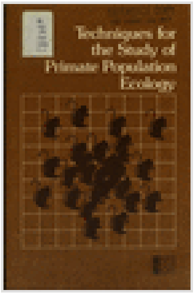

Techniques for the Study of Primate Population Ecology (1981)

Pages
255

Size
5 x 8

ISBN
0309031796

Subcommittee on Conservation of Natural Populations; Committee on Nonhuman Primates; Division of Biological Sciences; Assembly of Life Sciences; National Research Council

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NATIONAL ACADEMY PRESS
Washington, D.C. 1981

81-0176
c. 1

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This report has been reviewed by a group other than the authors according to procedures approved by a Report Review Committee consisting of members of the National Academy of Sciences, the National Academy of Engineering, and the Institute of Medicine.

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The primary support for development of this report was provided by Contract N01-RS-9-2117 with the Division of Research Services, National Institutes of Health. Additional support was provided by Grant RC-1W from the American Cancer Society, Inc.; Contract APHIS 53-3294-9-2 with the U.S. Department of Agriculture; Contract DNA001-79-C-0087-P00001 with the Defense Nuclear Agency; Contract DE-AM02-76CH93000 (Task Agreement DE-AT02-76CH93011) with the Department of Energy; Contract N01-RR-9-2109 with the Division of Research Resources, Animal Resources Branch, National Institutes of Health; Grant PCM-7921163 with the National Science Foundation; Contract N00014-80-C-0162 with the Office of Naval Research; and contributions from pharmaceutical companies and other industry.

Library of Congress Cataloging in Publication Data

Main entry under title:

Techniques for the study of primate population ecology.

Bibliography: p.
1. Primates—Ecology. 2. Population biology—Technique. 3. Mammals—Ecology. 4. Mammal populations. 1. National Research Council (U.S.) Committee on Nonhuman Primates. Subcommittee on Conservation of Natural Populations.
QL737.P9T43 599.8′045 81-11345
ISBN 0-309-03179-6 AACR2

Available from

NATIONAL ACADEMY PRESS
2101 Constitution Avenue, N.W.
Washington, D.C. 20418

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Preface

The need for basic data on population densities and trends for several species of animals has been increasing steadily as wild lands have been under pressure for the extraction of mineral, timber, and animal resources. The development of land for agricultural and industrial purposes has generally progressed without any regional planning and has resulted in the degradation or loss of native habitats, especially mature forests, and the fauna and flora associated with these habitats. In some areas the remaining tracts of wild land are becoming so restricted that management of animal populations has become necessary to safeguard their futures and to bring utilization of some of the species into line with the capacity of the habitat to support them.

The assessment of the status of wild primate populations requires immediate attention if primates are to be protected and managed as renewable wildlife resources. Little is being done to assemble the needed information systematically. Export restrictions imposed on primates over the past decade are in part a response to a concern for conserving wild populations. They are likely to remain in effect until scientific data become available that will justify changing them.

In the early 1970's a committee organized by the Institute of Laboratory Animal Resources, of the Division of Biological Sciences, Assembly of Life Sciences, National Research Council, was asked to study the status of wild primate populations. This was the Committee on Nonhuman Primates.

Under the leadership of R. W. Thorington, Jr., *Chairman*, and C. H. Southwick, *Vice-Chairman*, the committee set in motion a program of surveys, or censuses, to assemble data on primate populations in Colombia, Peru, Guyana, and Bolivia. Funds for supporting survey teams were provided by the Pan American Health Organization, the National Institutes of Health, and the U.S. Army Medical Research and Development Command.

When these surveys were compared with studies conducted by other investigators, it was obvious that lack of standardized procedures was causing serious inconsistencies in findings and that a manual would contribute significantly to accuracy and uniformity.

The Subcommittee on Conservation of Natural Populations, Committee on Nonhuman Primates, was organized to produce such a manual, and the present manual is the result of the subcommittee's efforts. It is hoped that the techniques and observations presented here will lead to increased understanding of forest ecosystems and will encourage worldwide efforts to develop conservation and management programs.

JOHN F. EISENBERG, *Chairman*
Subcommittee on Conservation of Natural Populations

Acknowledgments

In addition to the basic contracts supporting this work, the National Institutes of Health and other institutions supported preparation of certain parts of the report. The institutions that provided such support, the persons who received it, and the subjects dealt with in these persons' contributions to the report are as follows: National Zoological Park, John F. Eisenberg, habitat description; Smithsonian Institution, National Science Foundation, and National Institutes of Health, Richard W. Thorington, Jr., habitat use and collecting and marking techniques; Smithsonian Institution, National Science Foundation, National Institutes of Health, and the Deutsche Forschungs-Gemeinschaft, Wolfgang P. J. Dittus, sexing and aging animals, population analysis, and determinants of population density and growth; National Institutes of Health, Howard University, Johns Hopkins University, and National Zoological Park, Kenneth Green, remote-sensing techniques (Dr. Green also prepared a draft of a censusing manual and a background discussion of censusing methods.); and New York Zoological Society, National Science Foundation, and Na-

tional Institute of Mental Health, Thomas Struhsaker, censusing methods.

The Subcommittee on Conservation of Natural Populations is indebted to several persons who made suggestions concerning preparation of various sections of the manuscript. Special thanks are due Anne Baker-Dittus, T. Butynski, Lysa Leland, G. Caughley, J. Ballou, J. Frazier, and J. Russell. Artwork was prepared by Sigrid James-Brüch and Figure 1-1 by Carrie Thorington.

Contents

APPENDIXES

1

Introduction

This manual deals with methods and techniques applicable under field conditions often remote from the usual support facilities characteristics of this last quarter of the twentieth century. Alternating electric current, with constant voltage, is not readily available in areas that require the study of vertebrate ecology, especially in remote areas where a faunal survey must precede the establishment of a park or reserve. Thus, the technological support for faunal surveys normal for more settled regions is often lacking and one must fall back on techniques that to a large extent have been forgotten by biologists in recent decades. The compass, notebook, india ink pen, watch, scales, binoculars, and tape measure are still the basic tools, augmented by calipers, pliers, wire, camera, formalin for preservation of specimens, and tape or tags for marking trees (see Figure 1.1).

This manual outlines the basic steps for conducting preliminary studies of mammalian ecology. Several indirect census methods are available for studying large terrestrial herbivores; they are suitable for rapidly making rough comparisons of activ-

FIGURE 1-1 Typical collection of field equipment for undertaking primate censusing.

ity levels in large areas. Thus, fecal pellets, dung piles, and animal tracks can aid in estimating the abundance of a species being studied. Indirect methods have also been used to determine age classes and ranging patterns in some large terrestrial species and have been valuable additions to direct observational techniques.

Although observers should be aware of the value of using signs of activity to locate primates, no standardized methods are available that allow extrapolations from the abundance of feces around sleeping and resting trees, or from the amount of vegetative matter (fruits, leaves, petioles) dropped around feeding trees, to the number or species of primates that have progressed through an area. There are other situations in which extrapolation is a satisfactory censusing procedure. One is estimating the number of pygmy marmosets in an area by counting trees that have sap holes; another is estimating the baboon population by counting rock-cliff sleeping sites. The censusing of arboreal species, including most primates, continues to rely on standardized and relatively time-consuming visual counts of individual animals by observers.

The objectives of various types of censuses are stated later in this introduction. Chapter 2 discusses the selection of survey sites, and Chapter 3 is concerned with methods for identifying and describing characteristics of habitats that are essential to support the target species.

It is seldom possible to count all members of an animal population directly. Consequently, sampling methods must be used. Although typically social and diurnal, most primate species live in tropical forests where visibility is poor and movement by the observer is often impeded. Chapter 4 describes sampling techniques most useful for counting primates, emphasizing forest species because forested habitats contain the greatest number of species and pose the greatest number of practical problems.

The sampling method selected will depend on the objectives of the study; the characteristics of the study species; the habitat; and the availability of time, money, and personnel. Objectives often involve one or more of the following:

- Determining the presence (and abundance) or absence of particular species in relation to geographic and habitat features.
- Estimating densities of animal and plant populations.
- Compiling data on group sizes and the age and sex compositions of populations.
- Determining population trends.
- Determining microhabitat preferences of study species.
- Determining interspecific associations.

These objectives are fundamental to the development of conservation and management programs, as well as to the understanding of the biology of the populations and ecosystems concerned.

Three techniques for estimating population densities are discussed in this report: broad surveys, line transects, and detailed study of specific groups. Broad surveys are used as pilot studies in order to assess land uses, inventory species, and compare the status of populations in large areas in a relatively short period (Eisenberg, 1979; Scott *et al.*, 1976b).

The method best suited for obtaining data on the relative numbers of primate groups in forest habitats is the random compass line transect. Because of its statistical reliability, this method provides estimates that can be used for general management of species.

The most accurate method of estimating primate densities is the detailed study of specific groups. This method provides data on home range size, group size, and age-sex composition over time, and it provides a basis for intense species management and hypothesis testing.

Accurate estimates of the composition and use of space by a population are necessary before trends in population size can be understood. Therefore, techniques for aging and sexing primates are given in Chapter 5 and are followed by methods for evaluating habitat use in Chapter 6. Collecting data on the use of space, feeding habits, and time budgets is the most time-consuming part of observational studies. The use of life tables for the analysis of populations is described in Chapter 7. Finally, environmental and other factors influencing population size are discussed in Chapter 8.

2

Site Selection

MAPS AND PHOTOGRAPHS

Although most of the earth's surface has been mapped by foot survey, aerial photography, or satellite imagery, information on the distribution of vegetative cover in some tropical countries is not well documented. Thus, when working in a new area it may be necessary to spend time determining where the censuses should be made.

If topographic maps are available, they provide the logical starting point. Working from the best published map you can acquire, you should find the approximate position of the area you intend to survey. Typically, your starting point will be some major geographic feature (e.g., lake, river, mountain range). You may find that a map has a scale that is too large to include features such as tributaries, lagoons, hills, and outcroppings, which would be perfectly obvious to you on the ground.

It is important to examine vegetation maps, which enable you to become familiar with the range of habitats that can be expected in the survey region. Broad classifications are available for the neotropics in Holdridge (1967), for Asia in Puri (1960) and Richards (1966), and for Africa in Keay (1959).

If recent aerial photographs are available, they will augment the maps and provide details on the status of vegetation at potential survey sites. Such an analysis is cheaper than making an aerial reconnaissance in a small plane. Selecting a site can also be accomplished by ground travel, though this method is more time-consuming than the others. In areas for which detailed maps and photos are not available, it may be necessary to expand the scale of the preliminary mapping efforts described in Chapter 4 for establishing grids.

Images from LANDSAT satellites are being used increasingly for developing regional and national inventories of land-use patterns and for monitoring changes in vegetation. The large scale of the images makes them useful in selecting forested sites for surveys. Detailed interpretation of satellite photos depends on ground verification or on classification of vegetation types based on visits to the sites. Potential applications of satellite imagery techniques for the analysis of vegetation are discussed in Chapter 3.

