushes the thermoneutral zone toward low temperatures. Higher wind velocities move the thermoneutral zone toward higher air temperatures. A major response of birds towards transient weather conditions is to adjust their behaviour, where possible, to minimize the metabolic cost of environments outside the range of thermoneutrality. When these behavioural adjustments fall short, we see damage to avian survival and reproduction. Birds as flying machines also are affected by weather, particularly by winds during migration. Weather can interfere with the sensory systems of birds and determine the location and activity of prey items, thereby indirectly affecting the birds themselves.

Food-finding. Evolution appears to have selected for behaviour which promotes the net energy intake of foraging birds. Because net energy equals energy found minus the cost of searching, one should expect birds to minimize the energetic cost of foraging whenever necessary and possible. Small songbirds of hot, dry regions must often look for food in temperatures well above their thermoneutral zone. As they also must conserve water, evaporative cooling cannot be used profligately. With increasing ambient temperature, many small birds seek insect prey in increasingly shaded areas. In one study, above 45°C the Verdin *Auriparus flaviceps* confined 70% of its foraging to deep shade near the trunks of trees.

In winter, many temperate zone birds are confronted with the opposite problem, how to conserve energy below the thermoneutral zone. One mixed-species flock of tits *Parus*, nuthatches *Sitta* and woodpeckers *Picoides* wintering in a deciduous wood used several techniques to husband energy. In response to either decreasing temperature or increasing wind velocity, the birds descended from the canopy layer into the decreased wind velocities lower down. In very harsh weather, they confined their food-searching to the ground. They also used windbreaks more, switching to larger-diameter branches and to the leeward sides of substrates. Additionally, the windward sides of woodlands were abandoned in proportion to wind speed. As a bird moves more rapidly, it effectively finds itself in higher wind velocities. Consequently, lower temperatures and higher ambient wind speeds caused these species to curtail their own movements to reduce energy expenditures. Over a range of 30°C, one tit *Parus carolinensis* quadrupled its foraging speed. As expected, solar radiation had an ameliorating influence. Under similar regimes of wind and temperature, birds foraged farther away from windbreaks, nearer the windward side of the wood and at faster rates in sunshine than under a heavy cloud layer.

Quite independently of its consequences for avian energetics, weather can influence food-finding by interfering with birds' ability to perceive their prey. The Osprey *Pandion haliaetus* was less successful at catching fish when the water surface became rippled by wind. Ospreys also caught fewer fish under cloud than in direct sunlight. Since the reduction in catch coincided with a reduced diving rate, the ripples and cloud cover evidently interfered with the birds' visual perception. Also, under conditions of reduced visibility Ospreys took a higher proportion of silvery, highly visible fish and fewer brownish-coloured species. Some sea terns show markedly reduced success when strong winds and a rough sea conspire to force prey deeper and disrupt diving accuracy. Completely calm conditions can also be detrimental, facilitating the prey's vision of the overhead predator.

We know little of how other sensory systems employed by hunting birds might be influenced by weather. Do winds riffling forest leaf litter interfere with owls' location of running mice by sound? Does high humidity which enhances the aerial transmission of chemical scents, aid the olfactory location of food by kiwis *Apteryx*, Turkey Vultures *Cathartes aura*, petrels (Hydrobatidae), shearwaters (Procellariidae) and, possibly, oilbirds *Steatornis*? Weather induced changes in the distribution and abundance of prey strongly affect aerial insectivores. On warm, still days David Lack found Common Swifts *Apus apus* collecting insects between 6 and 30 m above open fields. Whenever a fresh breeze appeared, the Swifts hunted on the upcurrent of air at the windward edge of tree belts where insects were blown and concentrated from nearby fields and meadows. Rain stopped the Swifts' hunting flights by grounding their prey, but Spotted Flycatchers *Muscicapa striata* continued to hawk for insects sheltering under umbrella-like tree canopies. In certain parts of their winter range, American Kestrels *Falco sparverius* hunt insects during thaws and rodents and birds during freezes.

Roosting and perching. Birds can adjust their roosting and perching habits to alleviate the energy demands of weather. Treecreepers *Certhia* and Tree Swallows *Iridoprocne bicolor* roost nightly in compact masses within tree cavities in severe weather. The reduction in exposed surface saves each bird maintenance costs. In the laboratory, 50% of the birds in a flock of House Sparrows *Passer domesticus* roosted in contact at −10°C, while only 10% did so at 0°C.

Where birds select to spend the night can depend on the weather. In one winter study, Starlings *Sturnus vulgaris* roosted in pine stands rather than deciduous woods, presumably in response to the reduced wind velocities found there. The assemblage of birds roosted homogeneously throughout a pine wood in fairly mild conditions. On harsher nights, they abandoned the windward side and descended to a low height in the remainder of the woods. This adjustment placed them in the least windy habitat available.

During the day, perching or standing birds can reduce metabolic costs in hot or cold weather by selecting more benign microclimates and adopting certain postures. On bright cold days in winter, small woodland birds stop to rest, sleep or preen behind windbreaks and fully exposed to solar radiation. On cool mornings perching vultures (Cathartidae) and Anhingas *Anhinga anhinga* spread their wings perpendicular to the sun's rays. Roadrunners *Geococcyx californianus* below the thermoneutral zone capitalize on solar radiation by erecting body plumage to expose highly absorbent patches of black skin. Above their thermoneutral zone Herring Gulls *Larus argentatus* have been seen rotating their bodies east, south and then west through the day so as to face the sun continuously. This behaviour kept to a minimum the birds' surface area exposed to direct solar radiation while presenting the highly-reflective white head and breast to the sun's rays. In hot weather, vultures intentionally defaecate on their legs and feet, apparently to cool themselves by evaporation.

Migration. The components of weather impinge on birds commuting between reproductive and non-breeding sites. As in food-finding, both the energy cost of the migration flight and the ability of sensory capacities to monitor the environment are determined by prevailing atmospheric conditions (see MIGRATION).

Tail winds increase the ground speed of a flyer, thereby reducing the energetic cost of covering a given distance. At the very least, one would not expect migration in headwinds greater than the birds' airspeed. Crosswinds tend to displace migrants from their normal route and to reduce the ground speed of individuals compensating for wind drift.

Cloud cover is of uncertain significance for small nocturnal migrants. While some appear able to maintain a heading while enveloped in heavy cloud, radar work has revealed disoriented birds under such conditions of drastically reduced visibility (see MIGRATION; NAVIGATION). At minimum, disorientation would increase flight time with concomitant heavier energy demands. It could also lead to peril if birds wrongly flew out to sea or over such unsuitable areas as deserts.

Air temperature during flight is apparently of secondary significance. The southerly winds preferred by spring migrants are usually warm, while autumn movements are greatest on northerly winds, even cold ones.

Intense precipitation may penetrate plumage and destroy its insulating properties. It also adds weight to be kept aloft. This dual drain on energy usually restrains migration during inclement weather. Nonetheless, migrants have been driven to the ground or into the sea by rain, snow, hail and icing.

Weather cues available to migrants. In North Temperate latitudes, alternating high and low pressure areas move from west to east. Winds at the ground and aloft flow clockwise around high pressure centres and counterclockwise around low pressure centres. Thus, between a low to the west and a high to the east prevailing weather is marked by southerly winds and warmer temperatures. Between an easterly high and westerly low, winds are from the northern quadrant and temperatures are colder. As a rule, small birds begin migrating in the spring just after a high pressure system has passed when warm tailwinds prevail. Some reports describe long-distance flyers in particular taking off in the light, variable winds within a high. This behaviour would put them into a warm tailwind hours later as the easterly-moving weather crosses their flight track. In the autumn, songbirds begin migration under the northerly wind flow between low pressure to the east and a high to the west. Apparently, in the autumn a tailwind is selected even though birds could fly in warmer temperatures if they waited for a low to the west when winds would be warmer, but head on. Variations on the above theme occur among species depending on flight distance and preferred migration direction.

Swifts and swallows are exceptional in that, particularly in autumn, their low-altitude migrations often point against the wind. The explanation might be that these birds, which remain near the ground to catch insects en route, would be in danger in a tailwind if they stalled when overtaken by a sudden gust. Recent evidence indicates that wind velocity, when separated from direction, does not significantly influence the tendencies for passerines to migrate or remain aloft. However, hawks and other large diurnal migrants are concentrated along leading lines (lake and ocean shores, mountain ranges) if crosswinds are strong (see below).

Changes in temperature, atmospheric pressure and relative humidity are joined in a predictable way. A low pressure cell following a high brings increasing temperature and relative humidity and decreasing atmospheric pressure. As one would expect, falling pressure and high or rising temperature almost always accompany spring migration; the reverse is true in autumn. Rather inexplicably, radar studies of nocturnal migrants have shown that peak migrations in both autumn and spring can occur when relative humidity is low.

Waterfowl and shorebirds are much faster flyers than songbirds and many species are a good bit larger. Although these migrants generally respond to weather as do passerines, they show more variability, curlews *Numenius* leaving Finland in thunderstorms, vagrant shorebirds pushed well outside the normal range by crosswinds, geese *Anser* flying on into snowstorms in the spring. Sightings of this sort may be explained by the very long non-stop flights these species undertake. Snow Geese *Anser caerulescens* reportedly journey from James Bay in Canada to the Gulf coast of the United States without respite. American Golden Plovers *Pluvialis dominica* overfly the Pacific non-stop from Alaska to the Hawaiian chain. Variation in weather during these long flights would be extensive and greater than on the shorter flight paths of most songbirds. Also, their large size and greater energy reserves make the larger shorebirds and waterfowl impervious to weather a songbird would not survive.

The large-winged buzzards *Buteo*, vultures (Cathartidae) and eagles *Aquila*, *Haliaeetus* are adapted for soaring and gliding (see FLIGHT). Their migration is diurnal and is heavily influenced by weather and localities promoting the thermal or deflected updrafts on which soaring depends. Weather and topography interact to promote a complex variety of warmer, rising air formations from doughnut-shapes under cumulus clouds to banded patterns oriented parallel to the prevailing wind. Conditions promoting thermals useful to migrants occur under clear skies and light to moderate winds. Hawk flights north in spring are greatest then, particularly when winds are southerly. Most autumn flights also take place in clear weather and, like the songbirds, hawks in autumn seem to prefer a cold tailwind to a warmer southerly headwind. The well-known concentrations of migrating hawks along shores upwind of large bodies of water occur when wind-pushed thermals carrying them along diminish in intensity over water.

Mountain ranges astride prevailing winds are important corridors for soaring and gliding migrants. The Appalachian Mountains of eastern North America extend south-west from eastern Canada almost to the Gulf of Mexico. When northerly to westerly air meets this barrier it is deflected upward, providing a long wafer of air in which hawks glide in straight lines for many kilometres between wing beats. As gliding costs only a fraction of the energy spent in powered flight, hawks in autumn capitalize on these updrafts; the vast bulk of birds following mountain ridges goes past in the interval between a low and the next high pressure system on winds from the north to west.

Reverse migration. Reverse migration, as applied to the Northern Hemisphere, refers to flights south in spring and north in autumn, tendencies contrary to prevailing movements. This phenomenon is a consistent, though minor, component of seasonal passages. Its causes remain obscure, but in spring reverse migration is usually accompanied by tailwinds from the north, air that would strike head on migrants pursuing the normal path. This fact suggests that birds may retreat southward temporarily when they meet harsh weather, or that birds use wind direction as a cue in determining flight direction, or that migrants backtrack on favourable winds to reach destinations recently overshot. Reverse migration of songbirds in autumn is also known. Warm southerly tailwinds usually accompany these excursions, but their significance and causation are poorly understood.

Reproductive behaviour. In general, reproductive activities of temperate-zone species are under the fundamental control of photoperiod-induced changes in hormone levels (see BREEDING SEASON; ENDOCRINOLOGY AND THE REPRODUCTIVE SYSTEM). Prevailing weather conditions can inhibit or advance the timing of breeding behaviour, and if severe enough they may prevent successful reproduction.

The impact of weather on territorial singing in passerines diminishes as the breeding period progresses. Song Sparrows *Zonotrichia melodia* of North America cease singing in late autumn and remain silent in December regardless of weather. In January, singing is heard only during unseasonably warm spells. Low temperature becomes less a deterrent as spring progresses. During March, males sing in temperatures which silence them in January. Windy and cloudy weather also inhibits singing in January, but not later on.

Nest building and egg laying in songbirds are delayed by colder and promoted by warmer than normal weather. The onset of egg-laying by larger birds such as waterfowl and raptors appears little affected by weather. In regions with long dry seasons, precipitation is an important trigger for reproduction. Many birds of African and Australian deserts begin courtship and nest building within hours of the first rain.

In small birds, which are tied more closely to weather, length of the periods off the nest is directly related to ambient temperature. Several species have been found to spend shorter periods both on and away from the eggs in cooler weather. An explanation might be that in cool air the incubating bird becomes hungry more often, but the same weather stimulates it to return and cover the cooling eggs promptly.

During the nestling period, weather's principal action is to regulate the rate at which parents find food. Particularly affected are aerial insectivores and birds that must commute long distances between foraging and nest sites. Rain and cold weather ground flying insects. In the American Purple Martin *Progne subis* rain lasting 3 or more hours or temperatures below 13°C substantially reduced food delivery to nestlings. Certain species that are particularly vulnerable to adverse weather have evolved the ability to reduce nestling growth rates under starvation conditions and to survive unusually long periods without food. Starving nestling swifts, shearwaters (Procellariidae) and storm petrels (Hydrobatidae) use up fat stored in good weather, slow down feather growth, and periodically allow their body temperature to fall almost to air temperature. These qualities allow nestlings to survive without food for several days or more, while passerine birds without these adaptations starve to death in a few hours. T.C.G.

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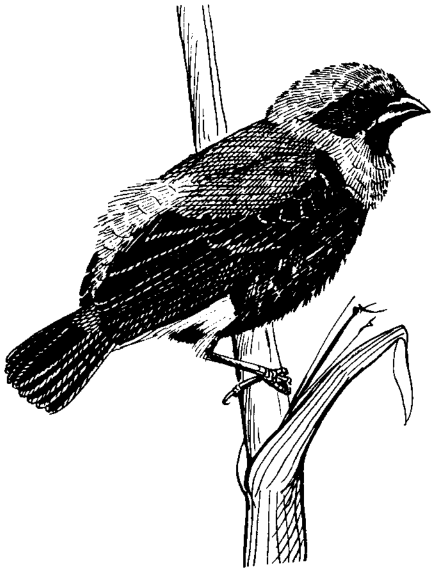
WEATHER MOVEMENT: see MIGRATION.

WEAVER: substantive name of many species of Ploceidae (Passeriformes, suborder Oscines). Most current authorities place the weaver-finches in a separate family Estrildidae (see ESTRILDID FINCH), and the sparrows in their own family Passeridae (see SPARROW), whereas formerly they were both considered subfamilies within Ploceidae. The viduine whydahs (alternatively indigo-birds, combassous, widow or widow-finch) have been considered a subfamily of Estrildidae by some, and of Ploceidae by others, and are treated separately (see WHYDAH (1)). A full review of the literature is given in Bentz (1979).

Here the weaver family is divided into the buffalo-weavers (Bubalornithinae), true weavers (Ploceinae), sparrow-weavers (Plocepasserinae) and scaly-weavers (Sporopipinae). The latter 2 subfamilies are the subject of a separate article (see SPARROW-WEAVER AND SCALY-WEAVER). The Ploceidae, an Old World and very largely African family, are finchlike birds 13–26 cm long, generally with rather short conical bills; they have rounded wings with 10 primaries (the outermost much reduced) and tail with 12 rectrices. All build roofed nests, and the tropical species breed mainly in the rainy season. Unlike the Estrildidae and Viduinae, the nestlings of Ploceidae do not have patterned mouth parts.

Within the true weavers, Moreau (1960) recognized 8 genera (number of species in parentheses): *Amblyospiza* (1), *Anomalospiza* (1), *Euplectes* (16), *Foudia* (6), *Malimbus* (10), *Neospiza* (1), *Ploceus* (57), and *Quelea* (3). Some of the species numbers have been modified and the São Tomé Grosbeak-weaver *Neospiza concolor* is possibly not a member of the Ploceidae. Nothing has been seen of it for many years and its life history is unknown. Within the large genus *Ploceus*, certain species groups can be recognized, some through similarities of nest structure, and some have been given generic status in the past. Eleven superspecies have been proposed within Africa by Hall and Moreau (1970). Insular isolation has not been important for speciation in Ploceinae, and the great rain forest that covers much of central Africa, from the Atlantic to Uganda, has



Black-winged Bishop *Euplectes hordeacea*. (*C.E.T.K.*).

acted as an efficient barrier to the spread of savanna species (see below).

In the buffalo-weavers 2 genera are recognized: *Bubalornis* (2 species) and *Dinemellia* (1 species).

Characteristics, distribution and habitat. Apart from 7 species in *Ploceus* and all species in *Foudia*, the true weavers are confined to the Afrotropical region, although one African species, Rüppell's Weaver *Ploceus galbula*, found in southern Sudan and northern Somalia, extends its range into western Arabia. Most of the *Ploceus* species of the drier areas of Africa, but not those of forest and wetter areas, have marked sexual dimorphism, with the females predominantly dull and streaky ('sparrowy') and the males, brilliant yellow in their plumage in the breeding season, assuming a similar dull plumage in the non-breeding season. As many species of *Ploceus* occur in Kenya and Uganda as occur in western and southern Africa combined. Of the 50 or so found in Africa, 8 have very restricted distributions and are rare. Most of the remainder inhabit savanna or fringing forest, the most widely distributed being the Village Weaver *Ploceus cucullatus* which also occurs in cultivation within the forest zone. The Giant Weaver *P. grandis* (22 cm), endemic to São Tomé, is considered to be derived from the Village Weaver (15 cm). Of the forest species, the Yellow-mantled Weaver *P. tricolor* is found in both the Upper and Lower Guinea forest blocks. It is strikingly coloured, black above except for a yellow patch on the mantle, and deep chestnut below except for a black throat. The Strange Weaver *P. alienus* is restricted to the middle canopy of montane forest above 1,600 m in eastern Zaire and Uganda. It is unusual in that the whole head of both sexes is black, the back, wings and tail are olive green, the upper breast deep chestnut and the rest of the underparts mustard yellow. The most distinctive feature is the long bill which is exceptionally broad at the tip and flattened on the culmen. The Black-necked Weaver *P. nigricollis* is found in evergreen forest in Zaire and West Africa but in savanna in southern Ethiopia, Kenya and Tanzania. A very distinctive forest group consists of 3 species, *P. insignis*, *P. preussi* and *P. dorsomaculatus*, which resemble each other in colour pattern (black wing and tail, yellow with black on the back, and underparts below the throat yellow), slender bill, and habit of foraging for insects on the bark of trees in the manner of a nuthatch.

The 5 Asian species in *Ploceus* are birds of paddy plains, open grasslands, cultivation and open woodland. They are all similarly coloured, with yellow and blackish heads and large areas of the body dull or streaky. The most widely distributed is the Baya Weaverbird *P. philippinus*, ranging throughout India, Sri Lanka, Bangladesh, south-west China, Burma, Sumatra and Java. There are 2 *Ploceus* species endemic to Madagascar, one, *P. sakalava*, inhabiting dry forest and the other, *P. nelicourvi*, inhabiting humid forest.

Except from the Red-headed Weaver *Malimbus rubriceps*, which inhabits woodland and acacia savanna, all the malimbes are found in evergreen forest in Upper and Lower Guinea. The sexes are generally unlike, and red and black are the predominant colours in all species.

The *Euplectes* group, the bishops and widow-birds (formerly *Coliuspasser*), live in open grassland and edges of swamps, often with several species occurring within a small area, but each ecologically separate. Thus the Red Bishop *E. orix* has largely the same range as the Yellow-crowned Bishop *E. afer*, but the latter appears more dependent on water. The bishop males, in breeding dress, look like brilliant coloured balls of either red or yellow and black as they display, and have short tails (50–70% of wing length). The widow-birds are less brilliantly coloured but have much longer tails. The largest of them is the Sakabula (Long-tailed Widow Bird) *E. progne* with a wing of about 14 cm and a black tail, some 50 cm long, that ripples behind the breeding male as he flies. The Yellow Bishop *E. capensis* is of interest as it is found in montane grassland throughout most of the northern part of its range but generally in lowland grassland elsewhere in East Africa, Zambia and Zimbabwe.