FAUNAL LISTS AND FLORAL INVENTORIES

Most major geographic areas have at least provisional faunal lists for the major vertebrate classes. Before undertaking a survey in a new area, you should make a provisional key based on published reports and museum specimens. Since many areas that you may wish to survey have strict regulations concerning specimen collection, the key must utilize field characters that are readily identified in an intact, living specimen. Of course, on occasion, it is necessary to collect and preserve voucher specimens (Chapter 3). The following field key for the primates of Guyana should suffice as an example:

KEY TO THE ADULT PRIMATES OF GUYANA

1.	Size small (< 1 kg) and squirrel-like; tail bicolored	2
1′	Size medium to large; tail color uniform	3
2.	Face and body dark, with hands and feet reddish; tail reddish proximally, black distally	*Saguinus midas*

2′	Contrasting black muzzle and light body; tail like legs and body golden brown, proximally with black tip	*Saimiri sciureus*
3.	Basic body coloration black	4
3′	Body coloration brown, gray, or reddish	6
4.	Large body size (> 6 kg); prehensile tail	*Ateles paniscus*
4′	Medium body size (~ 1.5 kg); nonprehensile, bushy tail	5
5.	Contrasting white fur on face; body pelage long	*Pithecia pithecia* ♂
5′	Typical body hair length; face dark and not contrasting to body color; conspicuous beard (♂)	*Chiropotes satanus*
6.	Tail bushy and nonprehensile; basic body color gray to agouti brown	*Pithecia pithecia* ♀
6′	Tail partially or fully prehensile	7
7.	Basic adult body coloration reddish; conspicuous beard	*Alouatta seniculus*
7′	Basic body coloration light brown or brown	8
8.	Conspicuous flat-topped black cap with tufts on head	*Cebus apella*
8′	Buff to brown cap; basic body coloration gray-brown	*Cebus nigrivittatus*

SPECIAL STUDIES OF INDICATOR SPECIES

A general knowledge of natural history is invaluable during initial attempts to characterize forests. Parameters of habitat quality, such as age of the forest, relative density of fruiting trees, and persistence of standing water, can often be assessed by keeping careful notes on other vertebrates present in the forest. Birds are conspicuous by their diurnal activity, voice, and often brilliant coloration. When you are transect walking, birds are often the most frequently encountered vertebrates. You can often make general statements by noting the frequency of bird sightings and the species identity. Consider the case where primates are rare in, or absent from, a forest block. If one has noted that large frugivorous birds, such as hornbills (in Asia), are present, there is reason to suppose that the lack of primates is not tied to a lack of fruiting trees.

A knowledge of frog calls can often aid in the assessment of the availability of standing water. Amphibians often have strict limits on their tolerance for aridity and temperature minima.

Trees may be useful as indicators of habitat quality. Certain trees are of pivotal importance in primate feeding (e.g., *Ficus*), and the presence or absence of fig species may correlate with the relative abundance of primates. Some species of trees are indicators of soil type or drainage patterns. For example, well-drained soils in northern South America are typified by Saman, *Pithecolobium*, whereas poorly drained soil may be dominated by mariche palm, *Copernicia*.

The presence of various rodents may also indicate the quality and disturbance of forest habitats. Muul and Lim (1978) described the association of Malaysian flying squirrels with forest type. They showed that 4 of 11 species of flying squirrels occur in primary and partially cut forests; another 5 species occur in disturbed forests, which range from secondary forests to mixed fruit and rubber plantations; the other 2 species occur frequently in both primary and secondary forests, but rarely in plantation areas. Similar correlations between habitat and species should be discernible for diurnally active mammals and birds. An awareness of such correlations will provide additional insight into understanding the community in which any censused species occurs.

During long-term studies, it is of great value to combine several projects at the same study site. Interchanges between workers who have concentrated on such diverse aspects of vertebrate ecology as bird feeding, amphibian reproduction, and rodent population dynamics often lead to the development of exciting new approaches in data acquisition and analysis. Many mechanisms of population biology are understood only for a few nonprimates. Indeed, rodents can be studied with great profit to aid our understanding of how tropical ecosystems function.

Rodent populations have been of interest to mammalian ecologists for many decades, particularly in temperate latitudes. There are several reasons why rodents and their population dynamics should be of interest to ecologists. First, rodents are common members of virtually all terrestrial ecosystems, where they play an important role as "key industry" animals in the transfer of energy from primary producers (plants) to secondary consumers. Second, rodents can have a considerable economic impact on human food supplies, particularly in tropical countries, where their destruction of crops and stored grain can run into millions of dollars annually. Crop destruction by rodents and insects may be many times greater than that caused by primates and birds. Third, various rodent populations serve as reservoirs for a diverse array of disease organisms that pose direct health threats to man. Plague, scrub typhus, Lassa fever, and various types of encephalitis and hemorrhagic fever are just a few examples of rodent-borne diseases that can affect the health of human beings and nonhuman primates. Finally, because they are ubiquitous and relatively easily studied, rodents and their populations can be used as "model systems" for studying the adaptive strategies of mammals in a wide variety of environments. Results of studies aimed at determining the basic operation of rodent populations under different environmental conditions have a direct bearing on our theoretical understanding of the evolution and maintenance of natural ecosystems.

3

Habitat Description and Specimen Collection

Accurate and standardized ecological information should be mandatory for any census or survey. A description of the physical features, community structure, and vegetation in a survey area is a necessary prerequisite for comparing densities of censused animals in different areas or in different habitats in the same area. The more detailed the habitat description, the more useful the census results.

It is necessary to emphasize that habitat descriptions can be either highly quantitative or just qualitative without very much field measurement. The type of data, as discussed for census procedures, will depend on the length of time available to conduct the survey, the personnel involved, and the level of sophistication desired. The methods for collecting habitat information should be decided when the census is planned.

If a small area is to be surveyed, attention can probably be directed toward microhabitat differences, such as flat terrain, hilly terrain, and flooded or unflooded areas. However, conducting a survey in larger areas will not permit attention to such detail, and it is advisable to evaluate habitat types in relation to the way census transects have been selected (see Table 3-1).

Ecological communities are frequently obvious to the researcher while conducting a census. For example, moist soil in a forest along a river indicates flooding. In a montane forest, if sampling covers a wide range of elevation, describe the habitat at every 50 m of elevation. Forests that have been logged or show signs of recent regeneration will require descriptions separate from those for undisturbed forest. Often, broad ecological communities are not apparent in the census zone, and the researcher may decide to describe the habitat at noticeable changes or every hour along the transect census. Whatever the choice, standardized descriptions of the habitat must be an integral part of the census.

HABITAT PROFILE

A physiognomic or structural classification of habitat types separates vegetation according to height and interdispersion of height classes. A sketch of a vegetation profile along transect lines has proved to be useful in augmenting detailed notes. Composite habitat profiles for an entire study area have also been useful in summarizing the relationship between animal abundance (based on sightings or signs) and habitat type (Figure 3-1).

In Sri Lanka, vegetation was classified into three major classes: (g) grass (and forbs), (Sc) scrub, and (T) trees. Mixtures of the three classes were indicated by the symbols (g, Sc), (Sc, T), (g, T), and so on. By use of transect sampling, it was possible to estimate the relative proportion of vegetation classes for the study areas (Figure 3-2). Scrub was arbitrarily defined as being composed of woody plants less than 2 m in height (Eisenberg and Lockhart, 1972). In adapting this scheme to other areas (e.g., the neotropics), the researcher should designate special vegetation categories, such as the palm (*Copernicia*) and savanna or tree savanna composed of *Pithecolobium*, *Acacia*, and grasses.

A habitat profile data sheet may help standardize observations by blocking out the habitat characteristics according to a scale that ranks the abundance of the feature from absent to rare, moderate, or dense. Undergrowth, epiphyte load, and foliage cover may be rated in this way. Information on such features as

TABLE 3-1 Estimates of Time Required for Field Work by Two Persons[a]

Type of Work	Area (km^2)	Days
Habitat survey		
General description	1	2
	10	10
Quantitative description[b]	1	8
	10	60
Density estimates (censusing)		
Crude		
Transect	1	6
	10	10
	20	20
Quadrat	1	6
	10	14
	20	40
Ecological		
Transect	1	6
	10	30
	20	40
Quadrat	1	6
	10	30
	20	60

[a] Does not include travel time to study areas; assumes work on foot; assumes forested habitat and some trail construction; assumes some familiarity with identification of flora and fauna.

[b] Nonpermanent grid.

the number of layers (shrubs, understory, main canopy, emergents), the light penetration through the canopy, the clumping of trees, and the presence of buttressed trees may also be listed. A visibility or obscurity score may be useful in comparing ease of observing primates between habitats. This may be as simple as ranking visibility as excellent, fair, or poor, but a better procedure is to place a 5- or 10-m striped stick at standard distances (10 m, 20 m, or more) from the transect path and determine the percentage of the stick that is obscured by the vegetation. A stick can easily be prepared by painting on it conspicuous stripes 1 m apart.

CHARACTERISTICS OF HABITATS

WATER AND DRAINAGE

The presence of water bodies, such as streams, lakes, ponds, and swamps, requires notation and brief description. Areas that retain standing water for prolonged periods, such as ponds and swamps, may also show unique vegetative characteristics requiring separate habitat profile descriptions.

Water drainage and quality may be indicated by characterizing a stream or river on the basis of color. Three major categories used in the Amazon basin are "white," "black," and "clear" and are important with respect to trace elements and suspended nutrients (Fittkau *et al.*, 1975; Soili, 1975). The color of a stream or river is not necessarily indicative of the soil and vegetation characteristics immediately adjacent to it. The color tells something about the dominant soil and vegetation in the major watershed feeding the river. The pH can be checked quickly with litmus paper (Table 3-2). Current evidence suggests that black-and clear-water drain-

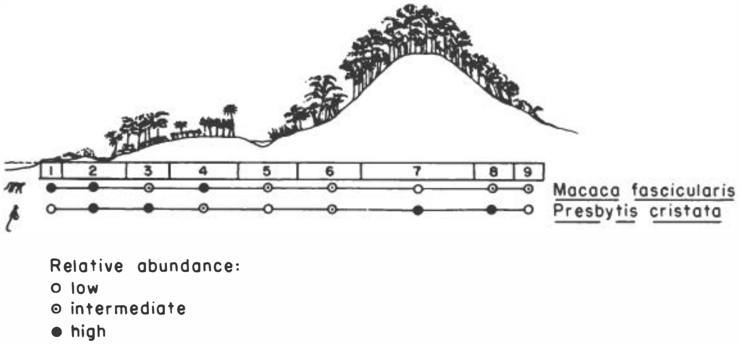
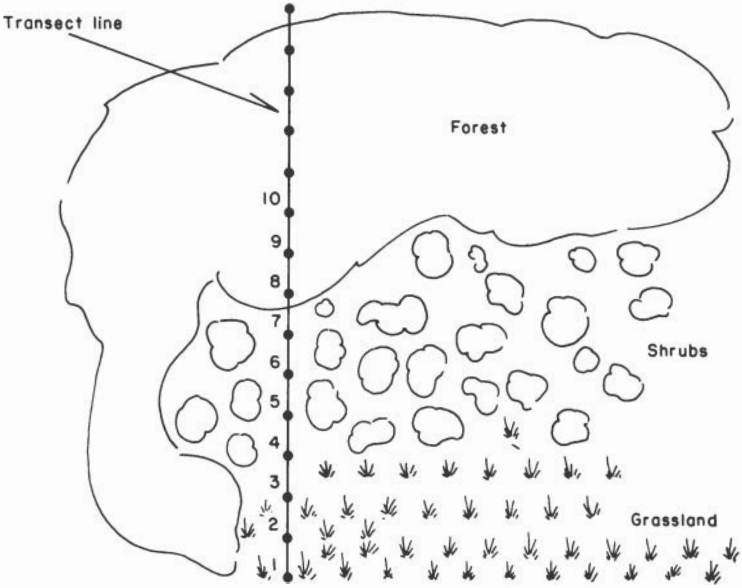


FIGURE 3-1 Primate abundance as a function of habitat type. A composite physiognomic habitat profile is a rapid way of summarizing which habitats support which species and whether all areas of available habitat are being exploited. The relative abundance of two primate species is shown for nine habitats in Java, Indonesia: 1. open sand; 2. *Barringtonia*, mangrove and tropical swamp forest; 3. alluvial forest; 4. plantations of coffee and rubber; 5. streambed vegetation; 6. bamboo/*Ficus*; 7. tropical rain forest; 8. transitional forest; and 9. bamboo/grass. Redrawn from Seidensticker and Suyono, 1980.



Station No.	Vegetation Type	Herbaceous Cover	Animal sightings (or signs)
1	g	90 %	Elephant feces
2	g	80 %	—
3	g	60 %	—
4	g	50 %	—
5	Sc	50 %	—
6	Sc	30 %	Axis deer (1)
7	Sc	40 %	—
8	Sc, T	20 %	—
9	T	< 10%	—
10	T	< 10%	Langur Monkey (2)

FIGURE 3-2 Preliminary transect sample of vegetation types in a survey area.

age areas have lower productivity than white-water areas. Black water may be caused by tannins and other compounds of plant decay as well as by eroded material.

SOIL TYPES

Soil science is an extremely specialized and important discipline, and in a survey of a new region only the most superficial notes can be taken; yet even brief descriptions can be of considerable value.

In a first-order description, soils are classified on the basis of color and particle size. Most nutrients generally occur in the humus and upper soil layers, which may be only centimeters in thickness. Soils are generally layered over bedrock, which varies in chemical composition. If a road has been cut through a hillside or if a natural landslide has exposed a "profile," a sketch or photograph with a scale can clarify soil depth, layers, and geological substrate. Color, depth, and layering are elementary data (Figure 3-3). In addition, some note should be made of the relative particle size. Claylike soils have extremely small particles and when dried out will harden and often crack with a characteristic hexagonal pattern. Sandy soils with intermediate particle size rarely show the reduced porosity when drying that claylike soils do. The presence of pebbles or rocks is important in understanding the nature of the overlying vegetational cover. Indeed, the whole rooting pattern and subsequent vegetational cover result from an interplay of soil type and duration of groundwater or moisture in the soil.

VEGETATION

Beyond a characterization of the habitat based on physiognomic features and a list of the common dominant plants, it is necessary to relate species composition to different forms of topography, drainage, and soil type. The frequency and dominance of species can be determined by using plotless or plot methods (Pandeya *et al.*, 1968).

The field worker need not be an expert botanist to compile quantitative floral data; however, in more detailed ecological studies, it is important to be familiar with the names of the com-

TABLE 3-2 Recording System for Water and Drainage[a]

Type of System	Map Location	Description	Water Quality	Substrate	Surrounding Vegetation
Lake	29° 40′-0° 10′	100 m × 150 m 2 m deep	pH 6.3 Color brown Turbidity high	Muddy bottom	Sandy bank to grass, brush, trees ~50 m from water
Stream	29° 40′-0° 11′	50 m wide Slow flowing 1.5 m deep	pH 5.2 Clear water	Gravel and stone bottom	Trees with submerged roots to 20 m Shorter stature with distance
Swamp	29°-0° 9′	Sedges to 2 m	pH 5.0	Muddy	Tangled brush before trees

[a] Headings are intended to suggest kinds of data to be recorded; entries are hypothetical.

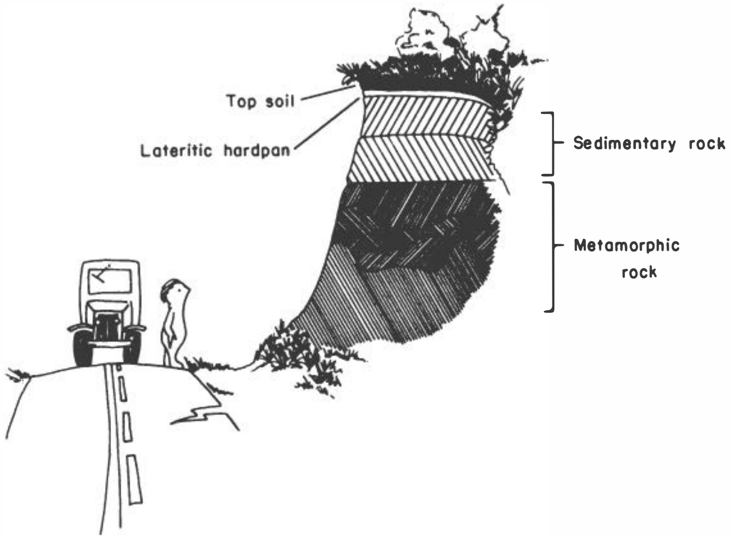


FIGURE 3-3 Profile of soils and underlying rocks.

mon dominant plants in the area. Common names are useful but in a final description Latin binomials should be given. It may be necessary to make a collection of each plant species, including leaves, flowers, and fruits, and then seek aid from a forestry official or botanist at a local museum. Equipment and materials useful for descriptions of vegetation include a tape measure, surveyor's tape, stakes, tree tags, paints, compass, and knife.

Three measurements are especially useful in preliminary studies of vegetation. These are the trunk diameter at breast height (dbh), tree height, and crown volume. Regardless of the vegetative sampling technique used, all trees above a dbh of 12 cm are usually identified. The measurement of dbh is useful in determining the maturity of a forest. Crown volume is an important measure of potential productivity if one is estimating the production of fruit or leaf crops. The dbh is positively correlated with the height of a tree within a given species and is the easier of the two size variables to measure.

Either a standard tape or a forester's tape may be used to determine the tree diameter. The circumference obtained in using a standard tape is divided by $\pi = 3.14$ to record the diameter. One scale on a forester's tape shows the diameter directly. Heights are visually estimated to the nearest meter. Tree height can be measured with a range finder, but pacing distances and angular measurements suffice in a preliminary description (Figure 3-4).

Crown volume is estimated with two pieces of information: the diameter of the crown and the general shape of the crown. Crown diameter may be determined by pacing and the shape by deciding whether the crown is best represented as a sphere, hemisphere, or some other shape (Figure 3-5). By dividing the crown diameter by 2 to obtain the radius, the volume of spherical canopies can be calculated from the equation $V = 4/3\ \pi\ r^3$. This volume is then divided by a fraction determined from inspection of the whole crown and determination of its approximation to a theoretical sphere (Figure 3-5).

Cover is the space occupied by all the individuals of a species or physiognomic class of vegetation. It is usually expressed as a percentage. Two types of cover are usually measured: canopy cover and ground cover. Canopy cover expresses the degree of closure or shading by adjacent trees. In a closed canopy where all crowns

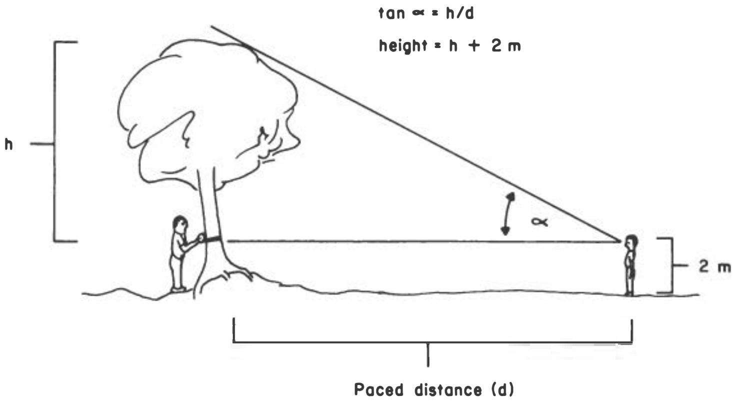


FIGURE 3-4 Measurement of tree height and diameter at breast height (dbh). Trigonometry is used to estimate the height of a tree from measurements of one angle and one leg of the triangle.

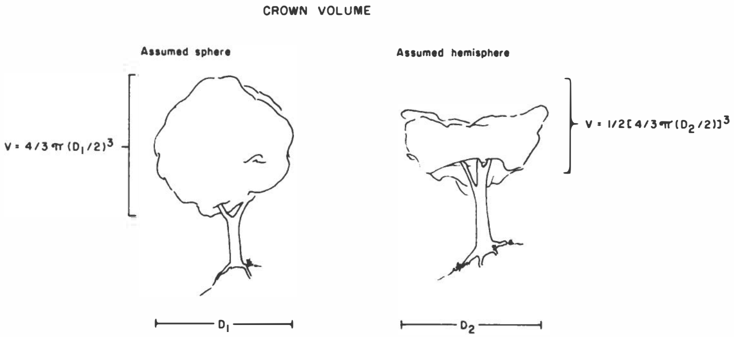


FIGURE 3-5 Measurement of tree crown volume. The volume of a tree crown may be estimated as that geometric shape that most closely approximates its shape, usually a sphere or hemisphere. The formulas for the volume (V) of a sphere and hemisphere require an estimate of the diameter (D_1, D_2) of the crown; $\pi \doteq 3.14$.

touch, the cover is 100%. Ground cover is estimated by sampling an arbitrary area (1 m^2) and estimating the amount of soil exposed. This is a useful measure in savanna habitats. In estimating ground cover a rating scale may be developed. For example, if one were estimating the amount of herbaceous plant growth within a 1-m quadrat, it could be expressed as 60%, 20%, or some other percentage. Usually one establishes a series of cover classes: one series for 0–24%, two for 25–49%, three for 50–74%, and four for 75–100%. For ground cover, a 1-m^2 area should be sampled at each 10-m interval.

Three methods frequently used to characterize vegetation are the strip, quadrat, and quadrant methods.

Strip Method

The strip method of vegetation analysis is commonly used by foresters and variations are used by primatologists (Dittus, 1977b; Struhsaker, 1976). This method is convenient because the vegetation sample strips are run along the animal census transect and are reliable samples of habitats (see Chapter 4). The analysis usually includes descriptions of trees and estimates of cover.

One problem is how much of the censused habitat should be vegetatively analyzed. Foresters using the strip method regularly sample 10%, but Struhsaker (1975) found that a sample representing about 3% of the home range of his main study group was adequate to characterize the forest composition.

Two procedures may be followed if a transect already exists. One is to sample all trees within a fixed distance of each side of the transect (5 m would be acceptable). However, sampling a transect longer than 3 km in this way would be difficult unless the observer had plenty of time. Therefore, where longer transects exist or there is considerable variation in vegetation, it is best to establish a sample swath every 100 m. Swaths 10 m wide are made through the study area.

Quadrat Method

The term "quadrat" generally refers to a sample area of a given shape and size used for analysis within a community. Sample plots should reflect the range of habitat types under study. By placing each sample plot at random within the study area, the data will be representative of the plant community as a whole. For example, if the area under study is divided into a grid and the plot squares are numbered consecutively, a table of random numbers can be used to select a sample of 10 from a grid of 100 squares.

A variation of this method is to divide the community into a series of rectangular plots and then sample at random within each of them. The total area of plots will not cover the entire community to be studied and may often be arranged in strips so that a certain proportion of the community is analyzed. In this way, one usually attempts to sample 5 or 10% of the total habitat.