The queleas are birds of the savanna, the most numerous being the Red-billed Quelea *Q. quelea* (see QUELEA CONTROL) which occurs throughout the Afrotropical region but is more numerous in east and central Africa. In wetter parts of its range it is replaced by the Red-headed Quelea *Q. erythrops*. In breeding dress the males are quite distinct, the one having a red bill and black facial mask, the other having a black bill and the whole of the head and throat bright red.

Of the monotypic genera, the Grosbeak Weaver *Amblyospiza albifrons* (18 cm) is found in rank grass and swamps in west, central and southern Africa. The males are mainly black with chestnut heads with a white patch on the wing and usually one on the forehead. The females in contrast are white with heavy brown streaks below and mottled brown above. The Cuckoo Weaver *Anomalospiza imberbis* has a similar wide distribution, but prefers drier more open grassland. It looks like a canary, the males having yellow-green upper parts streaked with dark brown and bright yellow underparts.

The fodies (*Foudia*) are found on Madagascar, Comoro, Aldabra, Mauritius and other islands in this group. The most widely distributed, often through introduction, is the Madagascar Fody *Foudia madagascariensis*. On the islands it inhabits, it is found in open plantations and near habitation. The breeding male is bright red on the head and underparts, streaked with black on the mantle and its wings are dark. Females and non-breeding males have streaky brown, 'sparrowy' plumage.

The 2 *Bubalornis* buffalo-weavers are large birds (25 cm) for the family and wholly black unless the feathers are ruffled to show their white base. The main distinction between them is the colour of the bill: black in the Black Buffalo-weaver *B. albirostris*, becoming white or pinkish and greatly swollen in the breeding season; and red in the Red-billed Buffalo-weaver *B. niger*. The former is found in acacia country south of the Sahara and its range extends into southern Sudan and Uganda. *B. niger* has two separate populations, one in southern Africa the other in Tanzania and northwards to Ethiopia and Somaliland. The White-headed Buffalo-weaver *Dinemellia dinemelli* is unmistakable with its white head, neck and underparts. The rump, upper and lower tail-coverts, and bend of wings are orange-red, and the rest of the plumage dusky brown. It inhabits dry areas in north-eastern Africa.

Movements. The forest species within the family are all considered resident. Some savanna species are known to be migratory in some parts of their range but resident in other parts. Thus in Nigeria, Heuglin's Masked Weaver *Ploceus heuglini* moves southwards in the dry season after breeding in the north, and is locally migratory in eastern Africa; but on the Accra Plains in Ghana it is resident. The movements of the Red-billed Quelea in Nigeria have been unravelled by Ward (1965). The birds move south in the early part of the wet season to find food but then return northwards to breed in the Sahel after the grasses there have fruited. Complex migrations also occur in other parts of its range (Ward 1971). In the Himalayas, the bulk of the breeding population of Baya Weaverbirds migrate to lower levels in the non-breeding season.

Food. Most ploceine weavers of open country eat both grain and insects, some only grain, whilst the forest species are predominantly insectivorous. Some weavers are known to take nectar from flowers. The buffalo-weavers forage on the ground for seeds, fruits and insects. All members of the family feed their nestlings with insects but the savanna species use seeds as well.

Behaviour. Crook (1964) recognized three main types of courtship within the family. (1) The male sings and chases the female, and the nest is built during or after this courtship period. This behaviour is typical of all evergreen forest species which are monogamous, such as the malimbes, and the nests are generally dispersed and rarely advertised by the male. (2) The male builds a nest and then displays at it to attract a mate. This behaviour is typically found in all African savanna species of *Ploceus* that are colonial and polygynous. The entrances to nests are on the underside of the structure and males display by hanging upside down at the entrance, flapping their wings and calling. If a female accepts a nest, she proceeds to line it with grass heads and other soft material before laying eggs. The male defends a small territory within the colony and subsequently attempts to attract another female to a new nest. The Asian weavers do not have such elaborate displays at the nest and, in some species at least, the male leads the female to the nest after a sexual chase. The males of those species with side entrances to their nests (such as the Grosbeak Weaver and queleas) advertise them with a flapping display while perched upright on or near their nests. (3) The male builds a nest and then seeks to attract a mate by an aerial display and song flight, and only after he has done so does he lead her to it. This is typical of *Euplectes* species, in which the species-specific plumage of the males is prominently displayed during the slow flapping flight over their territory. A unique exception is the display of Jackson's Whydah *E. jacksoni* of East Africa. The males have communal dancing grounds in highland grassy areas. Each male calls and leaps repeatedly into the air (0.7 m or more) within a circular patch (0.8–1.2 m wide) which has a central tuft of grass with two cup-like recesses on each side of it. The grass tuft is possibly symbolic of a nest, as visiting females show much interest in it. Copulation takes place at the dancing grounds, but the nests are built by the female not the male, usually at the base of a tuft of grass.

The fodies are monogamous. The male Toq Toq *Foudia sechellarum* quivers his wings while approaching the female but this changes to an upright wing-beating display on closer approach. The male Madagascar Fody has a similar flapping display but the body is held less erect. The nest invitation display of the latter consists of a retarded flight to the nest, the slow wing-beats interspersed with glides.

The Cuckoo Weaver *Anomalospiza imberbis* congregates into large flocks in the non-breeding season but is very pugnacious in the breeding season, holding individual territories. The buffalo-weavers are gregarious throughout the year and are usually found in flocks of 10–12 birds foraging like starlings. The Red billed Quelea forms gigantic flocks and their roosts often number several millions of birds. Ward (1965) has proposed that the roost acts as an information centre for the large areas prospected by birds seeking food, and this may well be true for other weavers that roost gregariously.

Voice. During the courtship displays that have been described, the males are very vocal. The calls are in the main high-pitched and individually have little carrying power, but the cumulative noise of a large breeding colony, an incessant chattering, is deafening. The notes and calls are usually described as chirps, buzzes and wheezy whistles. Some weavers are said to have melodious and elaborate songs (such as Heuglin's Masked Weaver) but very few have been studied. The buffalo-weavers are noisy both in flight and on the ground when feeding, and utter a variety of chatterings at the nest. The calls of the White-headed Buffalo-weaver are described as parrot-like.

Breeding. The fodies, queleas, *Euplectes* species and *Amblyospiza* build a vertical oval shaped nest with a side entrance, and, except for the fodies, nest in grassland or marsh. The nests of the fodies are more spherical and untidy than those of *Euplectes* which have a very thin, woven outer shell and a thick non-woven inner lining. In all *Malimbus* and *Ploceus* species, other than the Asian, the nest chamber is elongated in the horizontal axis, and the entrance is from below and separated from the egg chamber by a ridge that prevents the eggs from rolling out. This nest type is usually placed in trees and shrubs, often at the tips of twigs and palm fronds. They are often sited over water or close to habitations of either wasps, large birds or human beings (see NESTING ASSOCIATION). In several species the entrance tubes are very delicately woven, reaching 1 m in length in Cassin's Malimbe *Malimbus cassini*. The whole nest takes over a week to build, and is woven from long strips torn from leaves or stems of palm trees. Blobs of mud, sometimes cow dung, are invariably used by the Asian Baya Weaver and Black-throated Weaver *Ploceus benghalensis*, and the latter sticks brightly coloured flowers into the wet mud.

The buffalo-weavers build large untidy domed nests, entered from the side, of thorny twigs, which are highly protective and distinguish them from nests of all other weavers. In both *Bubalornis* species, the adults and immature males work in parties to build the large communal nest. The individual egg chambers each have one opening and are lined by the female with either grass seeds, green leaves or rootlets. The Black Buffalo-weaver is polygynous and this may also be true of the other species. In contrast, the White-headed Buffalo-weaver builds single nests, on the boughs of a thorn tree, often low down, usually in a scattered colony but sometimes clustered together.

Of the species for which breeding data are known, males of most savanna species in *Ploceus* are polygynous and alone build the nest. The female lines the nest with grass heads and other softer materials, incubates the eggs, and feeds the young with little help from the male. In West Africa, male Village Weavers give no help to the female but in central and southern Africa they help feed the nestlings. In consequence the male of the west African race builds more nests on average and has more mates than his counterpart in other parts of its range.

Generally, forest weavers (*Ploceus* and *Malimbus*) are monogamous; both sexes construct the nest and feed the nestlings. In Cassin's Weaver, the adults are assisted by one or two subordinate males during nest construction but these are chased off by the dominant male when the nest is complete. The fodies are also monogamous, and both sexes help in nest construction (in most species) and feed the nestlings.

In general, the clutch-size of insectivorous forest species (average 2.1) is less than that of granivorous savanna species (average 2.6). In the buffalo-weavers the clutch-size is usually 3–4. The known incubation periods recorded for the various genera are as follows: *Euplectes* 11–16 days, *Foudia* 12–14 days, *Ploceus* 12–17 days, *Quelea* 12 days. The corresponding nestling periods are respectively: 13–16 days, 11–15 days, 15–20 days, and 12–14 days. Incubation in the Red-headed Weaver is 12–13 days.

Eggs of *Foudia* and some *Ploceus* species are either white or pale blue, but the majority of the family has blotched or spotted eggs. In contrast, those of a race of the Black-headed Weaver *P. melanocephalus* are among the most variable of any bird, being recorded as white, pink, terra-cotta, brown, or green, with or without brown, reddish or purplish spotting. In the Village Weaver, the female consistently lays one type of egg and will throw out any eggs that differ markedly from her own. As the Didric Cuckoo *Chrysococcyx caprius* is a common parasite, this may be a protective behaviour; the cuckoo lays eggs with a somewhat parallel range of variations in colour and pattern. *Quelea* eggs are pale blue (in one species heavily streaked), those of the malimbes are plain white, or else white profusely spotted and blotched with brown or grey. The eggs of buffalo-weavers are generally dull white or pale green, heavily spotted and streaked.

The Cuckoo (or Parasitic) Weaver *Anomalospiza imberbis* parasitizes various species of *Cisticola* and *Prinia*. The few data available suggest that the egg colour mimics to a large degree that of the host. Not infrequently, 2 young of the weaver are raised in one nest, but the host young normally disappear.

(R.E.M.) L.G.G.

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WEAVER-BIRD: synonymous with WEAVER, or with weaver and ESTRILDID FINCH (weaver-finch) combined.

WEAVER-FINCH: see ESTRILDID FINCH.

WEAVER, SPARROW: see SPARROW-WEAVER AND SCALY-WEAVER.

WEB: a fleshy membrane between two toes (see LEG; and SWIMMING AND DIVING); or the vane of a feather (see FEATHER; VANE).

WEBER'S LINE: see ORIENTAL REGION.

WEDGEBILL: name applied to several unrelated species: *Schistes geoffroyi* (for family see HUMMINGBIRD); *Glyphorhynchus spirurus* (see WOODCREEPER); *Sphenostoma cristatum* (see RAIL-BABBLER).

WEEBILL: *Smicrornis brevirostris* (see WARBLER, AUSTRALIAN).

WEIGHT: see SIZE.

WEIGHT RECESSION: a phenomenon in which young birds lose weight during their development, first attaining weight above adult level, but thereafter decreasing towards an adult weight achieved around the time of fledging. See also GROWTH.

WEKA: substantive name, alternatively 'weka rail', of *Gallirallus* spp. (see RAIL).

WHALE-BIRD: sailors' name for various species of petrel (Procellariidae); applied in the Antarctic to the Dove Prion *Pachyptila desolata*, and in Alaska to the Short-tailed Shearwater *Puffinus tenuirostris* (see PETREL).

WHAUP: popular name in Scotland for the Curlew *Numenius arquata* (see under SANDPIPER).

WHEATEAR: substantive name of various *Oenanthe* spp.; used without qualification, in Britain, for *O. oenanthe*—the white rump of which is the origin of the name (see CHAT; THRUSH).

WHIFFLING: rapid descent in flight involving fast side-slipping first one way and then the other.

WHIMBREL: *Numenius phaeopus*, a species of curlew (see under SANDPIPER). See photos EGG-TOOTH; HATCHING.

WHINCHAT: substantive name of some *Saxicola* spp.; used without qualification, in Britain, for *S. rubetra* (see CHAT; THRUSH).

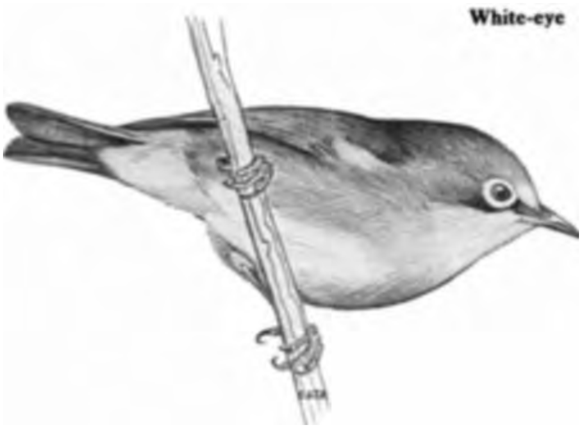
WHIPBIRD: substantive name of *Psophodes* spp. (see RAIL-BABBLER).

WHIP-POOR-WILL: *Caprimulgus vociferus* (see NIGHTJAR; also POOR-WILL).

WHISTLER: alternative substantive name for species of Pachycephalidae (see THICKHEAD).

WHITE-EYE (1): substantive name of most species of *Zosterops* comprising more than four-fifths of the Zosteropidae (Passeriformes, suborder Oscines); in the plural, general term for the family. Other names for species are 'silvereye', 'spectacle-bird' and 'zosterops'.

Characteristics. The white-eyes form a remarkable homogeneous Old World family of small birds (average length 12 cm) with generalized characters. They have slightly decurved, sharply pointed bills (short in nearly all the species), brush-tipped tongues, somewhat rounded wings with only 9 functional primaries and, in nearly all species, the white ring round each eye from which they take their name. This ring, often broken by black feathers of the lores, is formed of minute silky-white feathers, and it varies much in width. In a few species it hardly shows; at the other extreme, in certain of the African birds, it is enlarged to a big patch. Otherwise the plumage of the white-eyes is notably lacking in sharply defined pattern; most of them have the upper parts more or less green or yellow-green, the under parts grey or yellow, clouded with melanin—giving green or brownish on the sides. Yellow pigment has been lost in a number of insular populations, the entire plumage of some of them being reduced to greys and browns. The sexes are always alike; slight differences, if found in size (females smaller) or amounts of melanin or chromatin (female duller), are often overlapping within a local population and always masked by greater racial or clinal differences. There are no seasonal changes in plumage.



Green White-eye *Zosterops virens*. (*C.E.T.K.*).

Habitat. White-eyes are birds of forest edge and canopy, and frequent bushes in the gardens. They are found from sea level to the timber-line at about 3,500 m in tropical mountains, and from the acacias of south-western Africa to the mangroves of Australia and the edge of the richest tropical rain forest in south-east Asia. In the Great Barrier Reef they occur on wooded cays too small to support a breeding population of other passerines and may themselves reach very high densities (200 breeding pairs on 16 ha of Heron Island).

Systematics and distribution. There are about 85 species in the family Zosteropidae, the systematics of which are exceptionally difficult at the specific level though there is general agreement that most of them should be included in the genus *Zosterops*. This is because for the most part the genus *Zosterops* with well over 200 recognized forms varies only within narrow limits of plumage differences, and the populations found in different geographical regions may show striking resemblances as a result of convergence. For example, Madagascar and New Guinea *Zosterops*, *Z. lutea* of northern Australia and *Z. flavilateralis* of the East African lowlands, and *Z. griseovirescens* of Annobon in the Gulf of Guinea and *Z. natalis* of Christmas Island in the Indian Ocean are very much alike. Traditionally, the Zosteropidae of Africa and the neighbouring islands and those of the Indo-Pacific region have been treated separately, and the affinities within *Zosterops* of the two regions remain inscrutable. The most widespread and characteristic species are *Z. senegalensis* (range Senegal to Zululand) in the former and *Z. palpebrosa* (range Djalalabad in Afghanistan to Flores in Indonesia) in the latter region. The latest reviews recognize 4 highly polytypic species of *Zosterops* in Africa and 9 others in the islands on both sides of Africa, and 50 in the east from Pakistan to Samoa. *Z. japonica* has been introduced to Hawaii.

The family as a whole is distributed in the whole of the Ethiopian, Oriental and Australasian regions, and parts of the eastern Palearctic region, reaching their extremes of latitude in Ussuria on the Asian continent (*Z. erythropleura*) and Hokkaido in northern Japan (*Z. japonica*), and at the Cape of Good Hope (*Z. virens*) and Campbell Island south of New Zealand (*Z. lateralis*). On the continents of Africa, Asia and Australia, wide-ranging species follow Gloger's rule (melanin increasing with humidity) and Bergmann's rule (the cooler the climate the bigger the bird). In Africa the wing-length is known to increase with altitude irrespective of temperature.

Movements. White-eyes are highly mobile and have a strong tendency to migrate or disperse in flocks. The species breeding in the northern parts of Asia migrate to warmer parts in winter. Migration also occurs in eastern Australia where the individuals of the Tasmanian stock are found scattered between Tasmania and south-eastern Queensland in winter. White-eyes have established themselves on remote islands more widely than any other family of passerine birds. The most recent successful colonization is historical; in the 1850s Tasmanian birds of *Z. lateralis* crossed 1,200 miles of sea and reached New Zealand, where they have since become the commonest land bird.

In contrast with high mobility, some populations must have become profoundly sedentary as they exhibit high degrees of differentiation on oceanic islands and mountains, sometimes within sight of each other. Moreover, the speed of differentiation is remarkable in such isolated populations, which would account for high variability in insular birds. There are many examples of the double invasion of islands, and even of triple invasion (Norfolk Island), typically with one species differing much more than the other from the putative parental stock. Some, such as *Z. strenua*, a recently extinct Lord Howe Island endemic, and *Z.*

albogularis, a near extinct Norfolk Island endemic, have become 'giants'. *Z. modesta* of the Seychelles has lost its yellow pigment whereas *Z. cinerea* of the Caroline Islands and *Z. borbonica* of Mauritius and Reunion have lost both eye-ring and yellow pigment. Many combinations exist, of changes in size, in intensity of pigment, in shape of bill, and in eye-ring. Twenty-three species have been judged odd enough to be kept out of the genus *Zosterops*, and they are arranged in 11 small genera. Gigantism is found in *Speirops* in the Gulf of Guinea, *Woodfordia* at the south-eastern end of the Solomons, *Megazosterops* on the Palau Islands and *Hypocryptadius* on the mountains of Mindanao in the Philippines. The last mentioned, represented by a single species (*H. cinnamomeus*), is by far the largest, with wing-length reaching 9.5 cm and body-weight 31 g. *Chlorocharis emiliae* found on the mountains of Borneo has black eye-rings.

Food. They have a wide range of food—insects, spiders, nectar and fruit. Nectar and soft juicy fruit are obtained with the aid of the brush tongue; they are considered a pest by fruit growers. Although foliage gleaning is the commonest mode of feeding, they may also hawk, snapping the prey in the air, or may even scavenge on the ground. They often use their strong beak as a pivot to widen small crevices in clumps of leaves, bark, buds and old nests of other birds, in search of prey.

Behaviour. White-eyes are usually paired for life and breed in small territories. Most of them flock outside the breeding season and indulge in group activities of foraging, moving, bathing and resting, sometimes appearing in mixed species flocks. Flocking birds frequently perform mutual preening (allopreening) between pairs during the resting periods, and roost in clumps, huddling against each other on a perch. They have ritualized forms of aggression, the most common being wing fluttering and beak clattering. Courtship behaviour involves horizontal wing quivering and, at least in some species, motions of nest building without holding the material.

On the Mascarene Islands *Z. olivacea* (considered to have been derived from an earlier invasion) is specialized for feeding at flowers, and pairs remain territorial throughout the year, whereas *Z. borbonica* (considered to have been derived from a later invasion) is conspicuously social even during the breeding season and cases of communal feeding of young are known.

Voice. Most species seem to have a definite song at dawn throughout the breeding season. Some of them are kept in cages in Asian countries for their rich and melodious warbles. The courtship song is a soft warble.

The characteristic contact call is a high-pitched plaintive note, sometimes long-drawn and far-carrying. Soft contact notes are exchanged among members of foraging groups, and other distinct calls exist for alarm, aggression and distress.

Breeding. A cycle of breeding from nest building to fledging may be completed in as little as 3 weeks in some species, though post-fledging feeding may continue for up to 2 weeks. The nest is a deep cup of mixed plant material usually slung in a slender fork just below the canopy cover of vegetation, at any height above ground. The eggs, white or pale bluish, usually number 2 to 4. Both parents incubate, and feed the young. The incubation period and the nestling period are extremely short and similar in length (10–12 days). Young are fed with insects initially but by fledging their diet contains a significant portion of plant food.

See drawing ALLOPREENING. (R.E.M.) J.K.(2)

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WHITE-EYE (2): substantive name of certain pochards *Aythya* spp. (see DUCK).

WHITEFACE: substantive name of the species of *Aphelocephala*, a genus of Australian warblers (for family see WARBLER, AUSTRALIAN).

WHITEFRONT: colloquial short name for the White-fronted Goose *Anser albifrons* (see under DUCK).

WHITEHEAD: *Mohoua albicilla*, of New Zealand (for subfamily see WARBLER, AUSTRALIAN).

WHITETHROAT: substantive name of *Sylvia communis* and (Lesser) *S. curruca* (see WARBLER (1)).

WHITETIP: *Urosticte benjamini* (for family see HUMMINGBIRD).

WHOOPER: name sometimes used alone for the Whooper Swan *Cygnus cygnus* (see under DUCK).

WHYDAH (1): substantive name, alternatively 'widow' or 'widow-finch', of species of the genus *Vidua* (including '*Hypochera*', '*Tetraenura*' and '*Steganura*') Passeriformes, suborder Oscines. The name is also sometimes used in another sense; see WHYDAH (2). The name may have originated either because of the similarity of the long central tail feathers of some species to that of a widow's train, or from the locality Ouidah on the West African coast where they were found in the cage bird trade. The name indigo-bird (or the locally used alternatives combassou, indigo-finch or widow-finch) is used for the 6 species in the subgenus *Hypochera*. The name paradise whydah is used for the 4 species in the subgenus *Steganura*.

The viduine whydahs, a small group of about 14 species of African finches, all of them brood parasites of the Estrildidae, are of uncertain systematic affinities. They share some characteristics with the Ploceidae and others with the Estrildidae. Although some similarities between viduines and estrildids are due to mimicry, this does not preclude the possibility of a recent common ancestor as the primitive parasites may have originally parasitized a closely related species of estrildid. On the other hand, the egg white protein patterns of the viduines are perhaps closer to those of *Passer* than to those of the Ploceidae. A detailed systematic study of this group of finches is needed.

Characteristics, distribution and habitat. Viduines are birds of open woodlands, and occur in most terrestrial habitats in Africa except for the evergreen forests and the deserts.

The indigo-birds are all similar in appearance and size (10 cm long). The male in breeding dress is blackish with a metallic gloss of green, blue, or purple. The colour varies considerably within a species from area to area, and the variation has made it difficult to understand the species limits. The species also vary in colour of the wings, bill and feet. In the non-breeding season the male resembles the female in being streaked and brown. The tail is short throughout the year. The most widespread species is the Village Indigo-bird *Vidua chalybeata*, found throughout the drier areas of the Afrotropical region, including oases in the southern Sahara. The other species are the Variable Indigo-bird *V. funerea*, the Purple Indigo-bird *V. purpurascens*, Wilson's Indigo-bird *V. wilsoni*, the Barka Indigo-bird *V. larvaticola*, and the Jambandu Indigo-bird *V. raricola*.

The Shaft-tailed or Queen Whydah *V. regia* and the Straw-tailed Whydah *V. fischeri*, sometimes placed in a subgenus *Tetraenura*, have widely disjunct distributions, the former in southern Africa and the latter in north-east Africa. In the breeding season the males have red bills and the 4 central tail feathers are several times as long as the bird (total length 30–34 cm, female about 11 cm). The vane is nearly as narrow as the shaft but in *V. regia* it is flared at the tip.

In the paradise whydahs the tail of breeding males is extremely ornate, the central pair of long feathers being flattened and twisted into the vertical. In flight the males look like horizontal exclamation marks, the dot being the bird. The males are black except for a broad yellow or chestnut hind-collar, chestnut breast and buff abdomen. The most widespread is the Acacia Paradise Whydah *V. paradisaea* which occurs across the savanna belt from Senegal to Somalia and thence south along the eastern side of the continent to southern Africa. The West African races *orientalis* and *aucupum* are sometimes listed as distinct species. The Broad-tailed Paradise Whydah *V. obtusa* has a wide east-west distribution south of the Congo forest block, but does not reach southern Africa. The elongated rectrices are shorter, broader and untapered. The other 2 species *V. interjecta* and *V. togoensis* occur north of the forests, in central and western Africa.

In the 2 remaining species, the Pin-tailed Whydah *V. macroura* and Steel-blue Whydah *V. hypocherina*, the elongated rectrices of the breeding males are fairly narrow and taper to a point. The non breeding males and females are more heavily streaked than those of the paradise whydahs. The Pin-tailed Whydah is found throughout the Afrotropical region and even occurs in clearings within the forest zone which is exceptional for this family. The Steel-blue Whydah is confined to the arid areas of East Africa. The males in breeding dress differ markedly: the Pin-tailed is black and white, and the other wholly black with a high blue gloss above and below.

Movements. No long-distance migrations are known and in some areas the viduines are resident. However local movements occur in dry habitats. Marked Village Indigo-birds flock several km from their breeding areas, and some Variable Indigo-birds and Shaft-tailed Whydahs move more than 50 km from breeding season to dry season habitats.

Food. The viduines feed almost entirely on the small seeds of annual grasses. Seeds are taken on the ground, not from the seed heads still on the grasses. They uncover seeds in sand or dust with a quick kick of both feet. They occasionally take termites during emergences in the rains.

Behaviour. All members of the family gather into flocks during the non-breeding season. Social behaviour is best known for the Village Indigo-bird. Males space themselves several hundred metres apart and sing all day in traditional trees. Females visit several males in a day and are courted by each male in turn, in a bouncing aerial display. Females then return to one male and mate with him. The males also visit each other; the males who are unsuccessful at mating do most of the visiting and the most successful male has most of the visitors. There are usually 10–20 males in such a local breeding population, the most successful male being near the spatial centre of the population. The social organization resembles the dispersed lek of some other non-parental birds such as some birds-of-paradise. The most successful male in a local population usually gets more than half of all matings, involving perhaps 20 females in all. A few other males each account for the remaining matings. This highly polygynous mating system of the Village Indigo-bird was revealed by using colour ringed birds. Other viduines have not been studied in this way but it is likely that other indigo-birds, as well as the Shaft-tailed Whydah and the Straw-tailed Whydah, have similar social organizations, for they all have song dialects as does the Village Indigo-bird (see later).

The breeding behaviour of the Shaft-tailed Whydah and Straw-tailed Whydah is similar to the indigo-birds. The males mimic the songs of their host species and court females that fly to them on their call sites. In contrast, the male Pin-tailed Whydah and Steel-blue Whydah court their females on the ground and do not mimic songs, though the former then chases the female into a tree to continue the courtship display for many minutes. The paradise whydahs mimic the songs of their host species and some species have a conspicuous aerial display over their courtship area.

Voice. The songs of the viduines include the calls and songs of their host species, which they imitate from their foster parents, the only exceptions to this being the Pin-tailed Whydah and probably the Steel-blue Whydah. Wild hybrids (indigo-bird × paradise whydah) sing the same songs and calls as their local foster species and also the same songs and even alarm calls as the local paradise whydahs, indicating that they learned the songs both from their foster species and from the wild viduines that mimic the same foster species. The young viduines also mimic the begging calls of the host young, even when there are no host young in the nest; these mimetic begging calls are apparently innate. The host songs vary from place to place and these variations are faithfully reproduced by the local viduine population. Each male Village Indigo-bird mimics the songs of 3 or 4 different individual hosts (Red-billed Firefinch *Lagonosticta senegala*); the male may learn his foster father's song and then copy a few other firefinches or mimetic songs as sung by other male indigo-birds.

The viduines also have other alarm calls and chattery songs that are characteristic of their species groups and unlike those of the host species. In a local breeding population of Village Indigo-birds, the males share the same local variations of their own 22 song types with each other. These local dialects are apparently formed around the male who mates with most females, and his songs are copied by the other males around him. The adults sometimes switch songs when they move from one dialect neighbourhood to another.

Paradise Whydah *Vidua paradisaea*. (*M.W.*).

Breeding. All verified records indicate that most species of viduines are species-specific brood parasites. In all cases known the young of the parasite matches the young of the host species in the colour and pattern of the mouth. The mimicry involves the number and pattern of black spots on the palate, the colours (pink, lavender, blue, yellow) inside the mouth, and the colour of the highly reflective tubercles at the gape. These patterns differ among most species of estrildid finches, so each species of viduine is restricted to a single species of host. However, several species of waxbills (including Common Waxbill *Estrilda astrild*, Black-rumped Waxbill *E. troglodytes*, Fawn-breasted Waxbill *E. paludicola*, and Orange-cheeked Waxbill *E. melpoda*) all have the same pattern and all are parasitized by the Pin-tailed Whydah, whose young share this common pattern.

The parasite : host relationships that have been observed directly or that are known from song mimicry include the following: Village Indigo-bird and Red-billed Firefinch, Variable Indigo-bird and African Firefinch *Lagonosticta rubricata*, Purple Indigo-bird and Pink-backed Firefinch *L. rhodopareia*, Wilson's Indigo-bird and Bar-breasted Firefinch *L. rufopicta*, Barka Indigo-bird and Black-faced Firefinch *L. larvata*, Jambandu Indigo-bird and Black-bellied Firefinch *L. rara*, Shaft-tailed Whydah and Violet-eared Waxbill *Uraeginthus granatinus*, Straw-tailed Whydah and Purple Grenadier *U. ianthinogaster*, the Pin-tailed Whydah and several species of waxbills *Estrilda* (see above), Acacia Paradise Whydah and Melba Finch *Pytilia melba*, Broad-tailed Paradise Whydah and Orange-winged Pytilia *P. afra*, Exclamatory Paradise Whydah *Vidua interjecta* and Red-winged Pytilia *P. phoenicoptera*, Togo Paradise Whydah *V. togoensis* and Yellow-winged Pytilia *P. hypogrammica*. On distributional grounds alone, the Steel-blue Whydah probably parasitizes the Black-cheeked Waxbill *Estrilda erythronotos* (including *charmosyna*) in East Africa. This list accounts for all the known viduine species. Rarely, a viduine is raised in the nest of another host, perhaps as the result of an egg laid in the nearest estrildid nest when the usual host's nest is destroyed before the parasite has laid, and odd indigo-birds have been recorded singing the wrong host species' song, probably because their mother mislaid an egg.

Females, of all species, lay 3 or 4 eggs in a series or 'clutch', one a day, with an interval of several days between successive series. Sometimes only one egg and sometimes the entire series is laid in one nest. The eggs are white and slightly larger and rounder than the eggs of the host. The incubation period is 10 days in the Village Indigo-bird. Unlike most other brood-parasites, viduine nestlings make no attempt to evict the host's own offspring, and their close association with their foster-family may continue for an appreciable time after fledging. The nestling parasite grows faster than that of the host and sometimes crowds the host young. R.B.P.

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WHYDAH (2): substantive name, alternatively 'widow-bird', of some species of Ploceidae in the genus *Euplectes* (see WEAVER).

WIDEAWAKE: alternative name of the Sooty Tern *Sterna fuscata* (see TERN).

WIDGEON: obsolescent alternative spelling of WIGEON.

WIDOW: alternatively 'widow-bird', same as 'whydah' (see WHYDAH (1); WHYDAH (2)).

WIGEON: substantive name (usually unchanged in plural; the spelling 'widgeon' is practically obsolete) of certain *Anas* spp.; used without qualification in Britain for *A. penelope* (see DUCK).

WILDFOWL: general term for quarry species of birds other than 'game birds'; in the most common present usage in Britain it is confined to species of the family Anatidae (see DUCK; also GAME-BIRDS) but sometimes extends to waders (Charadrii) and other edible birds associated with water. In North America 'waterfowl' is more commonly used in this sense. In Britain the term 'waterfowl' embraces a larger group of birds ecologically dependent on water, including members of several orders of birds. The term 'ornamental waterfowl' is used principally for live Anatidae kept in captivity.

'Wildfowling' is the practice or sport of taking wildfowl, and is conducted by a 'wildfowler'; in the past the terms embraced many forms of capture, often involving the use of nets, but it is now generally confined to the shooting of wildfowl with shot-guns. 'Duck-hunting' and 'duck-hunter' are equivalent terms in North America, where the sport is more strictly controlled by law than in European countries. In Europe, wildfowl are shot principally while 'flighting', either naturally at dawn or dusk or under the moon, or when disturbed from a resting or feeding place. This method (known there as 'pass shooting') is used to a lesser extent in North America, where most wildfowl are shot when coming in to artificial models or 'decoy' birds, made of wood ('blocks'), cardboard, rubber or plastic, the hunter being concealed nearby in a 'blind'. Although such decoys are still relatively unfashionable in Europe, the practice of feeding certain ponds regularly with grain to encourage a 'lead' of ducks is widespread and results in large bags. In North America, where this is known as 'baiting', it is illegal, although crops are specially grown in certain areas to lure wildfowl to feed there.

An arduous old-time branch of the sport known as 'punt-gunning' persists in Britain. In this a large-bore 'punt gun' is mounted on a special shallow-draught boat in which the wildfowler, lying prone, stalks the birds—usually on the open mudflats of an estuary. It is variously curtailed by law in most European countries and altogether prohibited in North America. Large-bore guns mounted in fixed emplacements overlooking small ponds are still used in France ('huttiers').

The sale of some wildfowl for food is limited to certain months in most of Europe, the period varying in different countries, but has long been outlawed in North America.

The wariness of ducks and geese is such that wildfowling has been held to be one of the most exacting and exciting of field sports. The subject has caught the imagination of writers and painters, who have portrayed the romance of the wild marshes and the elusive quarry which frequents them. M.O.

WILDNESS: see under TAMENESS.

WILLET: *Catoptrophorus semipalmatus* (see SANDPIPER).

WIND: see ANTARCTIC; FLIGHT; MIGRATION; OCEANIC BIRDS; WEATHER AND BIRDS.

WINDHOVER: alternative name of Kestrel *Falco tinnunculus* (see FALCON).

WINDOW: a pale patch on the outer primary feathers of the wings of certain gulls.

WINDPIPE: see TRACHEA.

WING: the paired forelimb of birds, specially modified for flight. It was doubtless originally 5-fingered, although in *Archaeopteryx* it had already acquired tridactyle form but with the wrist bones as yet unfused (see ARCHAEOPTERYX).

The wing has become secondarily modified for swimming in penguins, Simpson's (1946) work proving that penguins were evolved from flying ancestors and were freed from any restriction on the ratio of body weight to wing and tail area when they took to an aquatic life. Similarly, the 'ratite' orders of running birds are thought to be derived from flying ancestors, as evidenced by the fossil *Eleutherornis helveticus*, the wing becoming secondarily reduced in these and other non-flying species (see EARLY EVOLUTION OF BIRDS).

Functions. The main function of the avian forelimb is FLIGHT. It is also used solely for swimming by penguins, as formerly by the flightless Great Auk *Pinguinus impennis* (and earlier by flightless auks of the fossil genus *Mancalla*). Certain flying species also use their wings while diving, notably the auks of the Northern Hemisphere and the diving petrels of the Southern. In these, the feet are used merely as rudders, but in such diving ducks as the scoters *Melanitta* spp., eiders (Somateriini), and the Long-tailed Duck *Clangula hyemalis*, both the wings and the legs are used as paddles under water and the wings are kept folded, but away from the body with the alula held in hyperextension (see SWIMMING AND DIVING).

All birds make use of their wings for balancing, particularly when perched on a moving object in a strong wind. During courtship and breeding, when the males of many species become pugnacious towards one another, the wings are frequently used as weapons of combat, the bird in most cases seizing the opponent with the bill and buffeting him with the wings. Spur-winged Plovers *Vanellus* ('*Hoplopterus*') *spinosus* fight while in flight, turning and striking with the wing, which, as it carries a spur, is capable of inflicting mortal injury. Although little is known about the use of wing-spurs in other species, such as the Spur-winged Goose *Plectropterus gambensis*, there seems to be little doubt that these are also aggressive weapons.

Wings play an important part in the displays of many species, and during these they are widely spread and may be vibrated in front of the hen bird, as in the Silver Pheasant *Lophura nycthemera* and related species. Many birds are brightly coloured, such as the birds-of-paradise and Sun-bittern *Eurypyga helias*, but the use of the wings in courtship display is not confined to colourful species and occurs in such sombre birds as Savi's Warbler *Locustella luscinoides*, the Grasshopper Warbler *L. naevia*, and the Dunnock *Prunella modularis*. The wings are also displayed in courtship flight by many waders (Charadrii), the Roller *Coracias garrulus*, and the Golden Oriole *Oriolus oriolus*, to mention but a few examples.

As a further function, mention must be made of climbing, with special reference to the nestling Hoatzin *Opisthocomus hoazin* (see HOATZIN). This bird climbs around its nest and the nesting tree, using its feet and wings in true quadripedal fashion. The thumb and first fingers possess large claws, the manus is relatively large, and there is arrested development of

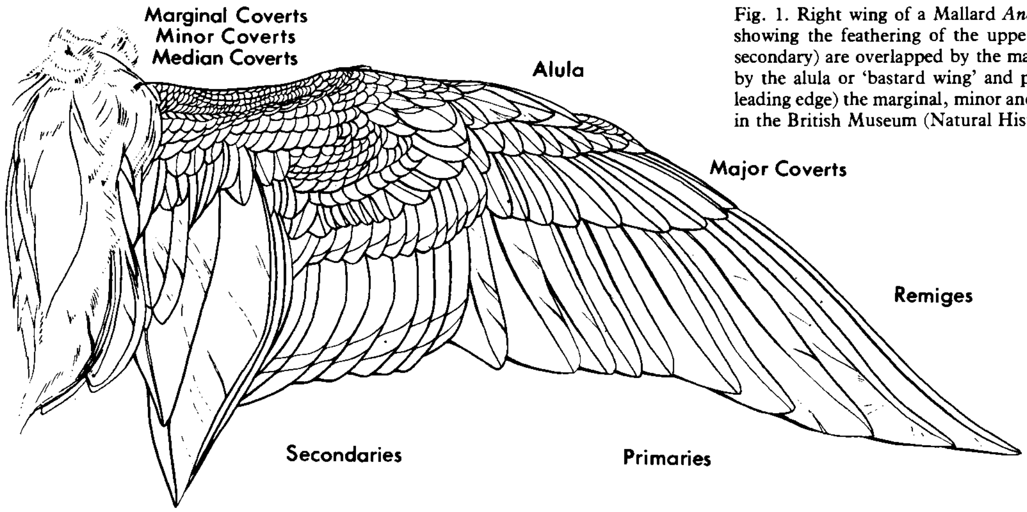

Fig. 1. Right wing of a Mallard *Anas platyrhynchos* in extended position, showing the feathering of the upper surface. The remiges (primary and secondary) are overlapped by the major coverts, and these in turn distally by the alula or 'bastard wing' and proximally by (in succession from the leading edge) the marginal, minor and median coverts. (From a preparation in the British Museum (Natural History)). (*M. Yule*).

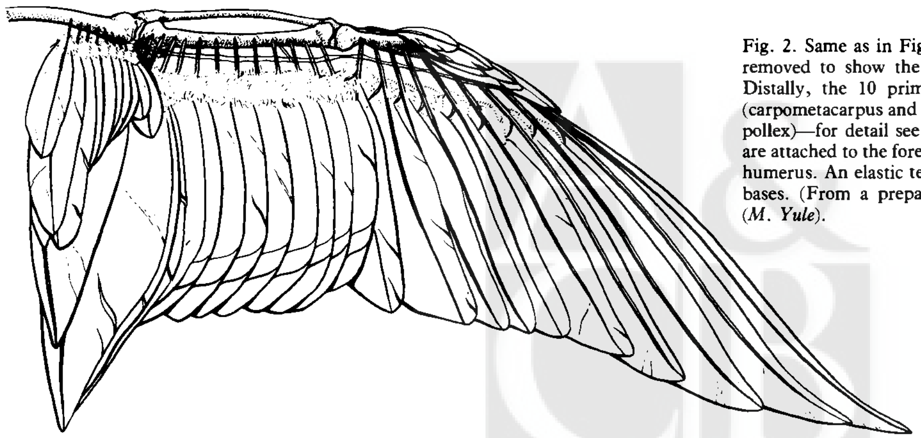

Fig. 2. Same as in Fig. 1, with soft tissues and covert feathers (tectrices) removed to show the relation of the main flight feathers to the bones. Distally, the 10 primary remiges are attached to the hand or manus (carpometacarpus and digital phalanges), which also bears the alula (on the pollex)—for detail see Fig. 3. Proximally to these, the secondary remiges are attached to the forearm (ulna), and the so-called 'tertiary' feathers to the humerus. An elastic tendon can be seen connecting the remiges near their bases. (From a preparation in the British Museum (Natural History)). (*M. Yule*).

the quill feathers of the thumb and fingers, thus enabling freer movement. The claws become absorbed in adult life and the manus assumes shorter proportions.