The number of quadrats used depends on the variation within the vegetation and the degree of accuracy required. As a rule of thumb, it is far better to analyze many smaller quadrats than a few large ones in a community. The "grain" of the analysis is important. If one is studying a community of small plant species, a quadrat may be as small as 1 m square. But larger quadrats are required in a study of tree distribution. For a discussion of quadrat sampling applied to sampling primate populations, see "Quadrat Censuses" in Chapter 4.

In a preliminary analysis, when all quadrats have been sampled, the number of times each species was present in each quadrat is tabulated. This figure is then divided by the total number of quadrats sampled to give the observed frequency of each species. This value is often expressed as a decimal or a percentage. Finding the frequency of occurrence is a quick way to determine relative composition over a wide area.

The density of a given plant species is expressed as the number of individuals of that species per selected unit area. It is one of the best measurements for a precise description of habitat. The number of individuals of each species in each quadrat is recorded and the average number per quadrat is then calculated.

Quadrant Method

In the analysis of tree communities, plotless sampling is frequently employed. This technique, which may be carried out rapidly, is called the quadrant method. Basically, one establishes a series of transect lines running in a given compass direction (e.g., north–south or east–west). Referring to a table of random numbers, one measures random distances along these lines, thus locating a series of random points. From each of these random points, one draws an imaginary line perpendicular to the transect line and thus establishes four quadrants. Next one measures the distance to the nearest tree or to the nearest tree of selected species in each of the quadrants. In general, the aim is to identify the species, measure the distance from the sample point to the nearest tree, and record the dbh and the area of ground covered by the base of trees. In any transect sampling of this nature, the worker must establish at least 100 points that yield measurements for 400 trees. After completion of the sampling, analysis can be made on the basis of individual species or for the set of trees as a whole. One can calculate the mean distance ($\bar{d}$) of trees or species from the point by summing all distances (d) and dividing the total by the number (n) of distances measured. The equation becomes $\bar{d} = d/n$.

One can convert the plotless method into a grid for calculating the density of a species by treating the distance from the random point to the nearest tree as the hypotenuse of a right triangle or as the diagonal of a rectangle that is twice the size of the triangle. The density is calculated as the reciprocal of the mean distance squared times a reference area to convert the densities to a uniform area (e.g., individuals per hectare). Thus, for species *A*, whose mean distance between the random points and the nearest trees is 4 m, the density $= 1/d^2\ (100^2)$ or $1/16\ (10{,}000) = 625$ trees/hectare of species *A*. Figure 3-6 portrays the quadrant method.

The relative density and relative dominance of different tree species can be calculated after the basal area of the trees and their densities are known.

$$\text{The relative density} = \frac{\text{number of individuals of a species}}{\text{number of individuals of all species}} \times 100$$

$$\text{The relative dominance} = \frac{\text{total basal area of a species}}{\text{total basal area of all species}} \times 100$$

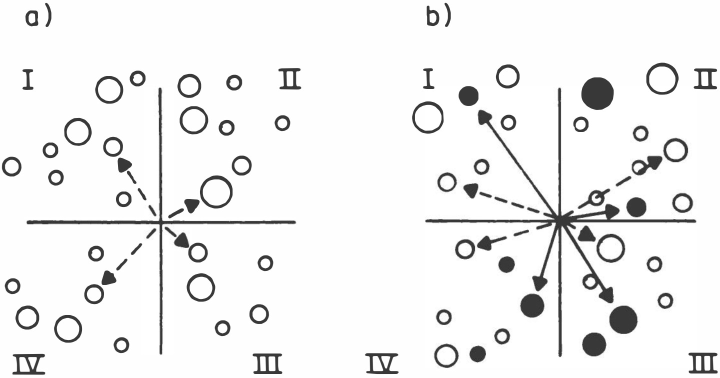


FIGURE 3-6 Plotless quadrant method for estimating relative tree densities. Random points are set along the vertical transect line. A perpendicular line is then drawn dividing the area into four quadrants, I, II, III, IV, that are numbered clockwise. (a) The distance (arrow) is measured from the random point to the nearest tree in each quadrant when an estimate of the relative density of all trees of a minimum dbh is desired. (b) The distances to specific tree species (solid and open dots) are measured when an estimate of the relative density of different species (in a two-species community) is desired. Adapted from Phillips, 1959.

OTHER INFORMATION

Certain other information pertaining to the status of the habitat, such as hunting and trapping pressure and history of land use, is important. This information is acquired by interviewing local inhabitants and government officials and consulting published records. The kind and degree of human influence in the habitat is evaluated by evidence of disturbance. Such evidence includes human settlements and agricultural and lumbering activities. This information is especially important for evaluating the present and future status of primate populations. (See Neville *et al.* (1976). An unpublished report by K. M. Green is also useful; to borrow a copy, write to K. M. Green, National Zoological Park, Washington, D.C. 20008.)

Photographs of the vegetation along the transect and several meters off the transect in the vegetation are useful. Black and white film is sufficient, but color film will provide more detail.

SPECIES MAPS

The preparation of species maps of large trees is a method for recording resource distribution. Mapping large areas of the study site or census zone is not always possible. Nonetheless, smaller vegetative sample plots or shorter transects will provide data from which rudimentary, but useful, profiles of habitats or forests can be prepared (Figure 3-1).

In study sites without existing transects, or if the researcher desires to sample larger areas, a compass and measuring tape are the basic tools to be used. Random directions are selected and followed with a compass and, by using a measuring tape or by pacing along a straight line, the desired distance is established. Surveyor's tape, blazes, or stakes can be used to mark the vegetation sample plots. For permanent identification of individual trees (which can be useful for future studies of phenology, succession, and animal resource utilization patterns), aluminum tree tags, numbered blazes, or paint are used. This permanent identification of each tree is mandatory to develop a vegetation map for long-term ecological studies. For an example of an elaborate vegetation map, see Figure 3-7.

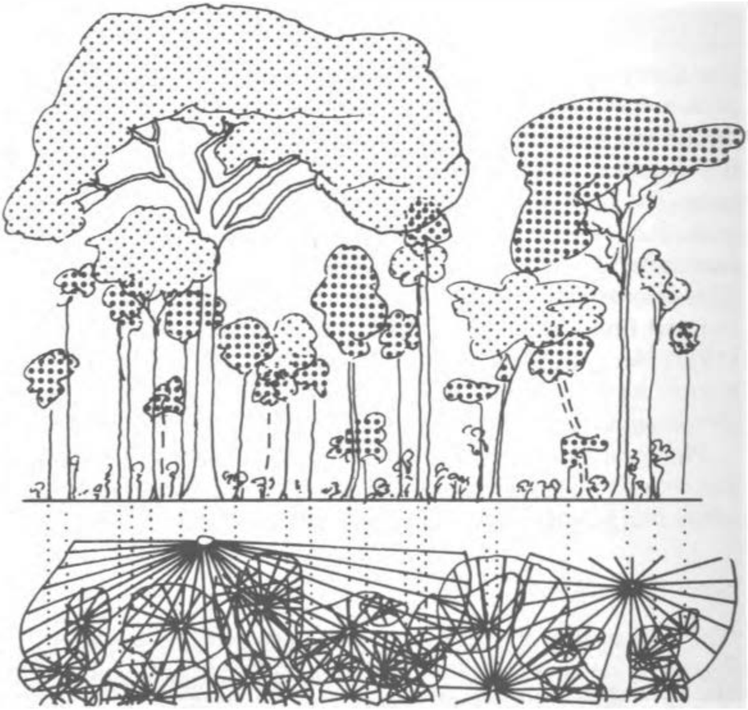


FIGURE 3-7 Species vegetation map with projected physiognomic vegetation profile. Vertical structure of the rain forest in Gabon along a portion of transect 90 × 5 m. Trunks shown by dotted lines are outside the transect width but support crowns included in the section. The horizontal structure is shown by the projection of the canopies and trunks in a wider sample area of 90 × 10 m. Canopies with lianas are represented by hatched areas on the profile. Identifications of tree species may also be labeled in these illustrations. Redrawn from Hladik, 1978.

Many study areas require vegetative analysis of shrub or grass in addition to the taller trees. This is particularly true for savanna-dwelling terrestrial primates in Africa and some Asian Colobinae and Cercopithecinae. For example, Dittus (1977b) analyzed shrub associations in Sri Lanka.

Struhsaker (1975) found that the strip-enumeration method is preferable for estimating the density of particular species in a large study area. He also found that, because of the aggregated dispersion pattern of many forest species, the quadrat method is better for evaluating densities in a local part of the forest, such as the home range of a group. In Struhsaker's strip method, all trees within 2.5 m of the trail and 10 m or more in height were identified; the taller trees were identified because the leaf-eating monkeys he was studying fed in those trees. Data from several strips through the home range of his red colobus study group were summed to obtain a strip that exceeded 2,800 m in length and 5 m in width. This strip corresponded to a sample area of 1.4 ha, with 469 trees and 51 species.

The diversity of a forest can be expressed by the Shannon Index of information content or uncertainty, H' (Pielou, 1969). The raw data for such an estimate are: S, the total number of tree species; N_i, the number of trees for each (ith) species; and N_t, the total number of trees in the sample of all tree species ($N_t = \Sigma_{i=1}^{S} N_i$) where $\Sigma_{i=1}^{S}$ = the sum values of N_i from 1 to the total, S.

The relative abundance (p_i) of the ith species is calculated as $P_i = N_i/N_t$, and diversity $H' = -\Sigma_{i=1}^{S} p_i 1np_i$, where $1n$ = natural logarithm to base $e = 2.718\ldots$.

The measure of diversity takes into account both the number of tree species and their relative abundances. H' measures the degree of uncertainty that an individual drawn at random from the population will belong to a particular species. H' increases with the number of species and, for a given number of species, will be greatest when all species have an equal number of individuals, i.e., when the distribution of trees among species is even. H' will be zero with only one species. H' can be applied equally well to estimating the diversity of primates or to estimating food items in the diet.

RECORDING CLIMATIC DATA

During a short survey the best that one can do is to record temperature, relative humidity, and frequency of rainfall. A maximum-minimum thermometer and a sling psychrometer will suffice. Long-term studies require a rain gauge and daily recording of the precipitation. If one has records for an annual cycle of daily rainfall and maximum and minimum temperatures, it is possible to plot these data on a single graph according to the method developed by Walter and Leith (1967); see Figure 3-8.

When an annual plot of precipitation and temperature is established, the drought periods are clearly delimited. When the precipitation curve falls below the temperature curve, this method of plotting reflects a drought in which plant growth is retarded. Average months of continuous drought are important; the longer the annual drought, the lower the annual plant productivity. The diversity of sympatric primate species clearly declines as the mean annual drought period increases over a range of geographic areas (Eisenberg, 1979).

COLLECTING AND MARKING SPECIMENS

Part of a habitat description may involve the assembly of plant and animal specimens. To be useful such collections must be adequately labeled and documented.

LABELING GUIDELINES

When collecting specimens it is important to get into the habit of keeping good notes and cross-references between the notes and the specimens. For this purpose it is useful to have tags that can be tied to the specimens. If specimens are being collected only sporadically, it may be adequate to number the specimens by date, since your notebook will probably be arranged chronologically. Specimen 7/II/79-2 would be the second specimen collected on the seventh of February 1979. Turning to the notebook for that date, one would find a description of the specimen and a note on where it was collected.