Structure. The wing consists of a light, variable vane for striking the air, the insertion of the wings being high up on the thorax, with the centre of gravity and the heavy internal organs well below the point of insertion.

The bones consist of the humerus, radius and ulna, and the bones of the hand or manus (see SKELETON, POST-CRANIAL). The latter are variable, owing to the loss of certain carpal bones and the fusion of others with the metacarpus. The radiale (or scapholunar) is present in all birds and the ulnare (or cuneiform) in many, exceptions being the emus and cassowaries and the kiwis. The 2nd and 3rd distal carpals are present in the young of most species, fusing in adult life with the metacarpal.

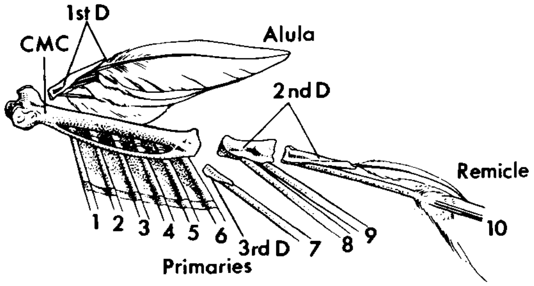

Fig. 3. As in Fig. 2, but left wing from below: detail of the manus area with the bones dissected apart. CMC = carpometacarpus; 1st D = digit or pollex (fused 1st and 2nd phalanges); 2nd D = second digit (1st phalanx and fused 2nd and 3rd phalanges); 3rd D = third digit. Feathers as marked. (From a preparation in the British Museum (Natural History)). (*M. Yule*).

Digits lost in the evolution of the typical avian manus are (on the most widely accepted view) V, IV, and the distal part of III. The second digit forms the major part of the manus in penguins, emus, cassowaries, and kiwis. The function of the hand, in general, has become largely subordinated to the provision of a firm basis for the primary feathers. The three parts of the wing—upper 'arm', forearm, and hand—can move only in one plane in relation to each other, a further adaptation towards stability.

The muscles present many problems in functional anatomy (see MUSCULATURE). Thus, the forearm and muscles of the manus are greatly reduced in kiwis, but in the Ostrich *Struthio camelus* there is little degeneration of musculature distal to the elbow. P.R. Lowe found that the only difference in the wings between the Flightless Cormorant *Nannopterum harrisi* (with almost no carina) and a flying cormorant *Phalacrocorax* sp. was in the general and relative proportions of wing to body; the Falkland Flightless Steamer Duck *Tachyeres brachypterus* has larger wings than the Flying Steamer Duck *T. patachonicus*, which is probably to be accounted for by their use under water when swimming. Penguins lack the biceps brachii muscle, but specialization of the pectoralis and tensor patagii longus takes over the function; other distal muscles of the wing are absent or reduced and the shoulder musculature is highly developed in response to the swimming action necessary.

The propatagium is a membranous fold of skin along the anterior margin of the wing, from shoulder to carpal joint; it contains flexor muscles and tendons. The metapatagium is a similar fold between the body and the posterior margin of the upper wing (see MUSCULATURE).

Feathering. The feathers of the wing (see PLUMAGE) have a definite arrangement as follows: the flight feathers or remiges are developed in the wing membrane (ala membrana) and point backwards, each feather partly overlapping the next. They are divided into the metacarpo–digitals or primaries, attached to the manus, and the cubitals or secondaries, attached to the ulna. There are typically 11 primaries, 6 attached to the metacarpus and 5 to the phalanges, but the outermost primary is often rudimentary ('remicle') or absent, while certain birds, notably the flamingos, grebes, and storks have 7 primaries attached to the metacarpus and 12 in all. The 5th secondary remex (numbered inwards from the carpal joint) was formerly thought to be absent in some species, but the modern view of this 'diastataxy' is that there is a gap between the 4th and 5th secondaries (see below and REMICLE).

In *Archaeopteryx* there were 9 primaries, as in a number of modern birds. The Ostrich has as many as 16, and the cassowaries have as few as 2 or 3. The primaries are best numbered outwards from the carpal joint, but as the opposite method is also practised it is necessary to specify which is being used (see PRIMARY).

The remainder of the wing is covered by three sets of wing coverts (tectrices) both on the upper surface and (constituting the 'lining') on the under surface, the major, minor, and marginales, the last in several rows covering the leading edge of the wing. Each major tectrix is attached in relation to one of the remiges, the bases of which are thus covered; the upper covert of the 1st metacarpal remex is generally rudimentary, as a requirement for folding the wing. The minor tectrices fill in the gap between the major and marginales feathers, overlapping the former and being overlapped by the latter. The shoulder region is covered by the humeral or tertiary feathers, and by the scapular feathers on the back and the axillaries underneath, thus ensuring a smooth feather contour at the junction of wing and body.

In the 'ratites', it is to be noted that the quills of the primaries are not fixed into grooves on the manus but lie loosely over the bones, their bases projecting beyond the bone margin. In penguins, the feathers have evolved a scale-like structure and there are no true primary feathers.

Alula or bastard wing. This, also called 'ala spuria', consists of a number of small quill feathers attached to the first digit. As mentioned, it is used in swimming by certain ducks; it is also used in flight, particularly by birds-of-prey, being of importance in the prevention of stalling (see FLIGHT). It is present in *Rhea*, providing further evidence of the flying ancestry of the 'ratites', as shown by de Beer (1956).

Claws. Three large digital claws were present in *Archaeopteryx*, and the presence of claws in modern birds must be regarded as primitive remnants, particularly as they are more commonly found in nestlings and are later absorbed. In structure, they are composed of horny epithelium, like other claws. They are found only on the 1st and 2nd digits, and persist in adult life on the 1st digit in the Secretary-bird *Sagittarius serpentarius*, the Black-necked (or Northern) Screamer *Chauna chavaria* and on all 3 species of finfoot (Heliornithidae); mention has already been made of the Hoatzin.

Spurs. These are used in combat. A spur consists of a conical bony core with an external horny sheath. They are invariably situated on the radial side of the carpus or metacarpus. The Spur-winged Goose *Plectropterus gambensis* is an example of a bird with a carpal spur arising from the scaphoid; the jacanas and the Spur-winged Plover *Vanella spinosus* have spurs arising from the first metacarpal, and the Black-necked Screamer has one on the 1st and the 2nd metacarpal. A carpal spur is present in sheathbills.

Ornamental plumes. These are occasionally present on the wing and are erected in display. Thus the Standard-wing *Semioptera wallacea* (Paradisaeidae) has 2 long plumes arising from the minor tectrices, near the distal end of the ulna. The remarkable 'sails' of the Mandarin Duck *Aix galericulata* are modified humeral feathers and are prominent in display. In some nightjars the innermost primary is greatly elongated, forming an ornamental train (with the second primary to a lesser extent) in the Pennant-winged Nightjar *Macrodipteryx vexillarius* and ending in a racket in the Standard-winged Nightjar *M. longipennis*. In cranes the innermost secondaries are elongated and incoherent plumes that, when the bird is at rest, droop over the hind end of the body. (For the wing plumes of male *Argusianus argus* see PHEASANT.)

Proportions. While one can point out certain principles in the shape and relative size of the wing, and correlate these with the mode of life of the bird, there are an enormous number of variations within these generalities.

Birds that spend most of their time in flight have evolved long, narrow wings (which tend to be pointed in sea birds but broader in land birds), with the primaries often separated to expose the 'slots' through which the air passes, thus reducing vortex formation over the wing tip. The relative lengthening of the wing has been brought about in the albatrosses (Diomedeidae) by the development of a humerus of great length with a short manus, whereas in the swifts the reverse is true and the primaries are relatively long; these are used in lateral steering and are, therefore, associated with the aerial insect-catching activities of swifts, whereas albatrosses simply glide in the air and feed off the water.

Slow fliers, and those that hunt in enclosed areas such as woodland, have relatively shorter and more rounded wings; excellent examples are the rounded wing of the Sparrowhawk *Accipiter nisus* compared with the pointed wings of the falcons (Falconidae), and the same applies respectively to the Jay *Garrulus glandarius* and the Rook *Corvus frugilegus*.

The frequency of the wing-beat increases as the size of the wing decreases, relative to body weight, reaching its maximum in the hummingbirds with up to 80 beats per second (see FLIGHT).

Diastataxis. This is an apparent absence of the fifth secondary remex in some groups of birds—also called 'aquintocubitalism'. In diastataxic wings every pair of major coverts except the fifth embraces a remex, and this effect is believed to be due to torsion of the feather papillae during embryonic life. Where the effect does not occur the condition is known as eutaxis.

The following are diastataxic: Gaviidae, Podicipedidae, Procellariiformes, Pelecaniformes (except *Nannopterum*), Ardeidae, Phoenicopteridae, Anhimidae, Accipitridae, Gruidae, Heliornithidae, Eurypygidae, Charadriiformes, Pteroclididae, Psittacidae, Strigidae, Caprimulgiformes, and Coraciidae.

Eutaxic forms include: Struthionidae, Galliformes (except Megapodiidae), Rhynochetidae, Cariamidae, Psophiidae, Cuculiformes, Meropidae, Momotidae, Todidae, Coliidae, Trogonidae, Piciformes, and Passeriformes. J.G.H.

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Berger, A.J. 1960. The musculature. *In* Marshall (as above).

de Beer, G. 1956. The evolution of the ratites. Bull. Brit. Mus. (Nat. Hist.), Zool. 4: 57–70.

Fisher, H.I. 1955. Avian anatomy, 1925–1950, and some suggested problems. *In* Wolfson, A. (ed.). Recent Studies in Avian Biology. Urbana.

Simpson, G.G. 1946. Fossil Penguins. Bull. Amer. Mus. Nat. Hist. 87: 1–99.

WING BAR: a line across the wing contrasting in colour with the rest of it.

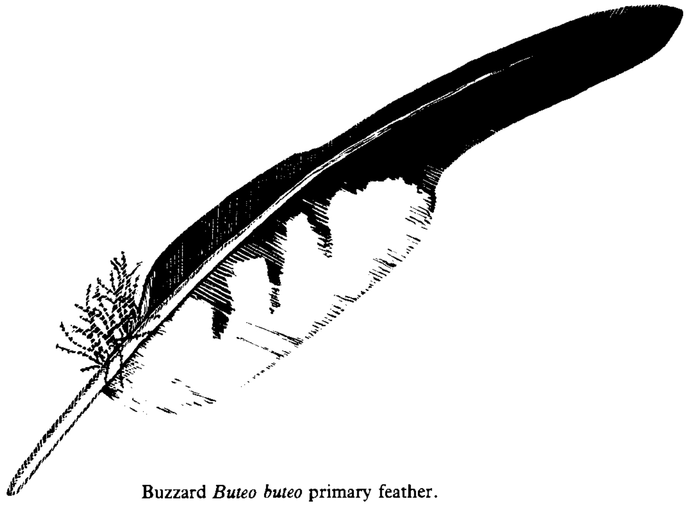
WING CLAPPING: raising the wings and striking them together to produce a loud crack (see MECHANICAL SOUNDS).

WING CLIP: see MARKING.

WING COVERTS: see TOPOGRAPHY.

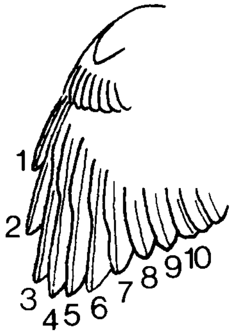
WINGED: wounded and unable to fly.

WING FORMULA: mainly mathematical representation of the shape of the distal part of a bird's wing. Wing formulae may be recorded from live or dead birds but may not be directly comparable through shrinkage of the dead bird's wing. Clear differences of wing formula exist between many closely related species whose plumage is very similar and, although there is considerable variation between individuals, such differences have also been demonstrated between races and populations of the same species (Busse 1967). Specific determination through wing formula characteristics is regularly used by bird-ringers to separate similar species, particularly among Sylviinae. In its fullest form the wing formula includes the distance (in millimetres) between the tip of the outermost primary and the longest primary covert and the distance between the tips of the rest of the primaries (and the longest secondary) and the wing point (tip of the longest primary). In addition the longer distal primaries may be notched or emarginated and this is noted. The emargination refers to the narrowing, which may affect either or both webs, towards the tip of the feather. On the outer web this may gradually slope outwards but on the inner web it may terminate abruptly at a notch. The example illustrated is a Buzzard *Buteo buteo* primary. The depth of such a notch may be measured, from the tip of the feather, and form an integral part of the overall wing formula. All relative measurements of feather length

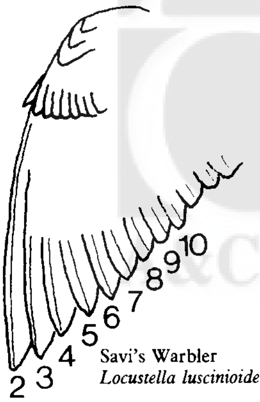


Buzzard *Buteo buteo* primary feather.

should be made on the closed wing because flexing causes alterations in the relative positions of the feathers as their points of attachment range along the metacarpals and phalanges. For the purposes of wing formula recording it is convenient and conventional to number the primaries from the outside inwards. In the example illustrated below slightly abbreviated wing formulae (measurements of some feathers are omitted) are given for two related species. The Cetti's Warbler *Cettia cetti* is predominantly a sedentary species and has a blunt, rounded wing but the Savi's Warbler *Locustella luscinioides* is a long-distance migrant with a sharp, pointed wing. In both illustrations the wings are shown partly opened but the measurements were taken from the naturally closed wings of museum specimens (Williamson 1968).



Cetti's Warbler *Cettia cetti*



Savi's Warbler *Locustella luscinioides*

Wing formula	*Cettia cetti*	*Locustella luscinioides*
1st primary	p.c. + 11 mm	p.c. − 1 mm
2nd	10 mm	Wing point
3rd	2½ mm	1½ mm
4th	Wing point	5 mm
5th	Wing point	7½ mm
6th	1 mm	10 mm
10th	9 mm	18 mm

Note that the first primary is measured in relation to the tip of the longest primary covert (p.c.), the other primaries in relation to the wing point or longest primary.

C.J.M.

Busse, P. 1967. Zastosowanie liczbowych wspolczynnikow ksztaltu skrzydla. Not. Orn. 8: 1–8.

Williamson, K. 1968. 3rd edn. Identification for Ringers 1, Tring.

WING LOADING: see FLIGHT (Adaptations for soaring).

WINGS, COMPARATIVE ANATOMY OF: the structure of the wing in birds as compared with that in other flying animals. The power of true flight, as distinct from gliding or passive 'ballooning', has been acquired four separate times in the course of evolution. Each method involves the use of wings that are analogous in being organs used in actively striking the air. The wings of insects, however, are not homologous with the others, being outgrowths from the dorsolateral areas of the two posterior segments of the thorax. In the other three instances, all among animals conforming with the general vertebrate plan, the wings are forelimbs adapted to the purpose; but the several modifications differ widely in detail. The bird's wing is unique in having the surface area composed of feathers, borne on an arm in which the bony elements of the manus are much reduced. In the extinct pterodactyls (Order Pterosauria, Class Reptilia) and in the bats (Order Chiroptera, Class Mammalia) the surface area consists of a membranous fold of skin borne on the arm and hand, the latter extended by elongated digits. In pterodactyls, represented in the geological record from the lower Jurassic to the upper Cretaceous, the extension of the skin was carried on an extremely elongated outermost digit (usually reckoned the 5th). In bats the larger part of the membrane is extended by elongated metacarpals and phalanges of digits 2 to 5 (the pollex being free, and clawed); a smaller part is anterior to the anterior margin of the arm, beginning from the side of the neck. In bats the wing is in fact more than a forelimb, as the membrane stretches down the side of the body and has its relatively small posterior part extended by the hind leg and the tail.

WING SOUNDS: see MECHANICAL SOUNDS.

WING SPAN: measurement from wing-tip to wing-tip across bird with wings fully extended—see FLIGHT. Standard measurements of wing-length taken from carpal joint to tip of longest primary cannot be used to assess wing span. Long-winged birds have generally evolved elongated inner wing bones (*radius* and *ulna* plus *humerus*) with extra secondary wing feathers attached. The maximum wing span for extant species approaches 4 m in the Wandering Albatross *Diomedea exulans* and may exceed 3 m regularly in the Andean Condor *Vultur gryphus* and Marabou Stork *Leptoptilos crumeniferus*. The first has a long, narrow wing adapted for dynamic soaring over the oceans and the other two long, broad wings with fingered primaries adapted for soaring over land (see FLIGHT). Fossils of extinct relatives of condors have been found with wing spans approaching 5 m, of an albatross-like species at over 7 m (see FOSSIL BIRDS) and of a flying dinosaur (the pterodactyl *Pteranodon ingens*) at about 8 m. All these creatures were soaring or gliding species not likely to have been able to sustain flapping flight. The larger size of the extinct birds is thought to be evidence that the atmosphere was more dense in former times. A 70% increase in density would probably allow birds with a mass of up to 25 kg to fly: the present-day limit is 10–15 kg (see FLIGHT). The big swans (Whooper *Cygnus cygnus* and Mute *C. olor*) have the largest wing span of current species which sustain flight almost wholly through active flapping—the biggest individuals may just exceed a span of 2.5 m.

C.J.M.

WING TAGGING: see MARKING.

WINNOWING: rapid wing beating through a very shallow arc in swift flight.

WINTER VISITORS: see VISITOR.

WIRE-BIRD: alternative name for the St Helena Sand-plover *Charadrius pecuarius sanctaehelenae* (see PLOVER (1)).

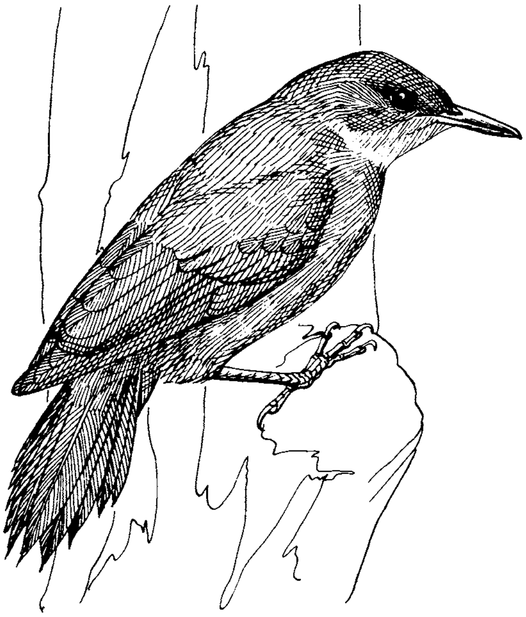
WIRETAIL: substantive name of *Sylviorthorhynchus desmursii*, a South American furnariid (for family see OVENBIRD (1)).

WISHBONE: the FURCULA; and see SKELETON, POST-CRANIAL.

WISP: see ASSEMBLY, NOUN OF.

WOODCHAT: name, alternatively 'Woodchat Shrike', of *Lanius senator* (see SHRIKE).

WOODCOCK: substantive name (commonly unchanged in the plural) of *Scolopax* spp. (see under SANDPIPER).



Ruddy Woodcreeper *Dendrocincla homochroa*. (*C.E.T.K.*).

WOODCREEPER: substantive name, alternatively 'woodhewer', of most species of Dendrocolaptidae (Passeriformes, infraorder Tyranni); in the plural, general term for the family. These birds are often treated as a subfamily Dendrocolaptinae of the ovenbird family Furnariidae from which they are derived. In size, plumage, and habits this Neotropical (primarily South American) family of nearly 50 species is rather uniform.