When specimens are being collected regularly or intensively, it is highly desirable to maintain a field catalog. The specimens should be numbered consecutively, preceded by your initials (e.g., RWT 735 or JFE 562). Never duplicate numbers. Keep the same series year after year. In both botanical and zoological collections, it is common to refer to the collector's numbers under the presumption that each applies uniquely to one specimen. Fruits and leaves bearing the same number are presumed to come from the same plant. The same would be true for a skull and leg

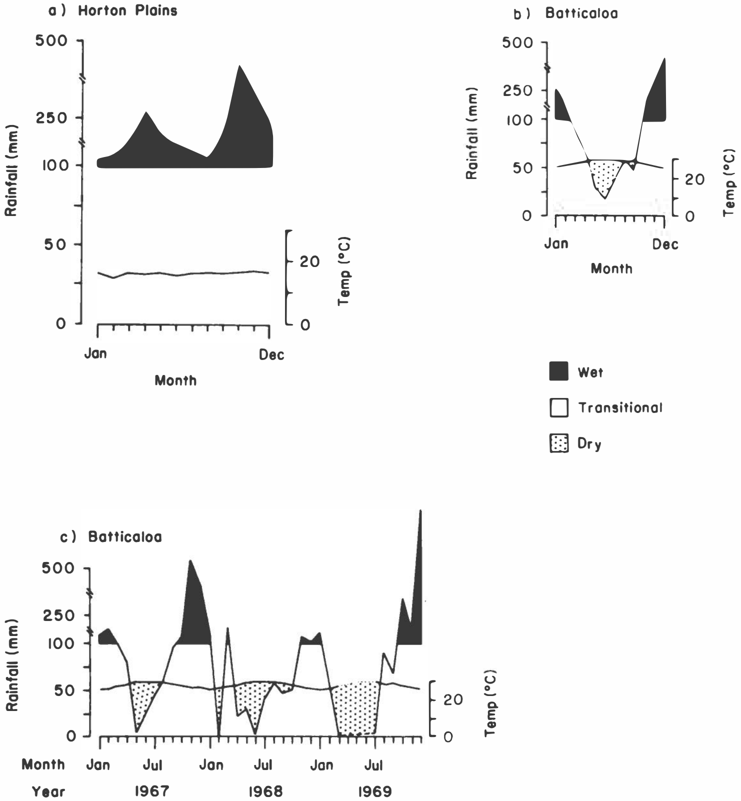


FIGURE 3-8 Climatic diagrams. This figure presents a rapid method from Walter and Leith (1967) for characterizing the seasonal variation in rainfall for two areas in Sri Lanka. In these diagrams, the temperature as a monthly mean is plotted in centigrade up to 50° on the left-hand ordinate. The scale is in 10° increments that correspond to increments of 20 mm of precipitation on the right-hand ordinate. Precipitation is plotted as the monthly total, and when the total for any month exceeds 100 mm the scale is altered to 200 mm in months. The abscissa is scaled in months.

The diagrams illustrate the differences between the climates of a wet-zone cloud forest at Horton Plains, which averages 2,000 mm of rainfall annually (Rudran, 1973a), and a coastal dry-zone forest at Batticaloa, which averages 1,699 mm of rainfall annually (McKay, 1973). The influence of monsoons on the amount and patterning of rainfall between years is striking in dry-zone habitats. This variability is illustrated in b and c, which contrast the data from individual years with 30-yr averages recorded by the Meteorological Department of Sri Lanka.

bones, all bearing the same collector's number. Examples of field catalogs, journals, and specimen labels are illustrated in many texts and pamphlets on mammalogy (e.g., DeBlase and Martin, 1974; Hall, 1962; Hall and Kelson, 1959; Setzer, 1963).

COLLECTING PLANT SPECIMENS

There are two main reasons for collecting plants used by the animals one studies. First, this enables one to identify the species of the plants. Second, it enables one to demonstrate that the identifications are correct. Thus, even if one "knows" what the plants are, it is desirable to have voucher specimens. Since most specimens will be examined by a botanist and deposited in a herbarium, it is important to collect and press specimens carefully. Botanists are far more helpful if one's specimens are well prepared. Herbaria appreciate being given specimens identified by their staffs, so duplicates should be collected if one wishes to retain an identified series. The herbaria of the world are listed by Holmgren and Keuken (1974).

The basic material needed is a plant press and the means to dry specimens. A plant press can be made from strips of wood fastened together to make a lattice. Two of these with straps around them constitute the press. Two boards and two pieces of light rope could also be used, as could a board and a big rock, but such presses make it harder to dry the specimens. The plants are placed between pieces of absorbent paper, such as folded newspaper, so that each sample, consisting of material from no more than one plant, is within its own fold. These are placed in the press between blotters, newspapers, or pieces of cardboard. Some sort of corrugated material, such as corrugated cardboard, is needed so that dry air can pass through the press. The corrugations should run the width of the press so that when the press is tightened and put on its edge over a source of low heat, the drier warm air will pass upward through the press.

When the specimens are collected, they should be numbered and an entry should be made in the field catalog. Note the size of the plant; describe the colors of flowers and sap, texture of bark, and so on. If you have numbered and labeled the trees in your study site, be sure to note these numbers also.

One should collect specimens with flowers and fruits whenever possible. The specimen should be large enough to show leafing and branching patterns, but remember that herbarium sheets are generally 11″ × 16″ and the pressed specimens must fit. Small plants may be collected whole—don't forget the roots. Large specimens may be folded, as long as important features are not obscured.

Press the plants as soon as possible, while they are fresh and unwilted. Under some circumstances specimens can temporarily be kept in plastic bags, preferably one specimen per bag so that they do not become mixed. When pressing specimens, arrange them so as to show the major features (e.g., both sides of leaves). Make sure the catalog numbers are with the plants in the press. To prevent molding, dry the plants as rapidly as possible in the press, but do not scorch them. Change wet blotters or newspapers as necessary, but do not remove the plants from their newspaper folders. It is best not to remove the plants from the folds of newspaper in which they are pressed until they are mounted on herbarium paper. The plants may be stored in newspaper, or they may be sent to a herbarium in newspaper.

Any arrangement simulating a warming oven may be used as a plant drier. Plants are often dried in a box. Make a series of small (0.5 cm in diameter) openings in the bottom and top of the box so that heat can rise. Place the box over a small light bulb (25 watts) or other heat source.

Each specimen sent to a botanist or a herbarium should have the following data included: data collected, collector's full name and his catalog number for the specimen, locality from which the specimen was collected, habitat (e.g., forest, savanna, swamp), and descriptive characteristics of the plant.

Fruits are commonly preserved dry. They may also be preserved in fluid: 70% alcohol or FAA (5% formalin, 5% acetic acid, in 70% alcohol). Large fruits may need to be lanced or sectioned to ensure rapid fixation. They can be stored in wide-mouthed mason jars. For shipping they can be wrapped in cloth dampened with the preserving fluid and sealed in plastic bags.

Botanists' collection techniques are described in more detail and illustrated in several books and pamphlets (e.g., Fosberg and Sachet, 1965; Shetler, 1963; Smith, 1971).

SCAVENGING ANIMAL REMAINS

During field work one occasionally finds dead primates or skeletal material. These specimens constitute a "graveyard sample" and can be very valuable. They can provide information on the ages at which animals die, data on nutritional stress, frequencies of fractures, and even the causes of sickness and death. These materials should therefore be saved and cataloged. The date, location, and state of decomposition should be recorded when the carcass is *first* encountered.

A smelly, maggot-ridden monkey cadaver is not an attractive acquisition. In some areas you can leave it until it has dried and then take possession; but in others it must be taken promptly—before it is removed by scavenging animals or birds. You can hang it from a tree to discourage vultures and small scavengers from dragging it away, but if it starts to fall apart, important parts may be lost. If wire screening is available, you can make a cage to put it in. Make sure that vultures cannot reach into the cage and pull parts of it out. If the cage excludes vertebrates but not invertebrates, the skeleton will soon be cleaned, but it may be necessary to soften the skin in water and cut it off the skeleton. Less desirably, the carcass can be buried for a few weeks, then exhumed. In some localities a cadaver can be left in slowly moving water, where invertebrate scavengers will clean it efficiently. If the cadaver is fresh, or one's stomach is strong, one can "rough it out" by removing the skin, viscera, and major muscle masses. Frequently this job is not as bad as anticipated if the viscera are first removed and disposed of. The skull should be separated carefully from the atlas, the eyes removed from their sockets, and the brain removed through the foramen magnum. The last can be done with a long-handled scoop, or a stick, or by injecting a jet of water inside the skull, as with a syringe. The "roughed out" carcass can then be dried, later prepared with dermestid beetles, or it can be boiled. The former is preferable.

Since the skull is generally the most valuable part, it should always be saved. Be careful not to loose the teeth, which can be used for estimating the age of the animal. The weight of the eye lenses also is frequently used to estimate ages of dead mammals.

In some areas and with some species of primates, there may be a risk of disease associated with handling dead animals. The risk is probably greatest among primates most closely related to man, and the risk probably decreases rapidly with the length of time that the animal has been dead. With freshly dead animals, one should take care not to be bitten by any of their ectoparasites. With all cadavers one should take reasonable precaution to avoid viral and bacterial contamination of oneself and one's colleagues.

The preparation of mammal skeletons for study is described in more detail by Anon. (1967), Hall and Russell (1933), Hoffmeister and Lee (1963), and Russell (1947).

PHENOLOGICAL PATTERNS

Phenology is the study of periodicity in the production of plant parts by individuals at a defined site and time. Typical phenophases that are discriminated include the vegetative parts (shoots, flush or young leaves, and mature leaves) and the reproductive parts (buds, blossoms, and unripe and ripe fruit). Fruit frequently changes color as it ripens. The period of leaffall is also monitored.

Plants differ in the seasonal periodicity and sequential patterning of their phenological activity. Trees may be ranked from evergreen to brevideciduous, semideciduous, or deciduous; the ranking depends on the type of leaf renewal and the extent and duration of leaffall. Evergreen species produce new leaves as they lose old ones. At the other extreme, deciduous species tend to be highly seasonal, and some renew their canopies only after a period of dormancy. These patterns are usually given operational definitions at each site. Plants may produce flowers and leaves simultaneously, alternately, or with some overlap of these activities.

Reproductive patterns are equally variable. Trees may flower continuously, seasonally at a regular period of the year, aperiodically, or gregariously; in gregarious flowering, neighboring individuals show the same rhythmicity. Trees may also remain inactive reproductively for extended periods (up to several years) until a critical stimulus is present or until a required dormancy is satisfied. Several tree species have separate male and female individuals. Care should be taken to select female individuals of dioecious species in order to develop an estimate of fruit availability.