Characteristics. The majority of woodcreepers are between 20 and 37 cm in total length, the genera *Glyphorhynchus* (wedgebills) and *Sittasomus* being exceptions and averaging about 15 cm. Characteristically the plumage is olive, with rufous wings and tail, light or buff striations on the head, and similarly striated or barred under parts. A few, such as the Narrow-billed Woodcreeper *Lepidocolaptes angustirostris*, are almost white below; others, such as *Sittasomus* and *Dendrocincla* spp., lack striations but, although the latter retain the standard plumage colours of olive and rufous, the former are pure dark grey or yellowish below. The shafts of the rectrices are characteristically stiffened and the whole tail developed as in woodpeckers for a support in climbing trees. The legs are short, with powerful feet and long sharp claws. The bill is mostly stout and well developed, often rather compressed, long or moderately so, and more or less decurved. The extreme development is in the scythebills (or sicklebills) of the genus *Campylorhamphus*, which have long (*c.* 7 cm), scimitar-shaped bills, representing about a third or a quarter of the total length of the bird. On the other hand, the wedgebills have short, straight bills with an upturned lower mandible. There are 4 genera of woodcreepers that show some intermediacy in anatomical and plumage characters with the subfamily Philydorinae of the Furnariidae (ovenbirds); in sequence leading to typical woodcreeper morphology, these are, *Dendrocincla*, *Deconychura*, *Sittasomus*, and *Glyphorhynchus*. The other woodcreeper genera, *Drymornis*, *Nasica*, *Dendrexetastes*, *Hylexetastes*, *Xiphocolaptes*, *Dendrocolaptes*, *Xiphorhynchus*, *Lepidocolaptes* and *Campylorhamphus* may be termed the 'strong-billed' woodcreepers, and appear to form a tightly knit group morphologically.

Distribution. The family comprises 13 genera and 48 species, and ranges from Mexico (Sonora Province, in the north-west) to northern Argentina, east and central Bolivia, and Peru; it also reaches Trinidad and Tobago, but is not found in the Antilles. Thus, the range is closely similar to that of the antbirds (Formicariidae) and is essentially Neotropical, largely South American. Most species are sedentary but the Narrow-billed Woodcreeper *Lepidocolaptes angustirostris* is said to be a summer visitor to the area of Buenos Aires.

Habitat and food. The family is well adapted for an arboreal existence and the birds generally behave much like treecreepers (Certhiidae). Woodcreepers of the genus *Xiphorhynchus* are fairly typical of the family. Although primarily forest forms, they also occur in semi-open situations and forest borders. Some occur in mangroves. They forage, like most woodcreepers, by hitching up the trunks of trees or along branches. They use the stiff, spiny tail as a brace in climbing, and with the feet positioned well out laterally from the sides of the body, the birds are well away from the surface of the tree. They hitch straight up the trees or in spirals, searching for insects, other invertebrates, or small cold-blooded vertebrates (small frogs, salamanders and lizards), frequently stopping to peer under loose bark, and into moss clusters, vegetation clusters, or epiphytic plants, looking up into the cracks and crevices of these situations with one eye, then proceeding. Although peering is more typical foraging behaviour, there are many instances of woodcreepers probing, prying, and pecking at bark and small objects. After 'completing' a tree, they fly in a strong, undulating flight to or near the base of another tree to begin the cycle again. Some species are found high in the forest, while others forage primarily at the lower levels. Several species have been recorded feeding on the ground. They are usually seen singly or in couples, often accompanying mixed species foraging flocks, and some species (especially *Dendrocincla* spp.) often follow army ant swarms, taking insects that are disturbed by the ants off the bark of trees, or fly catching for them. The Great Rufous Woodcreeper *Xiphocolaptes major* and the Scimitar-billed Woodcreeper *Drymornis bridgesii* are adapted to feeding on the ground.

Voice. The voice varies considerably, being recorded as loud, musical, and melancholy for the Narrow-billed Woodcreeper *Lepidocolaptes angustirostris*; a loud *whee-whee-whee* as well as challenging notes for the Scimitar-billed Woodhewer *Drymornis bridgesii*; and a long-drawn-out trill for the Streak-headed Woodcreeper *Lepidocolaptes souleyetii*.

Breeding. The nests and eggs of very few species have been described, but so far as is known all build nests of leaves and vegetable materials in old woodpecker holes, hollow stumps, and trees, between the leaves of epiphytes or palm trees, and in other such enclosed places. The eggs are always white and more or less glossy, and the clutch size is usually 2 and rarely 3. The incubation period has been observed only in the Streak-headed Woodcreeper, as 15 days; and the nestling period in that species and in the Spot-crowned Woodcreeper *Lepidocolaptes affinis* as 19 days. (S.M.) A.F.

Feduccia, A. 1970. Natural history of the avian families Dendrocolaptidae (woodhewers) and Furnariidae (ovenbirds). Jour. Grad. Res. Center, S.M.U., 38: 1–26.

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Dickey, D.R. & van Rossem, A.J. 1938. The Birds of El Salvador, Field Mus. Nat. Hist. Zool. Ser. 23: 321–328.

Skutch, A.F. 1969. Life histories of Central American birds. III. Pacific Coast Avifauna, No. 35: 374–418.

Meyer de Schauensee, R. 1970. A Guide to the Birds of South America, Wynnewood, Pa. 194–200.

Wetmore, A. 1972. The Birds of the Republic of Panama, 3. Smithson. Misc. Collect., 150: 2–56.

WOODHAUNTER: *Hyloctistes subulatus* (for family see OVENBIRD (1)).

WOODHEN: alternative name for the wekas *Gallirallus* spp. (see RAIL).

WOODHEWER: see WOODCREEPER.

WOOD-HOOPOE: substantive name now generally used for all members of the Phoeniculidae (scimitar-bill being an alternative name for some); in the plural, general name for the family. From 6 to 9 species are recognized; they are now often placed in a single genus, *Phoeniculus*, but the forms with very curved bills (scimitar-bills) are sometimes separated (as here) as *Rhinopomastus*, and the single species with a nearly straight bill as *Scoptelus*.

Characteristics. This small group (lengths *c.* 21–43 cm), restricted to sub-Saharan Africa (though known from fossils in Europe), is morphologically homogeneous and very different in appearance and behaviour from the better known true Hoopoe *Upupa epops*. They have long graduated tails and (in most forms) long decurved bills. The tarsi are short, thick and scutellate, and toes 3 and 4 are fused at the base. Primaries and rectrices number 10. Plumage colour of all wood-hoopoes is primarily black, with or without a metallic green, purple or blue gloss. White, buff or brown also appear on some species. The feet and bill are red, orange, yellow or black, depending on the species or population; these characters often vary with age. Sexual size dimorphism is pronounced in some species. The uropygial gland produces a strongly odoriferous substance when the birds, either adults or older nestlings, are frightened in the roost or nest cavity (as is also the case in the hoopoes). On the ground wood-hoopoes hop (unlike the hoopoes, which walk).

Habitat and distribution. Wood-hoopoes are primarily arboreal and are found in thick forests (e.g. *Phoeniculus bollei*), open acacia savanna (e.g. *P. purpureus*, *Rhinopomastus cyanomelas*), and along tree-lined water courses in arid country (e.g. *R. minor*). One species or species complex, the Green Wood-hoopoe *P. purpureus*, has a very large range which includes virtually all the Afrotropical region except the equatorial rain-forest of West Africa.

Food. Wood-hoopoes feed mostly on insects and other arthropods, but some at least occasionally also take succulent fruits, including berries. Although most foraging occurs in trees, primarily by bark-probing, Green Wood-hoopoes in Kenya also feed on the ground, tearing open the droppings of large mammals to uncover the insect fauna therein. The Violet or Grant's Wood-hoopoe *P. granti* has been seen to take the eggs of the Speckle-fronted Weaver *Sporopipes frontalis*.

Voice. Wood-hoopoes proper (*P. purpureus* and *P. bollei*) are quite vocal, their calls generally being rather loud and frequent; scimitar bills *Rhinopomastus*, on the other hand, tend to vocalize less and their calls have comparatively little carrying power.

Behaviour. Social systems range from solitary pairs, as exhibited by the scimitar-bills, to co-operative breeding in stable flocks that number from 3 to 16 in Green Wood-hoopoes. Within such flocks there is only one breeding pair, with other flock members ('nest helpers') usually being related to one or both breeders. A spectacular feature of their behaviour is the frequent social cackling (whence the Afrikaans name 'Kakelaar'), accompanied by fast, exaggerated bowing and whipping up and down of the tail.

Breeding. The nest is placed in either a natural cavity or an old woodpecker hole and little or no nest material is used. The eggs (2–4 or 5) are coloured, unusual for cavity nesting species, blue, green or grey. In *P. purpureus* the breeding female alone incubates, and she is fed both by her mate and by other flock members. The helpers may provide most of the food received by the female breeder and later the nestlings. The incubation and fledging periods for *P. purpureus* are 17–18 and 28–30 days respectively. Nest sanitation is not practised, but the young birds typically place their droppings at one edge of the floor cavity. After the young wood-hoopoes fledge they continue for some time to be cared for by the flock members. Later, sometimes within a few months, these young serve as helpers at the next nest. (D.A.B.) J.D.L.

Davidson, N.C. 1976. The evolution and systematics of the Phoeniculidae. Bull. Nigerian Orn. Soc. 12: 2–17.
Ligon, J.D. & Ligon, S.H. 1978. The communal social system of the Wood-hoopoe in Kenya. Living Bird 17: 159–197.

Green Wood-hoopoe *Phoeniculus purpureus*. (*N.A.*).

WOOD-IBIS: former substantive name of *Mycteria* (*Ibis*) spp., now more correctly known as wood-storks (see STORK).

WOODLARK: *Lullula arborea* (see LARK).

WOODNYMPH: substantive name of *Thalurania* spp. and *Cyanophaia bicolor* (for family see HUMMINGBIRD).

WOOD-PARTRIDGE: substantive name of several species of woodland gamebirds (see PHEASANT).

WOODPECKER: substantive name of most species of Picidae (Piciformes, suborder Pici); in the plural, general term for this family of about 198 species. There are 3 subfamilies of woodpeckers, the wrynecks (Jynginae) with 2 species, the piculets (Picumninae) with 27 species, and the true woodpeckers (Picinae) with 169 species, based upon Short's (1982) monograph of the family.

Several woodpeckers bear other names such as 'flicker' and 'sapsucker'; the tiny woodpeckers that do not apply the tail to the bark as they cling to it are known as 'piculets'.

Characteristics. Woodpeckers generally are the most specialized of bark-foraging birds, being adapted to cling easily to the bark and to move readily over tree surfaces where they are able not only to glean, probe and pry, but to excavate into the bark and wood to obtain insects. Their tapping sounds as they feed and their characteristic appearance with strong, straight bill and tail braced against the bark render them widely known and attract interest in them. Most species are small to medium-sized (15–33 cm in length), but piculets and a few woodpeckers are tiny (to 8.5 cm) and some are larger (up to 58 cm). The predominant colours are black, white, green and brown with patches of red or yellow; one or two colours usually mark the body and the head is often distinctively striped. The sexes are alike in a few species, and are markedly different in only 2 or 3 species, the chief difference commonly being the presence of a red or yellow patch on the head of the male that the female lacks. Dorsal streaking and barring are frequent and the wings and tail usually bear spots or bars paler than the dominant colour. Ventrally many species are streaked or spotted. Most species have an undulating flight.

Habitat, distribution and movements. Naturally woodpeckers are associated with trees and occur in diverse forests, woodlands, savannas, and scrub deserts. A few species are adapted for life in treeless grasslands, where they nest in holes in the earth. Some woodpeckers, especially smaller species, frequent gardens, tree-lined streets, parks, orchards, and vineyards. Most are strictly resident and maintain territories year-round, but a few species (especially of genera *Jynx*, *Sphyrapicus*, *Colaptes*) migrate extensively and some show periodic movements associated with insect abundance, or slight southward (temperate species) or downslope (montane species) post-breeding shifts. Woodpeckers range from the tundra-edge to southernmost Africa and South America, occupying Eurasia, the Americas and Africa. They fail to reach oceanic islands, Australasia, Madagascar, and of course Antarctica, although regularly occurring on islands of the continental slopes. They approach Australasia as closely as the Philippines and Sulawesi. In mountainous regions some woodpeckers regularly reach the limit of trees and even higher seasonally in the Himalayas (*Picus squamatus*), and the terrestrial Andean Flicker *Colaptes rupicola* (35 cm) spends its life entirely above tree line. Coexisting species of woodpeckers tend to compete, and less botanically diverse woods have fewer species, richer forests have more (as many as 13 species of woodpeckers may live sympatrically in tropical Malaya and perhaps Peru).

The world's largest woodpecker, the Imperial Woodpecker *Campephilus imperialis* (58 cm) of Mexico, is probably extinct, and a few individuals of its near relative the Ivory-billed Woodpecker *C. principalis* (50 cm) perhaps still exist in Cuba. Widespread North American species include the ground-feeding Northern Flicker *Colaptes auratus* (33 cm), the garden-haunting Downy Woodpecker *Picoides pubescens* (16 cm) and its larger, shyer relative the Hairy Woodpecker *P. villosus* (24 cm), the Red-bellied Woodpecker *Melanerpes carolinus* (25 cm), the omnivorous Red-headed Woodpecker *M. erythrocephalus*, the migratory Yellow-bellied Sapsucker *Sphyrapicus varius* (22 cm), and the still common, large, crested Pileated Woodpecker *Dryocopus pileatus* (40–48 cm). Tropical Middle America and South America feature large, crested species of *Campephilus*, several of *Dryocopus* and *Colaptes*, 2 species of *Picoides*, numerous species of *Melanerpes*, most species of *Celeus*, and a number of species of the endemic *Piculus* and *Veniliornis*. Cuba is the home of the highly coloured, endemic *Xiphidiopicus percussus*.

In Europe (most extend into Asia as well) are a number of species of *Picoides* (*Dendrocopos*) including the common Great Spotted Woodpecker *Picoides major* (23 cm) and the smaller, shyer Lesser Spotted Woodpecker *P. minor* (14 cm) of parks, woodlands and gardens, and 2 species of ground-feeding *Picus*, the Green Woodpecker *P. viridis* (31 cm) and the Grey-headed Woodpecker *P. canus* (25 cm), which extends to China and Sumatra. The large Black Woodpecker *Dryocopus martius* (45 cm) is still common in forested central Europe and in mountains one can find the Three-toed Woodpecker *Picoides tridactylus* (22 cm) that reaches Asia and North America as well, and the White-backed Woodpecker *P. leucotos* (25 cm), which occurs east to Japan.

Food. Although specialists at woodpecking, many species feed opportunistically on the bark surface of trees for insects, fly-catch for winged termites and other flying insects, go to insect-bearing dead, fallen branches on the ground, and eat available fruits and nuts. Rarely a few species prey on other birds, seizing young from an open nest or enlarging nesting holes of other birds to get at their young. Sapsuckers (*Sphyrapicus*) and a few species of *Picoides* (*Dendrocopos*) regularly feed on sap at special pits excavated and maintained in certain trees at some seasons. Ants are a favourite food of many woodpeckers that pick them from the bark, excavate for them into trees or rotten stumps, or take them from tree-ant nests; the ground woodpeckers (*Geocolaptes*, *Colaptes*) and some species of *Picus* regularly feed on the ground, mainly on ants.

Behaviour. Only a few species are social; woodpeckers commonly are seen singly, or occasionally in pairs (but also in family parties for a period following nesting).

Acorn Woodpeckers *Melanerpes formicivorus* (24 cm) of south-western North and Middle America are highly social, living in groups of up to a dozen birds including a primary pair and usually their offspring of one or several years. These groups nest communally, sharing incubation and feeding of the young. The life of the Acorn Woodpecker is based largely upon two foraging strategies, the harvesting and storing of acorns of several species of oaks, and in spring and summer, when weather conditions are suitable, upon flycatching. Entire tree trunks may be covered with pit-like holes excavated by the woodpeckers, into which they force the acorns. As they are largely dependent upon these acorns for much of the autumn, winter and spring, the members of a group vigorously defend their 'storehouses' against other Acorn Woodpeckers and other species of birds, and mammals. The related *Melanerpes lewis*, *M. erythrocephalus* and *M. carolinus* also store acorns, but not to the same extent and less systematically than the more social Acorn Woodpecker.

Tropical woodpeckers tend to remain paired throughout the year, as do some woodpeckers of temperate regions, but most forage alone. Paired birds maintain vocal contact. Adults are aggressive in defence of their territory, which often is proclaimed by drumming signals or by a long series of notes. The sexes respond sex-for-sex in territorial encounters, which are marked by a variety of vocalizations, and displays involving bowing and swinging movements of the head and body, and wing and tail movements.

Voice. Some tropical species are relatively quiet but most woodpeckers characteristically use the bill to produce a 'drumming' sound by tapping it against an appropriate tree surface as a means of communication (see MECHANICAL SOUNDS). As many as 18 different vocalizations have been ascribed to various pied woodpeckers (*Picoides*, or *Dendrocopos*) and most woodpeckers have call notes and often ringing or scream-like calls.

Breeding. Birds excavate holes in which to roost at any time of the year but, as the breeding season approaches, one or both members of a pair will excavate the cavity to be used for nesting (in some species the male's roosting hole becomes the nesting cavity, and a few species may use the same hole for several years). The height and situation of the nest vary, as does the time required to excavate it, although under stress the nest can be completed within several days. Starlings, toucans, other hole-nesting birds, and mammals often compete successfully for the woodpeckers' newly excavated holes. A few woodpeckers nest socially with as many as 20 nests in a single tree (*Melanerpes striatus*) or earthen bank (*Colaptes rupicola*). Small species utilize very narrow broken or dead stubs and branchlets too small to be used by larger woodpeckers or other competitors.

Woodpeckers' nesting cavities are lined only by wood chips and splinters. From 2–9 glossy white eggs are laid and incubated by both sexes alternately during the day, but by the male alone at night in virtually all species. The incubation period is 11–17 days. The naked, blind hatchlings develop rapidly. Both adults feed the young, first entering the nest, and later feeding at the nest entrance when the young are able to climb to it. The fledging period for the larger species is 2½–3½ weeks.

Fledglings are fed by the parents, whom they tend to follow about. The period at which the young become independent is critical, for the adults may force them out of the territory and they then lack holes in which to roost. In some tropical species there is long association with the parents, even after independence, and the young may remain on the territory, sometimes excavating roosting holes near those of the parents (*Chrysocolaptes lucidus*). The nest of some piculets becomes a 'dormitory', the entire family roosting together at night in it for a long period of time.

Moult. Moult takes place annually, after breeding, but may be protracted. Usually the largest, strongest tail feathers, the central pair, are moulted after all others have moulted and the new ones come in, rendering the tail maximally effective as a brace throughout the moult. The initial juvenile plumage is replaced in the postjuvenile moult beginning in the nestling stage, usually with abbreviated juvenile first and second primaries being shed and adult feathers coming in by the late nestling stage. The postjuvenile moult is usually complete, but it is incomplete in piculets and the juvenile secondary coverts of some woodpeckers (*Picoides* or *Dendrocopos*) may not be moulted until the bird is a year old. The juvenile plumage generally is similar to that of the adult, but duller and often with greater streaking; the outermost (reduced) primary is broader and longer than in adults. Juvenile-plumaged females often show more male-like head colouring than adult females, and the sexes are nearly alike in the juvenile plumage of some species. Sapsuckers (*Sphyrapicus*) and Red-headed Woodpeckers *Melanerpes erythrocephalus* (24 cm) have a juvenile plumage differing greatly from that of adults, and the moult into adult plumage may last 6 months.

Special features. Woodpeckers differ from the related barbets (Capitonidae) and other members of the order Piciformes in their straight, often chisel-tipped bill, thick bony skull, long, extensible, barbed and often sticky-coated tongue (sublingual glands secrete sticky mucus, which with the barbs and long tongue enables the woodpecker to extract ants or other insects from their tunnels within the tree), arrangement of pelvic muscles, and bifurcate manubrium of the sternum. The co-ordinated structure of the bill, skull, head muscles, tongue and glands forms an effective and unique food-securing system. Most woodpeckers have 12 rectrices, forming a hard, fairly rigid tail. *Sasia africana* has but 8 rectrices and other species of *Sasia* and *Campephilus pollens* have 10. The outermost pair is usually much reduced, and lacking in those woodpeckers with fewer than 12 rectrices. The tail of piculets and wrynecks is more flexible and less hardened along the shafts, but woodpeckers show a gradation from fairly flexible in less specialized to rigid in very specialized woodpecking species. The central pair are longest and most rigid but in a few specialized woodpeckers (*Campephilus*, *Reinwardtipicus*, *Chrysocolaptes*), the two central pairs are equally rigid. Woodpeckers have a tough, thick skin that probably serves to minimize effects of insect bites and stings. The legs of woodpeckers are short and strong, with sharp nails. Although zygodactylous ('yoke-toed', 2 toes forward, 2 behind), woodpeckers often splay the toes apart and very specialized species splay 3 or even all 4 toes forward (i.e., upward on tree) when climbing. The first toe (hind toe of most birds, the hallux) has been lost in some species of several genera (*Sasia*, *Dinopium*, *Gecinulus*, *Picoides* or *Dendrocopos*), and *Dinopium shorii* may have or lack a tiny hallux.

The bill tends to be slightly curved along the culmen (dorsal ridge) and pointed at the tip in ant-feeding, generally less specialized woodpeckers (*Colaptes*, *Campethera*, *Meiglyptes*), and straighter and more chisel-tipped in more wood-pecking species. The most specialized excavating species (e.g., *Campephilus principalis*, *Picoides arcticus*) have a broad-based bill with a deep chisel-tip. The nostrils are partly or fully covered by feathering in most woodpeckers and often are elongated and slit-like in specialized woodpeckers, protecting the nasal chambers from wood particles scattered as the bird excavates.

Jynginae. The wrynecks are peculiarly coloured in a cryptic pattern of tans, browns, grey and black. The sexes are alike. Wrynecks do not excavate nests but use natural cavities. More often than woodpeckers they perch crosswise, infrequently clinging to the bark. Twisting movements of the head and neck in display and alarm are responsible for their name. The 2 closely related species are the migratory Northern Wryneck

Jynx torquilla (16 cm) of Eurasia and North Africa, and *J. ruficollis* of tropical Africa. They probably represent a modified offshoot of primitive woodpecker stock.

Picumninae. The tiny piculets are poorly known taxonomically and behaviourally. Although the short tail is not used as a brace, they tap, feed, and drum like true woodpeckers. Most are brown, grey or greenish above, sometimes barred or spotted, with pale underparts marked with streaks, spots or bars. One species of *Picumnus* and 2 of *Sasia* occupy Asia, *Sasia africana* occurs in central Africa, the remaining 22 species of *Picumnus* inhabit Middle and South America, and the distinctive, large *Nesoctites micromegas* is endemic on Hispaniola.

Picinae. The true woodpeckers are most numerous in tropical America and South-east Asia. Africa, surprisingly, has rather few and no large woodpeckers. The classification used here differs in a few ways from that of Voous used elsewhere in this volume, and particularly in the case of use of *Picoides* instead of *Dendrocopos* for reasons given in detail in publications by Short (1971, 1982) and by Winkler and Short (1978).

One species of *Picoides* (*P. obsoletus*) aside, the two dozen African woodpeckers represent the endemic genera *Campethera*, *Geocolaptes*, and *Dendropicos*. Few species occur in heavy forest—most are woodland and savanna species. *Campethera* species are unspecialized, largely feeding on ants. *Geocolaptes olivaceus* is the terrestrial African Ground Woodpecker of southern Africa. *Dendropicos* contains more specialized wood-pecking species allied to *Picoides*.

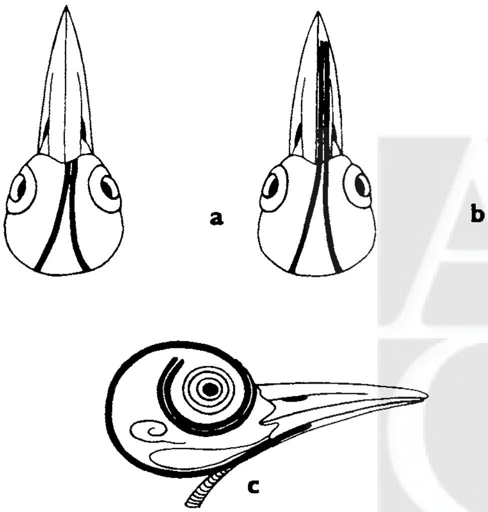

Fig. 1. Progressively different dispositions of the hyoid bones ('horns') in Picidae:
(a) the horns end at the base of the bill, as in *Reinwardtipicus validus*, *Chrysocolaptes* spp., *Picoides* spp. (including *Dendrocopos*), *Veniliornis olivinus*, *Picumnus* spp. etc.
(b) The horns end in the right cavity of the upper mandible, as in *Dinopium javanense*, *Colaptes* spp., *Picus puniceus*, etc.
(c) the horns end below, behind, or upon the right orbit, as in *Picoides villosus*, *Hemicircus concretus*, and *H. canente*. (*J. Steinbacher*).

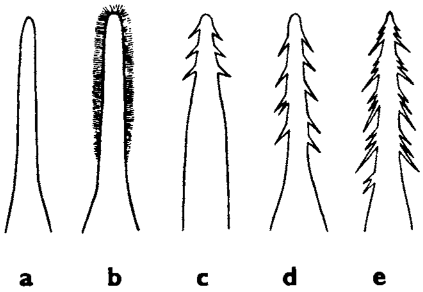

Fig. 2. Different forms of tongue-tips in Picidae:
(a) smooth, without any bristles (*Jynx*).
(b) brush-like (*Sphyrapicus varius*, *Melanerpes candidus*, *M. formicivorus*).
(c) with 2–3 barbs (*Colaptes melanochloros*).
(d) with 4–6 barbs (*Celeus flavescens*, *Veniliornis olivinus*, *Dryocopus lineatus*).
(e) with groups of barbs of different sizes (*Campephilus* spp. and *Melanerpes aurifrons*. (*J. Steinbacher*).

Powerful Woodpecker *Campephilus pollens*. (*P.J.K.B.*).

Tropical Asian woodpeckers are morphologically very diverse and include the endemic genera *Meiglyptes*, *Hemicircus*, *Mulleripicus*, *Blythipicus*, *Gecinulus*, *Dinopium*, *Chrysocolaptes*, and *Reinwardtipicus*, as well as numerous species of *Picoides* and *Picus*, one species of *Dryocopus* and a single species of *Celeus*. Of these some *Picoides*, *Dryocopus javensis*, *Hemicircus*, *Blythipicus*, *Chrysocolaptes* and *Reinwardtipicus* are most specialized for excavating. *Gecinulus grantia* feeds almost exclusively in bamboo. A distinctive, endangered woodpecker of Okinawa in the Ryukyu Islands, *Sapheopipo noguchii*, numbers about 200 birds.

See photos ALARM; FOOD STORING. L.L.S.

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WOOD-QUAIL: substantive name of *Odontophorus* spp. found in Neotropical woodlands (for family see PHEASANT).

WOOD-RAIL: in the plural, general term for certain genera of Rallidae (see RAIL).

WOOD-SHRIKE: name sometimes applied to species of Campephagidae or, in the plural, used generally for the family (see CUCKOO-SHRIKE); also, sometimes, similarly in respect of the Prionopinae (see HELMET-SHRIKE).

WOODSTAR: substantive name of *Chaetocercus jourdanii*, *Myrmia micrura*, *Myrtis fanny*, and *Philodice* spp. (for family see HUMMINGBIRD).

WOOD-STORK: *Mycteria americana*; also a general term for all four *Mycteria* spp., though the other three usually have 'stork' as the substantive name, e.g. Milky Stork *M. cinerea* (see STORK).

WOOD-SWALLOW: substantive name, alternatively 'swallow-shrike', of the species of Artamidae (Passeriformes, suborder Oscines); in the plural, in either form, general term for the family.

The family includes only the genus *Artamus*, which seems to have originated in Australia. As there is no recent monograph of the genus, the exact number of species can be given only as from 10 (Mayr 1962) to 15, of which 6 are wholly or partly Australian. The five purely Australian species share a number of features of plumage and behaviour not shown by those found partly or entirely outside it (Frith 1976). The latter perhaps represent a radiation in the Indo-Pacific region from an early ancestral stock of Australian origin. Their nearest relatives are uncertain, and they certainly are neither swallows (Hirundinidae) nor shrikes (Laniidae).

Characteristics. The wood-swallows are stoutly built birds up to 20 cm in length. The bill is stout, moderately long, slightly decurved, and pointed; it has a wide gape. The legs are short, the feet strong. The tail is blunt and rather short. The wings are long and pointed, reaching almost to the tip of the tail. The plumage colour of all species, except a partly chestnut Australian one, is a mixture of black, grey, and white. The sexes are alike or nearly so. They possess powder-down feathers, the tips of which break up into a kind of dusting powder, used by the birds in dressing the plumage; some of the Cotingidae have such feathers, but no other families among the passerines.

Wood-swallows may be identified from a long distance by their habit of huddling close together, 4 or 5 birds on a bare branch, and the tail is often waggled from side to side. The flight is exceedingly graceful, often interrupted by long periods of gliding, for which the wings are well adapted, and the larger species are able to soar on thermal up-currents. In some of the species the birds sleep in compact knots, one standing on another. They are very pugnacious, and will violently attack passing birds as large as crows or harriers (Circinae).

Habitat. Ranges from scrub, desert and agricultural land to clearings in montane forest according to species.

Distribution. The family is centred on Australia and the south-west Pacific. One species extends westwards to Malaysia, but without reaching the mainland of Asia; another is widespread in south-east Asia from eastern India and Sri Lanka, through Burma and Thailand, to western China.

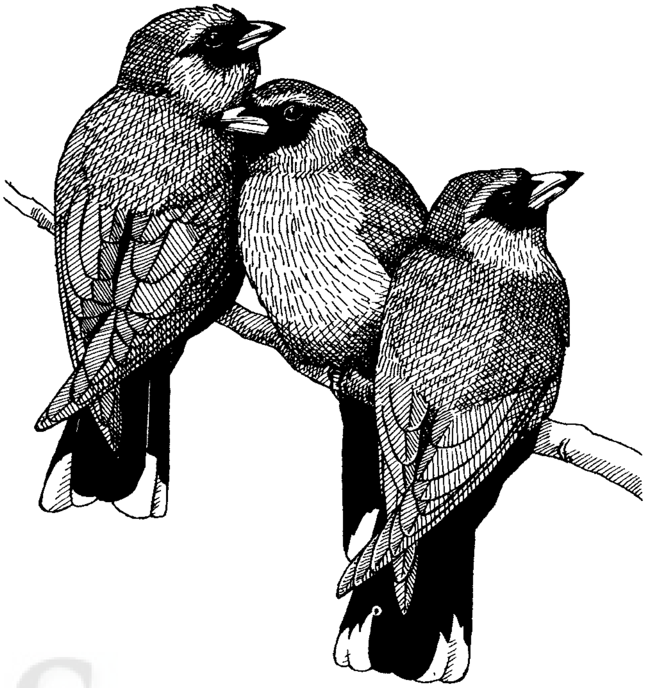
Movements. In South Australia, West Australia, and New South Wales, some species are migratory. Thus, the Masked Wood-swallow *A. personatus* described as invading the southern portion of West Australia on a large scale in some seasons, arrives in South Australia regularly in September in flocks, departing in January. The White-browed Wood-swallow *A. superciliosus* also arrives in South Australia in September. These two species form mixed feeding flocks and breeding colonies. Local movements of this type have been noticed in Northern Burma.

Food. Insects, from midges to large butterflies and beetles, usually captured in flight, though *A. cinereus* will take prey from open ground or foliage.

Voice. Harsh cries and twittering notes.

Breeding. Wood-swallows breed in colonies. The nest is usually placed on the top of a projecting stump or branch, occasionally in a hole; a favourite site is on a palm tree, either on the bases of the leaves or on the rough projections whence the leaves have fallen. The site is usually 10 m or more from the ground. Some Australian species, however, nest in shrubs or bushes within 3 m of the ground. The Little Wood-swallow *A. minor* haunts cliffs and broken country, where it nests in crevices among the rocks or on ledges in caverns.

The nest is a shallow, loose cup of fine grasses, roots, fibres, feathers, and similar materials, as a rule with no definite lining. The 2–4 eggs somewhat resemble those of shrikes, being spotted and blotched on a white to cream base. The nidicolous young are hatched with some down on the upper parts. Parental duties are shared by both sexes. Nestlings of the Greater Wood-swallow *A. maximus* have been observed being fed by 4 or 5 adults. B.E.S. and P.J.K.B.



Black-faced Wood-swallow *Artamus cinereus*. (*N.W.C.*).

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WOOD-WARBLER: alternative general term for the American warblers or Parulidae (see WARBLER (2)); also, in Britain, the name of *Phylloscopus sibilatrix* in the family Sylviidae (see WARBLER (1)).

WORMS, PARASITIC: see ENDOPARASITE.

WRECK: an occasional disaster affecting pelagic species of birds, e.g. storm-petrels (Hydrobatidae) and Little Auk *Alle alle*, when these are swept ashore or inland in large numbers by persistent gales (see OCEANIC BIRDS).

WREN (1): general term for birds in the family Troglodytidae (Passeriformes, suborder Oscines). 'Wren' without qualification, is usually assumed to refer to the Holarctic species *Troglodytes troglodytes*, which is also called the European Wren, or the Winter Wren in North America.

The family Troglodytidae is considered to contain 12–14 genera and 60–65 species, including the Black-capped Donacobius *Donacobius atricapillus*, which was formerly placed in the Mimidae. Except for the Holarctic *T. troglodytes* it is an exclusively New World family, probably having its origin in Central America where the greatest variety of genera and species is found. Indeed, only one species, *T. troglodytes*, occurs in the Old World, although it does comprise a large number of subspecies that differ in size and plumage coloration. Some of the most distinctive races live on isolated islands off the Atlantic coast of Scotland (e.g. Fair Isle and St. Kilda).

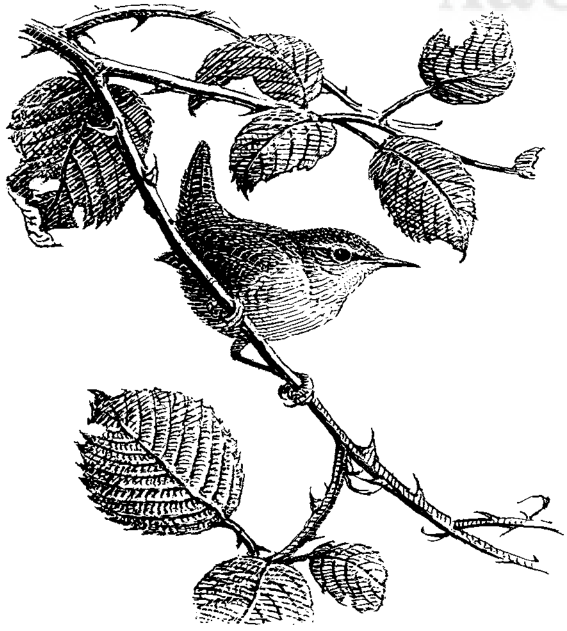
Characteristics. The wrens are mostly small (8–15 cm) with brown to rufous upper parts, a paler belly and, in many cases, a pale eye-stripe and a closely barred pattern on the flight and tail feathers. Their most distinctive characteristic, however, must be their tails, which are usually held erect to be moved vigorously back and forth in both territorial and mating displays. All wrens have rather short, blunt wings, making them poor fliers.

Habitat and distribution. Within their exceptionally wide New World range (from central Canada south to Tierra del Fuego) wrens of different species occupy almost every kind of habitat, though they are most characteristic of dense, low vegetation. Only a few species are found in lowland tropical forest, one of which, the Thrush-like Wren *Campylorhynchus turdinus*, is unusual in foraging among epiphytes high in the trees. At the other extreme such species as the Cactus Wren *Campylorhynchus brunneicapillus*, the Rock Wren *Salpinctes obsoletus* and the Canyon Wren *Catherpes mexicanus* live, as their names imply, in relatively dry and barren habitats, in the south-western United States. Typical farmland species in North America are the House Wren *Troglodytes aedon*, a common nest-box species, in the north, and Bewick's Wren *Thryomanes bewickii* in the south. The Marsh and Sedge Wrens, *Cistothorus palustris* and *C. platensis*, breed in reed marshes and sedge meadows respectively, the latter mainly in the north-eastern states. The Carolina Wren *Thryothorus ludovicianus* is particularly associated with dense understorey in forests.

Within the New World *Troglodytes troglodytes* breeds only along the north-western seaboard and in the area around the Great Lakes, where it almost always lives near dense shrubby cover on the forest floor. In Western Europe this is the type of ground it occupies at highest densities, but it also occurs in almost every other available habitat to some extent. Thus it is found breeding in disused buildings, drystone walls and broken cliff-faces in the west of Scotland, and in hedgerows, riverine scrub, urban gardens and all types of forest with appreciable understorey cover throughout the whole continent.

Food, populations and movements. Wrens, being small and almost exclusively reliant upon an invertebrate diet, are extremely susceptible to severe winter weather. Thus it is not surprising to find that many species undertake quite lengthy seasonal migrations in order to overwinter in milder conditions than are then found over some or all of their breeding range. In North America the House, Winter, Rock and Marsh Wrens show movements of this kind, which take the bulk of their populations either to the oceanic coastlines or to the southerly States for the winter.

In Northern Europe *Troglodytes troglodytes* may also move south for winter: exceptionally heavy birds, not thought to be members of the British breeding population, are sometimes caught in quite large numbers at ringing stations along the east coast of England during the autumn passage. The likelihood is that these birds breed in Scandinavia. In the south of England there are certainly local movements into especially productive habitats, such as reedbeds, for the winter.



Wren *Troglodytes troglodytes*. (*D.W.*).

The Wren in Europe has another habit which helps resident winter populations to survive periods of exceptionally inclement weather—communal ROOSTING for the night. As many as 50 birds may gather at dusk and cram themselves into a suitable cavity. They will often use Wren nests from the previous season, but also nest-boxes, hollow logs and eaves. Despite this special adaptation there are records of several dozen dead Wrens being found in and around roosting sites after a few days of continuous frost. Thus, Wren populations may undergo spectacular crashes over the course of severe winters (e.g. 1962–1963 in Britain) from which it takes them several years to recover.

Behaviour. The males of all the wren species so far studied in any detail are territorial during the breeding season, and perhaps for much of the rest of the year as well. In general only resident males confront vagrant or neighbouring males that trespass upon their ground. Fights are rare; most territorial disputes are settled conventionally, although precisely how is not known. Song is obviously involved because PLAYBACK of tape-recordings within occupied territories produces frenzied singing and overt aggression from resident males. Female and yearling Cactus Wrens join the male in the defence of their group territory.

Species living in or near the tropics are known or suspected of being monogamous in their breeding habits, but several Northern Temperate forms, including the House, European and Marsh Wrens, are known to be polygynous, quite frequently in productive habitats. The evolution of regular POLYGYNY has apparently resulted in some striking behavioural modifications to the presumed ancestral monogamous pattern.

First, at least in those northern species which have been well studied, the songs most characteristic of the polygynous species are long and complex, whilst those of the monogamists are simple, repetitive buzzing vocalizations (e.g. Cactus Wren). The European Wren produces an extraordinarily loud and long song for a bird of its small size. Each rendition usually lasts for more than 5 seconds and consists of several different types of high trill, which, together with other notes of great variety, make up a typical song of more than 100 notes in all. This wren and the next most frequent polygynist, the Marsh Wren, not only sing the longest, most complex songs in the family, but also sing for much more of the time, especially during the dawn chorus in Spring and Summer. At this season male European Wrens may sing for approximately one-third of the time for the first 3 hours after dawn. Neighbouring males can be heard answering one another for many minutes, whilst standing their territorial ground some 10–30 m apart.

Some tropical wrens have songs of outstanding beauty, especially those in the genera *Microcerculus* and *Cyphorhinus*. Thus the Nightingale Wren *M. marginatus* utters an extraordinarily slow sequence of pure flute-like tones, a complete song lasting for 30 seconds or more. Other tropical wrens habitually sing duets, the male and female of a pair singing either in unison or antiphonally.

Breeding. A second set of trends correlating with the variety of wrens' mating systems concern nest-building and the use to which the nests are put. The female Cactus Wren usually helps her monogamous mate to construct nests, but this has never been observed in either the European or the Marsh Wren. Cactus Wren nests are used as roosting sites throughout the year by the breeding pair and their offspring, as well as for housing the eggs and nestlings resulting from any breeding attempts. Male House, European and Marsh Wrens all build more nests in their territories than are ever used by breeding females. House Wren nests are usually in naturally occurring cavities in tree-trunks or buildings, and males quite frequently build 3 in a season. European Wren nests are domed and are also found at such sites, but they may also be bound to woody or herbaceous vegetation in forest understorey and other scrub. Males of this species quite frequently build 6, and sometimes as many as 12 nests in a single season. Some of these are used for breeding attempts by females, whilst others, which are sometimes referred to as COCK NESTS, are not. There is no obvious structural difference between these two types, at least to the human observer.