A tree species may maintain continuous activity of a particular phenophase through continuous production at certain sites, by asynchronous behavior between branches of an individual, or by asynchronous behavior between individuals in a population. As many as 27 types of reproductive patterns have been described for species of plants in a seasonal rain forest in Panama (Croat, 1975). The patterns of dispersing or concentrating resources over time and space have been considered adaptive strategies through which plant species attract pollinators and dispersal agents and augment chemical defenses for avoiding seed predators. The focus of attention on the interaction between plant and animal species has led to a new examination of phenological patterns that are only partly explained as responses to limiting climatic factors—for example, rainy seasons and dry seasons, and changes in temperature and day length. The strategies of different plants directly affect the daily ranging patterns of primates; these patterns include not only their foraging times but also spacing within groups during foraging and the distances they move between resources. For example, it may be advantageous for a tree to attract arboreal herbivores if they are also seed dispersers, but advantageous to discourage them otherwise. A number of phenological patterns have been described in recent studies conducted both in the New World tropics (Croat, 1975; Daubenmire, 1972; Frankie *et al.*, 1974a,b; Monasterio and Sarmiento, 1976) and in the Old World tropics (Hladik, 1978; Koelmeyer, 1959, 1960).

Phenological data are useful because they can be compared with observations on feeding in order to develop a picture of the availability and utilization of different food items. Therefore, plant species selected for monitoring should be important food items of the primate under study or common plants in the area. Many plants are eaten seasonally at restricted periods and may represent important food items at those times. Mapping of plant species and monitoring phenology with the grid established for vegetation analysis and within the home range of the main primate group increase the likelihood of observing the actual utilization of plants in the phenological sample. It is often necessary to use a sequential numbering system to identify the plants selected for the phenological sample prior to obtaining taxonomic identifications of voucher specimens (see Chapter 6). The more frequently selected plants are trees and shrubs; those less frequently selected are vines, epiphytes, and herbs.

Several individuals of each tree species are marked with numbered tags or tape for recognition at each sampling period. Mature individuals that do not show obvious signs of disease are selected. A sample consisting of 5–10 individuals per species may be as large a sample as can be recorded on a monthly basis. (You might be working with, say, 30 species, and you would have a sample of 300 trees if you selected 10 individuals for each species.) More frequent monitoring is necessary for some species.

Each phenophase is estimated as a percentage of the canopy. Percentages may be estimated broadly on a scale of 10 with each number representing 10% of the canopy. The data are recorded rapidly on prepared checksheets that provide columns for each of the phenophases (buds, blossoms, unripe and ripe fruits, young and mature leaves, leaffall) and a list of the identifications of the trees or other plants in the sample. The results are then tabulated or graphed and are contrasted with climatic variables that influence them (e.g., rainfall).

SATELLITE IMAGERY

Satellite analysis of land resources has been an expanding area of study in forestry, agriculture, and geology since 1972, when the Earth Resources LANDSAT Satellites began transmitting data collected by multispectral optical sensors to ground receiving stations worldwide. Photographic enlargements are made for study from the images, which were obtained at scales ranging from 1:3, 369,000 to 1:250,000 from the early LANDSAT satellite and are obtained at a scale of 1:125,000 from the current (1980) LANDSAT 3 satellite. The resolution at this scale means that 1 cm of the photograph represents 1.25 km on the ground and thus is much less than that available from recent aerial photographs or topographic maps.

Different surfaces on earth reflect characteristic amounts of light that can be discriminated as intensity differences in images. These reflective differences can be used to discriminate and clarify forests, crops, water bodies, and geologic features. Seasonal changes in maturing vegetation of well-known crops and changes in species composition within large forest tracts can be detected by using these methods. These classifications are developed in conjunction with observations at selected sites that provide "ground truth" for extrapolations to larger areas. The standardized Forest Survey Information Data Sheet is illustrated in Appendix C. It provides a means of describing habitats and has been used by the Royal Thai Forest Department for interpreting LANDSAT data.

Potential applications for satellite imagery increase as the technology moves from an experimental stage to one where the information can be used in evaluating changes in land-use patterns and in managing resources (National Research Council, 1977). Studies of tropical forests using remote-sensing techniques and guidelines for gathering ground truth information have been described at recent international symposia (International Symposium on Remote Sensing of the Environment, 1978, 1980). These studies include vegetation classifications and forest inventories in Brazil, Mexico, the Peruvian Amazon, Nigerian Forest Reserves, Thailand, the Philippines, and Indonesia. Initial applications of satellite imagery to primate studies may be in classifying forest types and in detecting and monitoring habitat loss for forest primates through deforestation. NASA has recently published a volume on monitoring forest canopy in tropical countries using LANDSAT imagery.

Data acquired by the LANDSAT satellite is transmitted to three receiving stations in the United States (located at NASA facilities in Greenbelt, Maryland; Goldstone, California; and Fairbanks, Alaska) to two stations in Canada and to one each in Brazil, Italy, Japan, and Sweden. Additional tracking and receiving stations are planned in Argentina, Australia, and China. The principal distribution facility in the United States for remotely sensed data is the EROS Data Center, Geological Survey, U.S. Department of the Interior, Washington, D.C. The Resource Planning Unit of the World Bank and the Remote Sensing Program of the U.S. Agency for International Development are important sources of information on remote sensing. Tropical countries that have LANDSAT programs include Bolivia, Brazil, India, Indonesia, Pakistan, Peru, the Philippines, Tanzania, and Thailand. Inquiries about the service offered and price lists for satellite images can be obtained from LANDSAT data distribution centers (see Appendix A). Private firms and academic institutions in the United States have also begun to provide image processing and interpretive series (see Appendix B).

4

Census Methods for Estimating Densities

BACKGROUND FOR CALCULATIONS DERIVED FROM TRANSECT CENSUSES

MEASUREMENTS FOR TRANSECT METHODS AND CALCULATION OF DENSITY

The aim of a census is to estimate the density of a sample population in a defined area so that the total population of a larger census area can be estimated. The basic formula for calculating density, which is the number of animals per unit area, is

$$\frac{\text{Estimated animal population, } N}{\text{Census area, } A} = \frac{\text{Number of animals seen in sample area, } n}{\text{Sample area, } a}.$$

When utilizing a transect, the area censused is found by multiplying the length by the width ($A = lw$). For sample areas based on transects, l = the length of the transect line and $2w$ = the strip width, which is twice the transect width—that is, the width located on one side of the transect line. The above relationship is usually solved for N, and the basic formula for estimating the number of animals in a population of census area $a = 2 \cdot lw$ becomes

$$N = \frac{nA}{2 \cdot lw},$$

where A is measured in the same units as the distance measurements. Several types of density estimates are recognized, and these are discussed in Chapter 8.

Transect width is estimated from the following measurements, which can be collected when an animal is sighted along a transect line:

P = the perpendicular distance, that is, the shortest distance from the detected animal to the transect line. It is often called the animal-to-transect distance.
S = the animal-to-observer distance, or sighting distance from the observer to the animal at the moment of detection.
θ = the sighting angle, or the angle between the transect line and the animal-to-observer line at the moment of detection.

The angle θ may be measured with a field compass.

On the basis of the trigonometric relationship $P = S \sin \theta$, any two of the three measurements shown in Figure 4-1 can be taken for convenience. Estimation errors can sometimes be caught when all three measurements are taken by using trigonometry to check accuracy. Usually a measurement is made only for the perpendicular distances or for both the sighting angle and the sighting distances from which the perpendicular distances can be computed.

Different methods for determining a valid transect width have led to a variety of formulas, usually through the substitution of w by some specifically defined value. The transect width has been variously defined as the maximum sighting or perpendicular distance, as the mean distance, and as some distance between the maximum and mean that is considered an effective strip width.

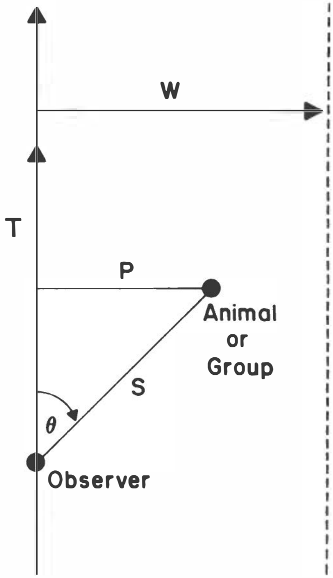


FIGURE 4-1 Measurements for perpendicular and sighting distances. Three measurements may be taken when an animal is sighted from a transect line: *P*, the animal-to-path distance; *S*, the animal-to-observer distance; and *θ*, the sighting angle. The length of the transect line, *T*, is a measured distance; the transect width, *w*, may be established as a fixed or variable distance.

These intermediate widths have been attempts to estimate a 100% detection distance or a distance at which observations become markedly less frequent.

It is obvious from the initial equation, $N = nA/2 \cdot lw$, that decreasing the size of the sample area relative to the sample population, n, has the effect of decreasing the denominator and thereby increasing the population estimate, N. Thus, formulas that utilize mean sighting or perpendicular distances will produce smaller estimates of the sample area and larger population estimates than will equations that utilize maximum values for these estimates of transect width. Formulas that are used to derive some estimate of effective strip width will provide intermediate estimates of population size. The latter formulas often rely on establishing a fixed width and excluding from analysis those sightings that lie beyond this fixed width. These estimates are made to avoid one of the problems encountered when using the maximum distance: the possibility that the maximum record represents an extreme value that is beyond the distance within which one could normally detect animals.

Burnham *et al.* (1980) reviewed census methods and tested several probability functions under the assumption that the probability of detection can be best expressed by a family of probability curves. Their estimates depend on use of a computer to generate probability functions and on access to a statistician. Although their methods will probably be used increasingly as census methods and analysis become more accurate and statistically robust, it is assumed that the investigator using this manual will not have access to a computer and will therefore be obliged to use the simpler analytical methods even though these may depend on some assumptions that only approximate the real situation.

A variety of methods were reviewed by Burnham *et al.* (1980) and Robinette *et al.* (1974), and additional discussions can be found in the references cited by them. Several of these methods are mentioned below. Selected methods that have been useful in censusing primates are discussed later in this chapter.

Robinette *et al.* (1974) reviewed several strip census methods that use either sighting or perpendicular distances. They conducted field tests in which they used stationary objects (blocks and carcasses) and found that all but three methods overestimated the actual numbers by more than 10%. Formulas based on sighting distances could be ranked by the size of the population estimates that they produced from lowest to highest as follows: King's method, which uses the arithmetic mean for the sighting distance; Gates III, which is based on a geometric mean; Hayne's method, which uses the harmonic mean of the sighting distance; and Gates II, which substitutes $2n - 1$ for n and uses the arithmetic mean for the sighting distance. The Gates II method gave population estimates that were almost twice that of King's.

Robinette and his colleagues found that several methods based on perpendicular distances also overestimated the population of stationary objects. These included Webb's method, the Gates I method, and Leopold's method. Webb's method uses the mean sighting distances and mean sighting angles to determine perpendicular distances; the other two methods use the mean perpendicular distances. The Gates I method also uses $n - 1$ for n. Methods developed by Kelker and Anderson and by Pospahala gave mean estimates within 10% of the actual numbers; in this way they were like King's method. Kelker used an estimated perpendicular threshold distance within which all animals were probably observed but beyond which some animals were probably missed, and he used an *n* in his formula that is equal to the number of animals seen within twice the threshold distance. Anderson and Pospahala also developed a correction factor for animals not observed.

ASSUMPTIONS FOR LINE TRANSECT SAMPLING

The theory of line transect sampling depends on four assumptions outlined by Burnham *et al.* (1980):

1. Animals directly on the line will never be missed. It is also understood that all of the animals in the sample area will not be detected, and the farther an animal is from the line, the less likely it is to be detected.
2. Animals are fixed at the initial sighting position; they do not move before being detected and none are counted twice.
3. Distances and angles are measured exactly, thus avoiding both measurement errors and rounding errors.
4. Sightings are independent events.