Nests of the House and European Wrens may be placed anywhere within males' territories, and single birds can have up to 4 ready for immediate occupation. Courtship in both these species involves the male attempting to lead any passing female to one or more of his nests; this he accomplishes by executing a frenzied dance over the female, whilst singing soft, abbreviated songs to her. The female will sometimes enter the nest she is shown and may remain within for some minutes. Soon afterwards she may be seen carrying feathers and other nest-lining materials to the site of her recent courtship. Usually this can be taken to indicate her intention to make a breeding attempt at that nest. All these facts make it seem highly likely that the nests of the European Wren have an important ceremonial function, associated with mate attraction by males in addition to their more conventional one. Indeed there is some evidence to suggest that the larger the number of vacant nests a male has in his territory, relative to his neighbours, the more likely he is to attract a prospecting female to breed in his territory.

The pattern is basically similar, though even more extreme, in the Marsh Wren. Males build a large number of nests in a cluster amongst reeds or bullrushes. Many of these nests are never completed and they are sometimes stacked on top of each other. These nest-clusters are known as 'courtship centres' because the male typically advertises them by singing nearby and leads any female that approaches to a number of the nests. He will usually build yet another nest, which is used by the female for breeding, away from the courtship centre at a location apparently specified by her. Additional females are often attracted to breed in the same territory after the construction of further courtship centres in different places. During the course of their 3-month breeding season males may routinely complete 30 or more nests and there is a positive correlation between the total number of nests completed and the number of females obtained per male. Thus most Marsh Wren nests appear to have only a ceremonial function, and the habit of nest-building on this prodigious scale is assumed to have evolved in males to increase their attractiveness to females (see BOWERBIRD). In general it seems that the singing and nest-building behaviour of some wren species has been greatly elaborated as a result of sexual selection acting through female mate choice (see LEK; MATING SYSTEM; SEXUAL SELECTION).

The clutch-size in tropical wren species is generally small (2–5 eggs), whilst that in northern temperate populations is of 6–10 eggs. Female wrens of all the well-studied species apparently incubate their clutches (14–15 days) unaided by the male, and there is little evidence of regular or substantial courtship feeding. The male shares responsibility for raising nestlings (16–17 days) and protecting and feeding recent fledglings in monogamous populations. But early broods of young Cactus Wrens have been seen helping their parents to feed later broods (i.e. their sibs) in the nest. Care of the nestlings by the male is much reduced or absent in the polygynous species. For instance, male European Wrens spend much of their time nest-building, singing and courting instead of feeding the nestlings they have presumably fathered in earlier breeding attempts taking place in their territories. This is but one illustration of the general principle that polygyny and male emancipation from the usual duties of an avian parent seem to evolve hand-in-hand (see PARENTAL CARE).

See photo DISPLAY. (E.A.A.) P.J.G.

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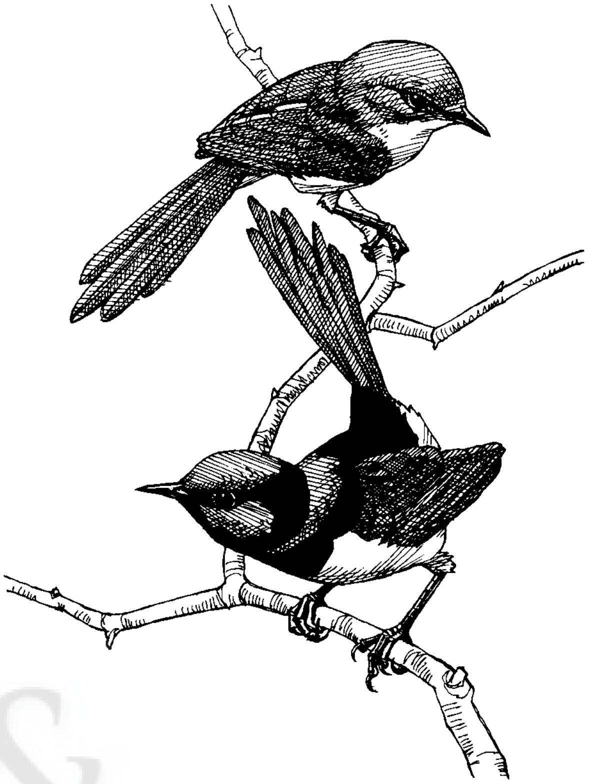
WREN (2): substantive name of many species in the former subfamily Malurinae (Muscicapidae, Passeriformes, suborder Oscines) in the form 'Australian wrens' or 'Australian wren-warblers'. This taxon has now been split into 3 groups, each with the rank of a family: the Maluridae (fairy or blue wrens and allies), Acanthizidae (scrubwrens, thornbills and allies; see WARBLER, AUSTRALIAN) and the Ephthianuridae (see CHAT, AUSTRALIAN). The genera *Cincloramphus* (songlarks) and *Eremiornis* (Spinifexbird) are excluded from these families and tentatively placed in the Sylviidae (see WARBLER (1)).

The Maluridae consist of 6 genera and 26 species. The largest genus, *Malurus* (fairy-wrens, 12 species) has a single endemic species in New Guinea, the rest in Australia. *Amytornis* (grasswrens, 8 species) and *Stipiturus* (emu-wrens, 2 species) are wholly Australian; and the remaining 3 genera (*Todopsis*, 2 species; *Chenorhamphus*, 1 species and *Clytomyias*, 1 species) are confined to New Guinea.



Superb Fairy-wren *Malurus cyaneus*. (*N.W.C.*).

Characteristics. Maluridae are small to very small, mostly semi-terrestrial songbirds (14–22 cm), wings are short and rounded, tail habitually cocked and usually more than half the total length, rectrices 'decomposed' in *Stipiturus* (hence the name 'emu-wrens'), bills fairly short, and fine except in some stout-billed *Amytornis* spp. and the broad-billed *Chenorhamphus* and *Clytomyias*. The plumage is basically brown with rufous and whitish tones, relieved or replaced in adult males of *Stipiturus*, *Malurus*, *Todopsis* and *Chenorhamphus* by blues, purples, black, chestnut, red and white in various combinations; females of last 3 genera may also have some blue. In *Malurus* at least, the bright colours of the adult males are assumed only in the breeding season. Plumage in *Amytornis* is cryptic, generally brown and cinnamon tones, streaked above and below, though some sandstone-haunting species are boldly patterned in black, rich chestnut and white. Legs and bills are brownish to blackish, irides usually brownish. Sexual dimorphism is pronounced in *Malurus*, *Stipiturus*, *Todopsis* and *Chenorhamphus*, usually slight in *Amytornis*. The young are unspotted.

An unusual character shared by all species is a gap (apterium) in the spinal feather tract. In addition, *Amytornis*, *Stipiturus* and some *Malurus* spp. have the *ala tympanica* conspicuously produced and inflated to form bullae, a development that presumably increases sharpness of hearing.

Habitat and distribution. The family is confined to Australia and New Guinea. The habitat range is extensive, from rain-forest (*Todopsis*, *Chenorhamphus*, *Clytomyias*) through forest- and mangrove-edge, riparian thickets and acacia woodland (*Malurus* spp.) to heath and swampy grassland (*Malurus* spp., *Stipiturus malachurus*) and arid hummock grassland, saltbush steppe and sandstone (*Stipiturus ruficeps*, *Amytornis*). The habitat preferences of the desert-living *Amytornis* spp. are of particular interest, and include sand dunes clad with the canegrass *Zygochloa paradoxa* (Eyrean Grasswren *Amytornis goyderi*), rocky hillsides clad with porcupine grass *Triodia* (Dusky Grasswren *A. purnelli*), relict lignum-swamps of *Muehlenbeckia cunninghamii* (Grey Grasswren *A. barbatus*), and sandstone terrain with *Triodia* (Black, White-throated and Carpentarian Grasswrens, *A. housei*, *A. woodwardi*, *A. dorotheae*).

Movements. Most species are apparently largely sedentary or make slight local movements; the arid-zone Rufous-crowned Emu-wren *S. ruficeps* and the Eyrean Grasswren, however, may undertake more extensive movements in response to the irregular changes in local conditions.

Food. Chiefly small arthropods and seeds: small centipedes, spiders, lacewings, bugs, ants, wasps, bees, flies, beetles, grasshoppers, moths, caterpillars, and small seeds mainly of grasses and chenopods (*e.g.* saltbushes). The thicker-billed species of *Amytornis* take a higher proportion of seeds, notably the Eyrean Grasswren, which feeds extensively on the seeds of the canegrass *Z. paradoxa*. The swamp-living Grey Grasswren eats, in addition to insects, a significant amount of lignum seeds and tiny water snails.

Behaviour. Most aspects of behaviour are poorly known, except in a few relatively well-studied species, e.g. the Superb Fairy-wren *Malurus cyaneus* and the White-winged Fairy-wren *M. leucopterus*. *Malurus* spp. breed co-operatively, are strongly territorial and remain in their social groups throughout the year. In *Malurus* also, courtship feeding of the female by the male has been described, and a simple display in which the male crouches with contour-feathers laterally spread and concealing the dull-coloured wings, while the head is extended horizontally and the tail drooped. A 'rodent run' distraction display has been observed in *Malurus*, *Stipiturus* and *Amytornis*. An unusual habit in *Malurus* is direct head-scratching.

Malurus, *Stipiturus*, *Todopsis* (*cyanocephala*), *Chenorhamphus* and *Clytomyias* forage on the ground and in the lower stages of vegetation, and *Amytornis* almost entirely on the ground, in monospecific groups. *Todopsis wallacii*, on the other hand, regularly joins mixed feeding parties of warblers and flycatchers, and forages up into the lower canopy.

Whereas most *Malurus* spp. are generally not timid, and show themselves a good deal, *Amytornis* and *Stipiturus* are notorious skulkers, though individuals may occasionally assume a vantage point atop a bush or tussock to sing. Progression is by weak, usually short flights, and by hopping; in the rodent-run, however, a scuttle is affected.

Voice. *Malurus* spp., in addition to various churring and scolding notes, have a distinctive reeling trill, especially well-developed in *M. leucopterus*. *Stipiturus* also has a reeling trill, though much higher and fainter, and also a rapid call of 4–5 high piercing notes. The repertoire of *Amytornis* spp. is particularly varied, elements recorded for *A. goyderi*, for instance, including a high sharp *seep seep*, an upward-inflected buzz, silvery cadences, pips, trills and long bursts of piercing staccato. In addition, this and other *Amytornis* spp. occasionally give forth a short but rich and melodious song.

Breeding. Nests are usually no more than a metre or two above ground (once as high as 6 m in a Superb Fairy-wren), in tussock or shrub. In *Malurus* and *Stipiturus*, the nest is globular or oval, domed, with side entrance, of grass, bark and other vegetable matter, sometimes spiders' cocoons, and lined with feathers and plant down. The only nest of *Chenorhamphus* reported was in moss, low on a tree-trunk, and had a side entrance. Nests of *Amytornis* are generally less domed, more often half-domed or truncated spheres, made of grass leaves, stems, roots, and sometimes fine twigs, placed low in a grass tussock or saltbush. The 2–4 eggs are generally white or pinkish white in ground colour, spotted with light greys, browns and reddish browns, often more heavily towards the larger end. In *Malurus*, nest-building and incubation are by the female alone, though the male may help to choose the site; incubation is 13–16 days, nestling period 12–14 days. There is usually more than one brood a year; nest-duties are shared by the family group (young of previous broods, subordinate males). *Malurus* spp. are heavily parasitized by cuckoos. (D.L.S.) S.A.P.

Harrison, C.J.O. 1969. The affinities of the blue wren genus *Malurus* and related genera: with special reference to the grass-wren genus *Amytornis*. Emu 69: 1–8.

Parker, S.A. 1982. Remarks on the tympanic cavity of *Malurus*, *Stipiturus* and *Amytornis* (Passeriformes, Maluridae). S. Aust. Orn. 29: 17–22.

Parker, S.A., May, I.A. & Head, W. 1978. Some observations on the Eyrean Grasswren *Amytornis goyderi* (Gould, 1875). Rec. S. Aust. Mus. 17(24): 361–371.

Rowley, I. 1965. The life history of the Superb Blue Wren *Malurus cyaneus*. Emu 64: 251–297.

Schodde, R. 1982. The Fairy-Wrens. A Monograph of the Maluridae. Melbourne.

Tidemann, S.C. 1980. Notes on breeding and social behaviour of the White-winged Fairy-wren *Malurus leucopterus*. Emu 80: 157–161.

WREN (3): substantive name of 3 out of the 4 species of Acanthisittidae (Passeriformes, suborder Oscines); in the form 'New Zealand wrens', general term for the family (also called Xenicidae). This distinctive group is peculiar to New Zealand and is believed to represent one of the most ancient avian colonizations of that country during the Tertiary Period. Although formerly placed in the suborder Tyranni near the Pittidae, recent studies (C.G. Sibley) indicate that they have no close living relatives and may be best placed in their own Infraorder. The 4 known species, one now extinct, are placed in either 2 or 3 genera. They are the Rifleman *Acanthisitta chloris*, the Bush Wren *Xenicus longipes*, the Rock Wren *X. gilviventris* and the Stephens Island Wren *Traversia* ('*Xenicus*') *lyalli*.

In both Rifleman and Bush Wren a North and a South Island subspecies have been described, differing only slightly; but in the Bush Wren a third and more distinctive subspecies known as Stead's Bush Wren (*X. l. variabilis*) developed on Stewart Island (formerly) and its neighbouring islets. The status of the 'Alpine Rifleman' '*A. c. citrina*' recorded from South Island wet mountain areas and of the 'Fiordland Rock Wren' '*X. g. rineyi*' is doubtful.

Characteristics. In the Rifleman the the sexes differ in both plumage and size, the difference being apparent even in nestlings. Female Riflemen weigh about 7.5 g and males about 6.0 g (length *c.* 8 cm), the reverse of most passerines that show sexual dimorphism. Bush and Rock Wrens (*c.* 9.5 cm) and Stephens Island Wren (*c.* 10 cm) are larger, and males and females differ little in plumage, though males are brighter.

Habitat and distribution. The Stephens Island Wren, discovered in 1894, became extinct almost as soon as it was discovered, the population on the small island being destroyed by a cat. About a dozen specimens were collected. It attracted much attention because it was supposed to be flightless; if so, it would have been the only flightless passerine. Although weak flight is suggested by the short rounded wings and soft plumage, the anatomy of the specimens received little attention and there is no clear evidence of flightlessness. The only observations were those of the lighthouse keeper on the island who saw the birds but twice, in the evening when disturbed from holes in the rocks; they ran like mice and did not fly at all. Subfossil bones, believed to be of *Traversia* have recently been found by P.R. Millener in the North Island and indicate that formerly the bird was distributed more widely.

The Rifleman and the Bush Wren originally occurred widely in both North and South Islands, the Rifleman evidently being much the more abundant. The numbers and range of many species of birds in New Zealand were reduced after European settlement in the mid-19th century; destruction of forest and introduction of predators and disease probably all contributed to the reduction. Changes brought about by settlement have obscured the former ecological relationships of the Rifleman and the Bush Wren, for early reports suggest that they were widespread from high altitudes to sea level. The Bush Wren may now be extinct, and the last known population of Stead's Bush Wren became extinct in 1965 after *Rattus rattus* reached Big South Cape Island. The Rifleman, however, is abundant in *Nothofagus* forest which still clothes

Rifleman *Acanthisitta chloris*, female and male (below). (*N.W.C.*).

much of the mountain chains of both islands, the wet region of Fiordland, and the comparatively dry eastern slopes of the South Island. It is less abundant in mixed forest at low altitudes, the extent of which is much reduced. The Rifleman appears to be adapting to man-modified habitats and enters forests of exotic pines. The Rock Wren is restricted to alpine and subalpine habitats of the South Island and its numbers have probably changed less than those of the other species.

Movements. All species probably are, or were, sedentary.

Food. So far as is known, members of the family are largely insectivorous but Riflemen and Rock Wrens eat some fruit. The Rifleman obtains much food from bark crevices and from epiphytic mosses and lichens on trees and shrubs, although it explores all parts from the bole out to the twigs, and on fallen logs, but seldom on the ground. The Bush Wren, of which little has been recorded, apparently has less creeper-like habits than the Rifleman. It feeds less on trunks and more amongst foliage, and sometimes on the ground. The Rock Wren obtains its food on and beneath the rocks of open screes, rock falls, and moraines. To some extent it enters subalpine scrub to feed, and in larger measure for shelter. In winter it does not move to lower altitudes but probably continues to feed under the snow in the air spaces among jumbled rocks and scrub.

Behaviour. Both the Bush Wren and the Rock Wren have the habit of bobbing the whole body, a vigorous action repeated frequently on alighting; this action, in the Rock Wren, varies in different portions of the range.

Voice. The Rifleman's main note is a high-pitched *zee* and the Rock Wren's a less frequently repeated *zipt*.

Breeding. Breeding habits are, as far as known, uniform. The birds are all hole-nesters and their domed nests consist of abundant material, loosely woven, usually lined with feathers and with a side entrance. Rifleman and Bush Wren nests are concealed in holes in trunks or branches and Rock Wren nests in rock crevices in comparable sites, to those of the arboreal species. Eggs are white in all species.

Rifleman and Rock Wren lay 2–5 eggs in a clutch, but Bush Wrens may have smaller clutches. The eggs of the Rifleman are large—each is about one-fifth of the female's body weight and is laid at 2-day intervals. The Rifleman has long incubation and nestling periods of 19–20 days and *c.* 24 days respectively; growth rates are extremely low but chicks at fledging are considerably heavier than adults. One or two broods are produced in a season. Both birds of a pair share in incubating and feeding; M.F. Soper and G.E. Sherley have observed that at some nests additional adults and juveniles of both sexes help to feed the young. Little is known about the breeding biology of Rock Wrens or Bush Wrens. (E.G.T.) B.M.F.

Bull, P.C., Gaze, P.D. & Robertson, C.J.R. 1978. Bird Distribution in New Zealand. A provisional atlas 1969–1976. Wellington.
Falla, R.A., Sibson, R.B. & Turbott, E.G. 1979. The New Guide to the Birds of New Zealand. Auckland & London.
Gray, R.S. 1969. Breeding biology of rifleman at Dunedin. Notornis 16(1): 5–22.
Oliver, W.R.B. 1955. New Zealand Birds. 2nd edition. Wellington.
Sibley, C.G., Williams, G.R. & Ahlquist, J.E. 1982. The relationships of the New Zealand Wrens (Acanthisittidae) as indicated by DNA–DNA hybridization. Notornis 29(2): 113–130.
Soper, M. 1976. New Zealand Birds. 2nd edition. Wellington.

WREN (4): an alternative substantive name, popularly misapplied to certain birds of small size other than those mentioned above, e.g. the 'Willow Wren' (Willow Warbler) *Phylloscopus trochilus*, 'Wood Wren' (Wood Warbler) *P. sibilatrix*, and 'Golden-crested Wren' (Goldcrest) *Regulus regulus* (for all of which see WARBLER (1)), and babblers in the genera *Microura*, *Spelaeornis*, and *Sphenocichla* (see BABBLER); also forms part of various compound substantive names as shown below.

WREN, ANT-: see ANTWREN; and ANTBIRD.

WREN-BABBLER: see under BABBLER.

WREN, BUSH-: see WREN (3).

WREN, GNAT-: see GNATCATCHER.

WRENTHRUSH: *Zeledonia coronata* (see WARBLER (2)).

WRENTIT: *Chamaea fasciata* of western North America, a bird of much-debated affinities treated in this work as belonging to the family Timaliidae (see BABBLER).

WREN-WARBLER: substantive name of *Prinia* spp. (see WARBLER (1)); also, in the plural, alternative term for the Maluridae (see WREN (2)).

WRIST: see under SKELETON, POST-CRANIAL; WING.

WRYBILL: or Wrybilled Plover, *Anarhynchus frontalis* (see PLOVER (1)).

WRYNECK: substantive name of *Jynx* spp. (see under WOODPECKER).

X

XANTHOCHROISM: alternative term for flavism. See PLUMAGE, ABNORMAL.

XANTHOTIS: substantive name sometimes used for *Meliphaga polygramma*, a New Guinea HONEYEATER.

XENICIDAE: synonym Acanthisittidae, a family of PASSERIFORMES, suborder Oscines; WREN (3).