The investigator attempts to design the study and the data analysis to minimize violations of these assumptions.

It is assumed that a plot of the sighting data, like the frequency of many classes of measurements, approximates a normal distribution. Figure 4-2 illustrates a normal distribution fitted to a frequency histogram. The value x is the mean or the sum of all values divided by the number of individual measurements, $\bar{x} = \Sigma x/\Sigma n$. The standard deviation, s, indicates the dispersion of the values for the measured variable around the mean. The usual notation for the mean plus or minus the standard deviation is $\bar{x} \pm s$. One calculates s by the formula: $s = \sqrt{s^2}$ where s^2 is variance. The variance is calculated from the following formula:

$$s^2 = \frac{\Sigma(x - \bar{x})^2}{n - 1},$$

where x is any measured value in your sample, $\bar{x}$ is the mean, and n is the number of observations. In practice, the term $(x - \bar{x})^2$ is reduced to:

$$\Sigma(x - \bar{x})^2 = \Sigma x^2 - \frac{(\Sigma x)^2}{n}$$

$$s^2 = \Sigma x^2 - \frac{(\Sigma x)^2}{n} \Big/ n - 1$$

$$s = \sqrt{\Sigma x^2 - \frac{(\Sigma x)^2}{n}} \Big/ n - 1$$

A census method that can be used for data that are not normally distributed but follow a Poisson distribution is given on p. 65.

A good census is one that avoids bias and is both accurate and precise. The introduction of bias due to terrain, vegetation, or human activity is avoided by selecting transects in a way that randomly distributes them in the census area. The use of existing roads as transects strongly biases the counts because a road system almost never randomly traverses an area. Roads are generally constructed along rather than across contours. In addition, roads affect the exposure of animals and habitat to human activity by providing an access to nearby areas for hunting, cutting for firewood, and lumbering. Lastly, road or river edge habitat is very different from nonedge habitat because of the increased light penetration and prevalence of secondary growth species. There are a few special situations, e.g., the flat agricultural plains of the upper Gangetic Basin in India, where roads provide valid transect routes for surveys of primates in rural areas (Southwick *et al.*, 1965).

An accurate census is one in which the estimate of a population closely approximates the true value; a precise census is one in which repeated measurements or replicates of the same quantity

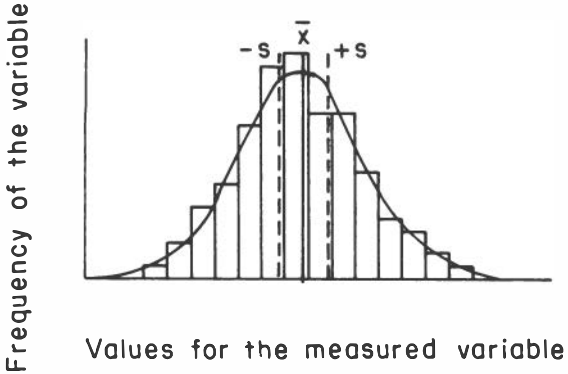


FIGURE 4-2 A normal distribution. The diagram shows the observed frequency of a variable in the form of a histogram (rectangles) together with a fitted normal distribution (smooth curve). Data may show some variation from a bell-shaped curve and still be considered as normally distributed. The $\bar{x}$ = the mean, the s = one standard deviation.

(in this case, the number of animals present) are close to each other. To obtain a census that is both accurate and precise, it is necessary to determine the sample size, the number or length of transect lines, and the number of sightings (sample points) from inspection of preliminary data drawn from the sample area. Examples are given in subsequent sections of this chapter. Tables of random numbers can be found in general statistics texts, and an elaboration of these statistical concepts can be found in discussions of population estimates in Burnham *et al*. (1980), Caughley (1977), Norton-Griffiths (1975), and Overton (1971).

Several examples of primate censuses illustrate that there can be considerable variability in the results, but the estimates tend to increase in accuracy and precision with replication. Thus, Neville (1976) showed that counts of a population of howler monkeys in Venezuela doubled between the 50th and 80th hours of observations. Altmann and Altmann (1970) found a clear-cut tendency for censuses to become more accurate with time when they measured the amount of sampling error by matching the results of censuses against the true composition of groups of baboons determined by independent methods. MacKinnon (1974a,b) calculated the density of orangutans as 0.8 individuals per km^2 on the basis of a count of nests along a transect, but increased the estimate to 4.6 organutans per km^2 after making a more detailed count of all nests in a plot within the same census area.

Not all census methods have high accuracy or precision but represent compromises between size of survey area, cost, time, and manpower. Southwick *et al.* (1965) "calibrated" roadside surveys by repeating runs over 168 km of Indian roadside. The counts, based on 10 replications of the trip, ranged between 3 and 11 groups with an average of 7. Later they found that 14 groups lived in the census zone, indicating that for small sample sizes roadside surveys of rhesus macaques have low accuracy and, on the average, underestimate actual numbers by half.

Assumption 3 emphasizes the theoretical importance of estimating distances to the nearest unit of measure, such as a meter, because grouping distance measurements into classes, as the data are taken, sets the limits for data analysis and requires that the data be analyzed as frequency counts rather than as a set of continuous measurements. Thus, an observation should be recorded as a sighting at 36 m rather than as one in the interval between 30 and 40 m. Burnham *et al.* (1980) point out that there are valid statistical methods for estimating densities on the basis of grouped perpendicular distances, but none have been developed for analyzing grouped sighting distances and angles.

Assumption 2 presupposes that animals do not move before they are detected. Movement away from an observer by animals initially close to a transect line has the effect of increasing width estimates (such as means) and thereby decreasing density estimates. Such bias is suggested in graphed data (Figure 4-3) whenever the number of close sightings is less than the number of intermediate sightings (Janson and Terborgh, in press). Figure 4-3 also illustrates a method for determining a reliable detection distance by using the graphed data to identify the distance at which the frequency of detections drops sharply. Where there is no sharp separation between a plateau and a decline in observation distances, it is useful to compute density estimates for more than one possible maximum cutoff distance and to present the range of resulting density estimates.

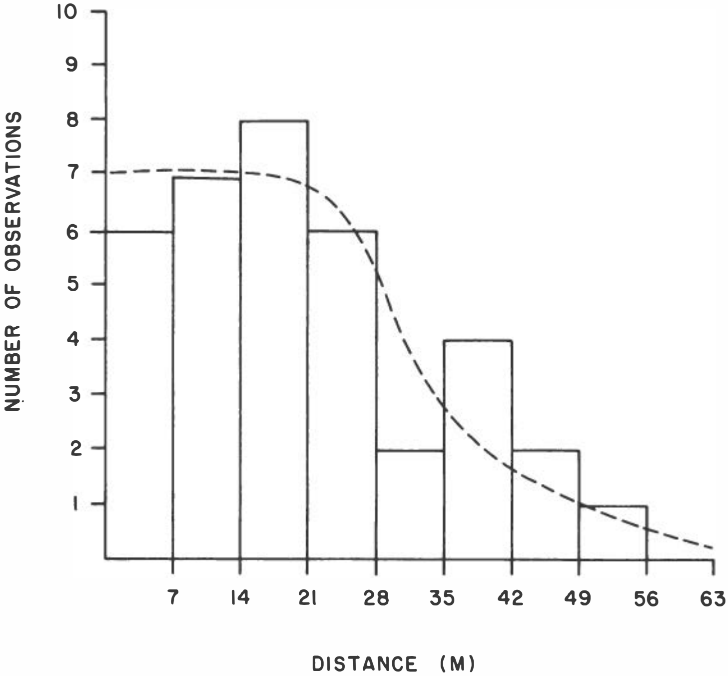


FIGURE 4-3 Distribution of perpendicular sighting distances for *Cebus*. Redrawn from Janson and Terborgh (in press).

Burnham *et al*. (1980) recommend the use of perpendicular distance data and believe that when sighting distances are used they should be used with sighting angles. Robinette *et al*. (1974) also recommend the use of methods based on perpendicular distances but note that there are some conditions, such as uneven terrain, in which sighting distances are useful because measurement of perpendicular distances from the transect lines is difficult. Thomas Struhsaker reports finding a high frequency of sightings over the transect line. In such instances, the use of methods based on sighting distances is preferred over those based on perpendicular distances because the latter underestimate the area (the perpendicular distance overhead is a "zero" width) and overestimate the number of animals.

The fundamental problem in utilizing the perpendicular distance from the transect line derives from the fact that primate habitat space is three-dimensional. We are in effect attempting to estimate density in terms of area rather than density within a volume. The problem becomes critical when the sample size is small and the area surveyed is restricted in size. Large sample sizes over wide areas reduce the vertical dimension relative to the transect length and width and thus reduce apparent variability, but the problem is a genuine one in small transect survey operations. Density expressed as numbers of animals per volumetric units are common in fisheries but have seldom been applied to terrestrial vertebrates. In most primate surveys of limited scope, the observer-to-animal distance will probably yield the most useful results for estimating density per unit of area, but the recording of perpendicular distances as well as sighting distances and angles will provide the greatest flexibility in later statistical analyses of the data.

GENERAL GUIDELINES AND FIELD PROCEDURES

Standardization of methods is essential to minimize the variables and thereby allow comparisons between investigators and study sites. Unless distances are to be measured with a tape, an observer should develop experience and confidence in pacing and visually estimating metric distances prior to starting a census. Pacing is an effective method for determining horizontal distance provided the terrain is relatively level and unobstructed. A pace may be empirically determined by counting one's steps along a straight line premeasured by a metric tape and then dividing the paces into this linear distance. A person can accurately determine his average pace or step by pacing the measured line several times and by using care in regulating his stride.

Experience and interobserver reliability also are gained by estimating horizontal and vertical distances in the habitat where the census will be done and by making visual estimates along measured distances. The trick is to think in multiples of known distances and heights, whether the basis of comparison is an imagined 90-m football field or an 8-m two-story building. An 18-m tree can be considered simply as a tree that is 12 times the height of your 1.5-m-tall partner, who is standing at its base. Measuring treefalls is another way of developing a sense of scale. After measuring a few 50-m treefalls with a metric tape, it becomes easier to recognize the standing height of comparable emergents and to estimate the height of smaller trees as a fraction of the tallest trees in the forest.

Censuses should be made at about the same time of day. The first 4 to 6 h and the last 3 h of the day are recommended because these periods are usually coincident with peak activity of primates. Published surveys show that primates are easier to detect when they are active than when they are resting (Freese, 1975; Green, 1978a,b). It is not possible to census during rainstorms or windstorms.

During a census the observer moves along a transect line and stops frequently (every few minutes or meters) to listen and scan the surrounding area. The optimal walking pace is about 1 km/h. By noting in your notebook the distance paced at every stop or every hundred meters, or by punching a number counter, you can accumulate an accurate record of the total distance paced. It may be advisable to work a transect line alone in order to reduce the noise from the movement of other people, but under some conditions the eyes and ears of a partner increase the chance of detecting primates.

When a primate group is seen, a standarized time should be spent observing it (10 min is recommended). It is suggested that the observer remain on the census route and not follow the animals away from the predetermined line.

When beginning each transect, the observer should record several standard items including the location, date and starting time, weather, census method, and participating personnel. These items can be recorded on a data sheet modified as necessary from the sample provided in Appendix C for all types of transects, from broad surveys to random compass line transects. Each time an animal or group of animals is encountered, the observer should record the following information:

- Species.
- Number of individuals actually counted. In addition, the

group size should be estimated when conditions prevent a complete count.