XENOPS: generic name used as substantive name of *Xenops* spp., sometimes called 'recurved-bills' (see OVENBIRD (1)).

XENOPSARIS: substantive name of *Xenopsaris albinucha*, a South American bird of uncertain affinities now generally placed in the tyrant-flycatcher family (for family see FLYCATCHER (2)).

XEROPHILOUS: adapted to living in a dry climate.

Y

YAFFLE: alternative name for the Green Woodpecker *Picus viridis* (see WOODPECKER).

YAWNING: an involuntary action in which the mouth is opened and a deep breath taken. While there is no doubt that yawning movements, superficially resembling those of mammals, do occur in most birds, it is not certain that these include the inhalation and exhalation of air in all species. Some writers have argued that yawning birds do not inhale, and that 'jaw-stretching' is therefore a more appropriate term for this action. Heinroth (1930) was the first to take this view, and many subsequent students of animal behaviour (including Konrad Lorenz) have accepted this interpretation. However, Sauer and Sauer (1967) in the most comprehensive study of yawning in any bird, clearly observed the inhalatory and exhalatory components of the yawn in the Ostrich *Struthio camelus*. Moreover, Ainley (1974) was able to distinguish both a jaw-stretch (without any appreciable opening of the throat) and a yawn (with inhalation) in both Brandt's Cormorant *Phalacrocorax penicillatus* and the Pelagic Cormorant *P. pelagicus*. Simmons (1977) likewise recognized a separate jaw-stretch and yawn in the Great Crested Grebe *Podiceps cristatus* and Brown Booby *Sula leucogaster*. The jaw-stretch is easier to observe in cormorants and sulids because the upper mandible can be flexed upwards at the naso-frontal hinge. In most other species in which yawn-like movements have been described in detail (including penguins, ducks, geese, waders Charadrii, warblers Sylviinae and finches) it has so far proved impossible to determine whether these movements are jaw-stretches or true yawns because of the difficulty of observing whether or not the throat opens and inhalation occurs.

Yawning occurs early on in the development of the Ostrich, being first seen in chicks which have just rested after freeing themselves from the egg shell and egg membranes. Thereafter, in both adults and young, it occurs most frequently at times when movement is reduced to a minimum and when birds are just about to fall asleep or have just awoken. It is often associated with other COMFORT BEHAVIOUR movements such as stretching, preening, scratching, head shaking (to remove mucus from the nostrils) and defaecation. During the yawn itself, the eyes are often fully or partially closed, the neck is often stretched and some head feathers are erected. In other species of birds, yawning (or jaw stretching) is broadly similar in its occurrence, and it thus shows remarkable parallels with the situation in mammals.

The physiological function of the true yawn remains a mystery. It has been suggested that in mammals it serves to purge the deeper parts of the lungs of carbon dioxide accumulated during shallow, restful breathing. However, if any such accumulation occurs during sleep, it is apparently innocuous, since no yawning occurs then. Filling the lungs with fresh air could provide a means of enhancing alertness during drowsiness (to help prevent sleep) or of speeding up the transition to an active state after slumber. Jaw-stretching presumably fulfils a similar function to the stretching of other parts of the body, though this function is itself something of an enigma. It has been suggested that stretching stimulates the blood supply to muscles as a prelude to activity, but this fails to explain why animals often stretch before sleeping.

Yawning in an individual bird often stimulates surrounding individuals of the same species to yawn, just as it does in mammals. The function, if any, of this 'snowball' effect is by no means clear, but it could serve to synchronize certain kinds of communal activities such as sleep itself, or the departure from a roost. Yawning and jaw-stretching may sometimes occur as DISPLACEMENT ACTIVITIES in apparently inappropriate contexts, such as in the middle of bouts of fighting.

Care needs to be taken to distinguish yawning or jaw-stretching from other kinds of gaping activities such as panting, threatening displays (which often involve opening of the mouth) and persistent gaping due to infection with syngamid nematodes (gapeworms). Some garden birds may appear to yawn in the presence of a human observer when waiting to be fed at a bird table. In fact this is probably a case of soliciting for food by gaping—a form of behaviour shown by altricial young both before and after fledging, and used by some adult females to elicit food from the male. P.N.F.

Ainley, D.G. 1974. The comfort behaviour of Adélie and other penguins. Behaviour 50: 16–51.

Heinroth, O. 1930. Über bestimmte Bewegungsweisen der Wirbeltiere. Sber. Ges. naturf. Freunde Berl. 1930: 333–342.

Sauer, E.G.F. & Sauer, E.M. 1967. Yawning and other maintenance activities in the South African Ostrich. Auk 84: 571–587.

Simmons, K.E.L. 1977. Further studies on Great Crested Grebes. 2. Maintenance activities and routine. Bristol Ornithology 10: 175–196.

YELLOWBILL: *Ceuthmochares aereus* (for family see CUCKOO); also used for another African species, *Anas undulata* (for family see DUCK).

YELLOWHAMMER: name, alternatively 'Yellow Bunting' (compare German 'Ammer' = bunting), of *Emberiza citrinella* (see BUNTING); colloquially applied in North America to the Flicker *Colaptes auratus* (see WOODPECKER).

YELLOWHEAD: *Mohoua ochrocephala* of New Zealand (for subfamily see WARBLER, AUSTRALIAN).

YELLOWLEGS: substantive name of 2 American species of *Tringa*; in British usage sometimes unnecessarily altered to 'yellowshank' on the analogy of 'redshank' and 'greenshank' (see SANDPIPER).

See photo LOCOMOTION, TERRESTRIAL.

YELLOWSHANK: see above.

YELLOWTHROAT: substantive name of species of *Geothlypis*; used without qualification, in North America, for *G. trichas* (see WARBLER (2)).

YOLK: see EGG.

YOLK-SAC: see DEVELOPMENT, EMBRYONIC.

YOUNG BIRD: a rather vague term applicable to a bird from the time of hatching (when it ceases to be an embryo) until the attainment of sexual maturity; the use of a more exact term is generally preferable. The bird is technically a 'pullus' ('pull.') until it is full-grown and flying; the ability to fly is the usual criterion, except in flightless species, but does not suffice alone in birds that have precocious flight. During the same period a bird may, in ordinary speech, be called a 'chick', especially in species where the pulli are active; or a 'nestling' while remaining in the nest. After the pullus stage a bird is described as 'juvenile' while wearing its first plumage of true feathers. Thereafter a bird may still be 'immature' (the beginning point is vague) until it attains sexual maturity, the usual criterion of which is the assumption of full 'adult' PLUMAGE (and see MATURITY); in some species this immature stage lasts for a few years, and the successive plumages may be distinguishable one from another (see also under MOULT).

Colloquially, there are special terms for the young of certain species (see CYGNET; DUCKLING; EYASS; GOSLING; OWLET).

Certain terms describe the condition of pulli in different kinds of birds. The young of some species are 'precocial', i.e. capable of locomotion more or less immediately after hatching; others are 'altricial', i.e. incapable of locomotion. The young may be 'ptilopaedic', i.e. covered with down, usually dense, when hatched; or they may be 'psilopaedic', i.e. naked or with only sparse dorsal down (and usually blind) when hatched. Young that leave the nest immediately or soon after hatching are termed 'nidifugous'; those that remain in the nest are termed 'nidicolous'. Nidifugous young are necessarily both precocial and ptilopaedic, but nidicolous young are not in all the species psilopaedic or even wholly altricial.

Nice (1962), in an important monograph on the development of behaviour in young birds, classified the state of maturity of 'hatchlings' as follows:

Precocials—eyes open, down covered, leave nest first day or two

1. Independent of parents (e.g. Megapodiidae)
2. Follow parents but find own food (e.g. Anatidae, Charadriidae)
3. Follow parents and shown food by them (e.g. Phasianidae in part)

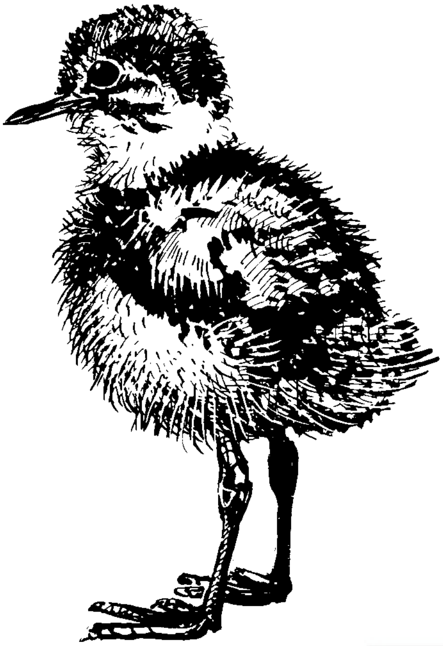


Fig. 1. Newly hatched Lapwing *Vanellus vanellus*—precocial, nidifugous, ptilopaedic, and open-eyed. (*K. Shackleton*).

4. Follow parents and are fed by them (e.g. Podicipedidae, Rallidae).

Semi-precocials—eyes open, down covered, stay at nest until able to walk, fed by parents (e.g. Laridae).

Semi-altricials—down-covered, unable to leave nest, fed by parents

1. Eyes open (e.g. Ardeidae, Falconiformes)
2. Eyes closed (e.g. Strigiformes).

Altricials—eyes closed, little or no down, unable to leave nest, fed by parents (e.g. Passeriformes).

Precocial and semi-precocial birds are actually or potentially mobile, while semi-altricial and altricial young are sedentary. Semi-precocial birds are physically well developed, but because of the feeding habits of the adults must stay on or near the nest until fledged. Semi-altricial and altricial young are physically unable to leave the nest, but the former are well provided with down from the start and some are hatched with their eyes open. Only in the first three kinds of precocials are the young not fed by the parents, and only in the first two are they not even shown food. Thus there is a progression from chicks so developed in every respect that they need no parental care to chicks so helpless that they demand prolonged and specialized care.

Fig. 2. Newly hatched Blackbird *Turdus merula*—altricial, nidicolous, psilopaedic, and blind. (*K. Shackleton*).

The newly hatched chick of the domestic fowl has only about 3% of the weight of an adult; yet growth to full size is achieved in a remarkably short time. In some small passerines the period is as short as 10 days. On the other hand, young King Penguins *Aptenodytes patagonicus* hatched late in the season have a period of arrested growth during the winter and may lose half their autumn weight during that time (see PENGUIN).

For characters and behaviour particularly associated with the pullus stage see especially BEHAVIOUR, DEVELOPMENT OF; BROOD-PARASITISM; EGG-TOOTH; FLIGHT, PRECOCIOUS; GROWTH; HATCHING; PARENTAL CARE.

See photo FLIGHTLESSNESS. A.L.T.

Nice, M.M. 1962. Development of behavior in precocial birds. Trans. Linn. Soc. N.Y. 8: 1–211.

YUHINA: substantive name of the species of *Yuhina*, a south-east Asian genus of small BABBLERS.

Z

ZONE: see LIFE ZONES.

ZOOGEOGRAPHICAL SPECIES: a species or superspecies (i.e. group of closely related allopatric species) which for purposes of zoogeographical analysis may be treated as a single unit.

Mayr, E. & Short, L.L. 1970. Species Taxa of North American Birds. Cambridge, Mass.

ZOOGEOGRAPHY, THEORY OF: the description and causal explanation of patterns of geographical distribution of extinct or living animals are the subject matters of zoogeography, a science that has changed considerably since the days of Schmarda (1853) and Wallace (1876). The texts of Darlington (1957), Udvardy (1969) and Pielou (1979) among others reflect both the growth in breadth and the evolution of concepts in zoogeography in a little more than a century. Keast (1977) and Vuilleumier (1975) reviewed the history and development of zoogeography especially from an ornithological perspective.

History. Zoogeography seems to have gone through three major phases. During the first phase the description of zoogeographical regions (Palearctic, Ethiopian, Oriental, Australasian, Neotropical, and Nearctic) and the delimitation of their subdivisions was the main focus of study. This phase is largely a thing of the past now, although the analysis of distribution patterns by means of multivariate statistics has allowed several authors to refine or re-define the older zoogeographical regions, their components or their boundaries. Regions and sub-regions may now be defined by non-arbitrary criteria which permit one to compare similarities or differences in distribution patterns between different taxa within the class AVES or to compare Aves with other animal groups.

The second phase corresponded to the identification of faunas and the determination of faunal elements. An avifauna is the sum of species of birds living in a given geographical area (for instance North America) or ecological zone (the boreal forests). A faunal element is made up of one or more species having a given pattern of geographical origin. Thus the North American avifauna is composed, according to Mayr (1946), of Pantropical, Panboreal, Old World, North American, Pan-American and South American elements. Among the variants of this kind of analysis one may cite the recognition of dispersal centres (Müller 1973) made by plotting the ranges of many species and inferring areas where taxa have originated according to the areas of greatest species density or congruence.

The third phase in the evolution of zoogeography began when general and conceptually simple theories of distribution were used to make specific predictions about geographical distribution. These predictions are verified by checking specific details of distribution. If distributional evidence is contrary to prediction, then the theory is falsified. This rigorous way of using theory and empirical evidence is considered by modern zoogeographers to be much more scientific than previous endeavours. For example the theory of insular or equilibrium zoogeography (MacArthur and Wilson 1967) is derived conceptually from the mathematical theory of birth and death processes in population ecology. Colonization and extinction are two processes that in the absence of SPECIATION (formation of new species) operate against each other and jointly determine the number of species on an island or a patch of habitat, such as a mountain top. A prediction from this theory is that turnover of species (the balance between colonization or immigration and extinction) should occur at certain rates. Empirical validation or invalidation of the equilibrium theory thus hinges in part on the measurement of turnover rates. The practical difficulties of measuring colonization or extinction rates and of calculating turnover rates from them have not so far permitted unequivocal tests of the theory. Some results giving very low or zero values of turnover have been published and could be construed as falsification of the theory.

Contemporary schools of thought. Zoogeography has not, however, evolved smoothly over the years, one phase leading gradually into another. Instead it has developed by leaps and bounds, and the three phases actually overlap largely in time. Zoogeography is a heterogeneous science composed of several contrasting points of view, within three main schools of thought.

The first school of thought corresponds to what some authors call the 'centre of origin' theory. The geographical origin of species or other taxa (for instance genera) is sought and their subsequent distributional history is reconstructed. By analogy with the neo-Darwinian view of evolution this point of view could be called neo-Wallacean because its antecedents can be traced in large part to the work of Wallace. The practitioners of the second school of thought, called 'vicariance biogeography' (Nelson and Rosen 1980) ask similar questions but use a methodology based on a special form of taxonomic analysis (cladism). Whereas in both schools great weight is placed on solid taxonomy as the necessary foundation for zoogeographic analysis, there is no agreement about how the taxonomic work should be carried out. Cladism attempts to classify taxa in a scheme of relationships based on a rigid analysis of taxonomic characters (usually morphological differences between individuals in populations, species, or other categories). Characters are divided into primitive or derived ones and the relative occurrence of each sort among closely related taxa permits one to draw a branching diagram called a cladogram (see CLADISTICS). In vicariance biogeography cladograms are used together with the mapped distributions of the organisms so classified to understand their geographical history. Furthermore, proponents of vicariance biogeography believe that active dispersal of organisms is either unimportant or far less significant in their geographical history than the movements of the land masses on which they live or lived. The movements of land (by continental drift) or of habitat (because of climatic changes through time) thus determined or made up the 'vicariant events' that are the primary causal factor of disjunct distribution patterns. This concept is quite different from the one held by members of the centre of origin school of thought, who envisage dispersal as an extremely important factor in distributional histories. Their view is based in large part on the common observation that modern bird species do not have a static distributional area but instead show either dynamic range expansions (the Cattle Egret *Bubulcus ibis* for instance) or range contractions (see RANGE CHANGES).

The members of the third school of thought, or equilibrium biogeography, not only consider dispersal to be an important factor in zoogeography but try to quantify it together with its opposite force, extinction, to determine the state of equilibrium or disequilibrium of faunas, especially insular ones. The idea that a balance between colonization and extinction influences the species composition of insular faunas did not originate with MacArthur and Wilson, but they expressed this relationship in mathematical models analogous to the differential equations of population dynamics. Their presentation opened the way to numerous studies and produced a revolution in the field of zoogeography.

Plate tectonics as a model of continental evolution have been used by zoogeographers to explain faunal histories (Cracraft 1974). Plate tectonic theory rallies together zoogeographers who otherwise prefer one or the other of the three schools of thought outlined above. Thus vicariance explanations of faunal history have been amalgamated by some workers with plate tectonic history, whereas other authors have used equilibrium models in conjunction with plate tectonic models. However, proponents of the centre of origin school have usually maintained that the history of modern faunal elements does not need plate tectonics, because drift of land masses took place earlier than the evolution of the taxa in the elements.

Future developments. Many of the differences of opinion between the various points of view embodied in the prevailing schools of thought could be resolved if zoogeographers realized more clearly that, although they all work in a framework of space and time, they do not consider the same scales or the same taxonomic levels. Thus in equilibrium biogeography time and space are both very small and populations of species are the biological unit used; in vicariance biogeography time and space are much larger and species or even higher taxonomic categories are considered. There seems little doubt to zoogeographers who study birds in the field that both dispersal and vicariant events are important in determining their ranges.

It seems also clear that several theoretical concepts and several methods can be employed to study zoogeographic problems. A large range of techniques is now available and it should be normal practice to carry out research along several lines. As zoogeography evolves, some of the theories that now seem solid will doubtless be discarded and new methodologies will be invented to permit testing of predictions from new theories. For example, recent advances in the biochemical systematics of birds (using DNA-DNA hybridization or other techniques, such as gel electrophoresis) permit the measurement or estimation of the degree of relatedness between species or genera. Such information should be used in analyses of geographical distribution of these taxa; it will be most interesting to find out whether the conclusions drawn from the older systematics match those obtained from the modern data. The contribution of paleornithology to zoogeography will also be larger in the future. Discoveries of new FOSSIL BIRDS, including both island and mainland taxa, as well as re-evaluations of fossil taxa described long ago have already given us a rich source of information that has hardly been tapped for zoogeographical reconstructions. F.V.

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ZOOLOGICAL RECORD: an annual publication of the Zoological Society of London, the 'Aves' and other sections being obtainable separately. This is an essential tool for keeping abreast of the current literature, or searching the past literature, in any branch of zoology. As complete a list as possible of books and papers published during the year is given alphabetically under authors' names; and there are elaborate indices to this under subject, geographical, and taxonomic heads. The series goes back to 1864; Alfred Newton was the first recorder of the ornithological literature. See also BIBLIOGRAPHY.

ZOOLOGY: the scientific study of animals; as such, one of the main divisions of BIOLOGY. Zoology may be subdivided according to the particular classes of animals under study; thus the study of birds (Class AVES) is a branch of it (see ORNITHOLOGY).

ZOONOSIS: general term (plural 'zoonoses') for any disease naturally transmitted, directly or indirectly, between other vertebrate animals and man. Birds are in some cases the other vertebrate animals concerned; psittacosis (ornithosis) is an example of a zoonosis transmitted directly from birds to man, and some types of virus encephalitis are transmissible from birds to man by an insect or other arthropod vector (see DISEASE; PSITTACOSIS; VECTOR).

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ZOSTEROPIDAE: a family of the PASSERIFORMES, suborder Oscines (see WHITE-EYE (1)).

ZOSTEROPS: generic name often used as common name (see WHITE-EYE (1)).

ZUGSCHEIDE: German term, sometimes used in English writings for a 'migratory divide', i.e. a line (or more or less narrow zone) on either side of which the breeding populations of a species migrate in different, divergent directions; best known in the White Stork *Ciconia ciconia*, which has a *Zugscheide* in central Europe, the birds to the west migrating south-west in autumn, and those to the east migrating south-east.

ZUGUNRUHE: German term, sometimes used in English writings, for pre-migratory restlessness (see MIGRATION).

ZWISCHENZUG: German term, difficult to translate, for nomadic movements performed by birds of some species between the breeding season and true migration. 'Between migration' not being a possible expression in the English language, either in grammar or sense, the nearest literal equivalent is probably 'interim movements'.

ZYGAPOPHYSIS: one of the articulating processes of a vertebra (see SKELETON, POST-CRANIAL).

ZYGODACTYL: having two toes directed forwards and two back (see LEG). When toes I and II instead of I and IV are directed backwards, the condition may be called 'heterodactyl'.

ZYGOMATIC ARCH: the bony arch of the cheek (see SKULL).