- Mode of detection (whether by sight, vocalization, or sound produced by the animal moving through the vegetation).
- Time sighted.
- Observer's location along the transect.
- Animal-observer distance. This is the distance from the observer's position to the animal when it is first detected. It is frequently referred to as the sighting distance.
- Shortest transect-animal distance. This is the perpendicular distance from the transect line to the animal. Both the sighting distance and the perpendicular distance should be checked by measuring or by pacing until confidence and reliability in estimating distances are built up through experience.
- Height of the first animal sighted.
- Activity when first detected.
- Age (body size relative to adults) and sex of individuals in each group. Since one is rarely able to make a complete group count of forest species within 10 min, in the final analysis one is concerned primarily with the number of social groups and solitary animals encountered.
- Vocalizations. Tabulating bouts of loud calls may be useful in evaluating relative abundance in study sites.
- Time encounter ended.

Carbon copies of field notes are a cheap form of insurance against loss when the original is held by the observer and the copy is sent back to the institution supporting the study. Blank sheets and notes of the day are best carried in an aluminum loose-sheet holder, which are available in a variety of sizes from most American forestry suppliers. Daily field notes should be cataloged on summary census sheets at the end of each day and summarized at the end of each week or month. Catalog entries should include date, location, species sighted, number of individuals, page number of the entry in the daily notes, and a brief description of what the specific entry contains. Daily cataloging permits rapid reference to specific events and greatly facilitates data analysis. The catalog entries can be stored in ring files (looseleaf notebooks). The catalog entries are greatly expanded in long-term studies to include whatever behavioral topics are the focus of attention, such as interactions between specified age and sex classes or individuals, feeding observations, vocalizations, progressions, or group encounters.

ASSESSING THE IMPACT OF HUMAN ACTIVITIES

In conducting initial surveys, investigators will find that interviews with local inhabitants, government officials, and biologists help determine the amount and selectivity of hunting pressure, the utilization of forest products, and the extent of recent land clearing. In many parts of both the New and Old World tropics, monkeys are hunted for food for local consumption and for markets, which can be visited to verify interview reports. Where primates have been subjected to continuing hunting pressures, their detectability will be seriously altered. A field investigator should keep in mind that more precise methods of data gathering and analysis can be used in protected areas than in hunted areas where reliable estimates of depleted populations may be beyond the scope of an initial survey.

When entering an unprotected census area in which animals are hunted, investigators will want to know what species are hunted, for what purpose primates are hunted, and about how many animals are killed each year. This information is usually available from local inhabitants. Several interviews may be necessary. If hunters are active in the area, it may be a good idea to accompany one of them.

The value of the interview method is illustrated by the results of a survey that J. F. Eisenberg (1976, unpublished) conducted in an area of Territorio Amazonas in Venezuela, where six species of primates were known from museum collections to have occurred 15 yr previously. It quickly became apparent from interviews that local hunters had removed great numbers of primates to support a population of colonists. The bearded saki (*Chiropotes*) was rated as extremely palatable, as were the spider monkey (*Ateles*) and howler monkey (*Alouatta*). The hunters confessed that the capuchin monkey (*Cebus*) was very unpalatable and that the squirrel monkey (*Saimiri*) was too small to be profitably hunted with a rifle. The night monkey (*Aotus*), because of its nocturnality and difficulty of detection, seemed not to be worth the effort for sustained hunting. Again its small size made it somewhat uneconomical. As could be predicted from this information, the only primate species seen during diurnal boat surveys were the less favored species *Saimiri* and *Cebus*. The other larger species and the highly prized bearded saki were not detected by normal survey techniques.

BROAD SURVEYS

The broad survey attempts to cover large geographical areas in a relatively short period of time (Scott *et al.*, 1976a,b). When dealing with forest habitats, the most one can hope for in this kind of survey is data on geographic distribution, relative abundance in different areas of habitats, and limited information on age and sex composition of the populations. In open-savanna habitats and certain types of rural and urban settings, one may be able to collect relatively accurate data on group size, age and sex composition, and density, but it is difficult to collect these data in most situations (Southwick and Siddiqi, 1977; Struhsaker, 1976).

For broad surveys in forests and with little time available, observations are usually made along existing roads, trails, or footpaths. In special situations, counts may also be made from canoes along streams and in swamps. If time permits, a rough trail can be cut through the forest, preferably in a straight line and 4 km or more in length. No attempt should be made to census the same day that rough trails are cut.

For broad surveys in open habitats and along river edges, vehicles and boats or canoes greatly expand the area that can be censused, but the detectability of animals may be reduced in areas where animals move back from the edge in response to motor noise.

Vehicles have been used extensively in India (Mukherjee and Mukherjee, 1972; Neville, 1968; Southwick and Siddiqi, 1966; Southwick *et al.*, 1961, 1965) to survey primates along rural roads and canal banks. Modifications of this procedure have also been used in Malaysia (Southwick and Cadigan, 1972), Indonesia

(Wilson and Wilson, 1974), Bangladesh (Green, 1978b), and Africa (Taub, 1977; Altmann and Altmann, 1970).

In most forest regions, suitable roads are limited in their extent and distribution and may be impassable during the wet season. Also, noisy vehicles reduce auditory cues from the animals. The practicality of counts from vehicles is therefore restricted. Favorable conditions include good visibility, accessibility, and reasonable tolerance of vehicles by primates. Vehicles may be the only reasonable method for surveying large land areas, and they are well suited for surveying in savannas and agricultural areas.

Researchers have censused by canoe or motorized boat areas not otherwise accessible. Flood plains that can be surveyed by foot during dry seasons may be passable only by water transport during the rains. Therefore, censusing in different seasons may require two survey methods.

The approximate distance traveled on a river can be computed by determining the time required to travel a measured distance along a shoreline (e.g., 1 km), both upstream and downstream; computing the speed (km/h) at which the measured distance is traveled; and multiplying this speed by the total travel time.

APPLICATIONS OF LINE TRANSECT CENSUSES IN AN AFRICAN FOREST

Many of the data identified in the previous section can be used in a comparison of relative abundance of animals in study sites. However, because results of primate censuses along the same route are extremely variable from one day to the next, the data from broad surveys cannot give an accurate estimate of the absolute density. To reduce variability in transect censusing, a large number of censuses must be made over the same census route and over a long period of time (usually a year or more). But this is beyond the scope of the broad survey.

The number of transects established and the distance between transects depend on the size of the study area, the heterogeneity of the habitat, and the distribution of the primate community within the study area. Although there is no fixed rule on this point, the following discussions of the number of censuses to be made and of estimating densities are relevant to planning an accurate census program. Clearly, more research needs to be done on this aspect of censusing forest primates. The same methods and precautions listed in the preceding sections of this chapter should be followed.

In the line transect census, the trail should be of predetermined length and established randomly within the study area. It should not be biased according to terrain, vegetation, or other factors (e.g., hunting) that may affect primate abundance along the transect. One usually establishes a transect along an arbitrary compass bearing and assumes that the area included will be representative of the vegetation types of the site. For instance, if the forest encompases 80% forest, 10% grassland, and 10% swamp, then ideally the transect will reflect this.

Straight-line transects are preferable to routes following a circle, square, or rectangle because they reduce the chances of inadvertently counting the same animals more than once. A transect of about 4 km is appropriate for a morning's census.

ZONATION

If the vegetation along a transect varies in type (e.g., forest and swamp, woodland and savanna), it is important to divide the transect into zones or strata within which the vegetation is homogeneous. Censuses and density estimates are made for each zone (habitat type) and weighted according to the proportional representation of each zone in the study area. This technique, called zonation or stratification, is intended to reduce variability between samples and thereby increase precision. Although developed and used most extensively in aerial counts of large mammals, in principle it should be applicable to any kind of line transect census (Caughley, 1977). Use of this method usually requires prior knowledge of the habitat types, their abundance, and the habitat preferences of the animals.

In most cases the technique has been of limited value in censuses of tropical forest primates because this kind of information has not been available. Observers should keep accurate notes on the exact locations of sightings along the transect line and the type of vegetation so that it is possible to zone the census transect after the censuses have been completed.

Zonation techniques are most applicable when dealing with a mosaic of strongly contrasting vegetation types in which one can quickly form impressions about primate densities from preliminary walks through the study area. For example, this technique would be employed when comparing low-stature swamp forest with contiguous upland tall forest or a block of undisturbed mature rain forest with an adjacent forest that has been selectively felled for timber. One can, of course, zone the census transect after it has been established and after the cenuses have been completed as long as accurate notes are kept on the exact location of each sighting and the vegetation is described accordingly. In this way one can combine segments of the transect that are similar in vegetation. Such zonation would not only increase the precision of density estimates by reducing variability between censuses for each zone but would also reveal habitat preferences of the primates being censused.

Two outstanding problems are posed by the line transect method: (1) determining the appropriate sample size (length) and (2) estimating densities (width) from the data. As mentioned earlier, the extreme variation in counts from one day to the next makes it necessary to conduct several counts along the same transect.

SAMPLE SIZE DETERMINED BY 95% CONFIDENCE LIMITS

How many censuses should one make along a particular transect? This will depend on the precision required, which in turn depends on the variability of the censuses. Although, basically, the larger the sample size, the more precise the results, a point is usually reached where more samples will not reduce variability significantly. Since this point cannot be determined before the study has begun, one must analyze the data as the study progresses so that the results and estimates of precision can be monitored. As outlined by Norton-Griffiths (1975, pp. 34–36), the precision of an estimate is the 95% confidence limits expressed as the percentage of the estimated mean. In the case of censuses of primate groups, precision can be expressed as the 95% confidence limits divided by the estimated mean number of groups per census multiplied by 100. The lower this percentage, the more precise the estimated mean. One then plots this estimate of precision against the cumulative number of censuses completed. The point on the curve where any further increase in effort is not repaid by a proportional increase in precision can either be calculated exactly or found where the curve begins to flatten out.

An example from the Kibale Forest, Uganda, demonstrates the value of computing estimates of precision (Table 4-1). A total of 44 censuses were made over an 18-mo period on a single 4-km census transect that traversed relatively mature tropical rain forest. No samples were made in 4 mo, and 2–4 censuses were conducted during each of the remaining 14 mo.

TABLE 4-1 Results from 44 Censuses of Red Colobus Along the Same Transect

Census Number	Number of Red Colobus Groups Seen (x)	Census Number	Number of Red Colobus Groups Seen
1	7	23	3
2	3	24	4
3	5	25	4
4	2	26	3
5	3	27	0
6	5	28	3
7	2	29	3
8	2	30	3
9	3	31	3
10	5	32	1
11	6	33	3
12	4	34	6
13	8	35	4
14	7	36	2
15	4	37	3
16	3	38	3
17	6	39	5
18	3	40	0
19	4	41	6
20	3	42	3
21	5	43	4
22	6	44	5

Confidence limits were computed for the mean number of groups seen per census for the two most common primate species (red colobus and redtails). Although this could have been done at the end of each census, for simplicity the censuses were divided into units of 10.

Calculating the standard deviation (*s*) was the first step in calculating the 95% confidence limits. An example of the calculations for the *s* of the first group of 10 red colobus samples is shown below from the original census data provided in Table 4-1.

$$s = \sqrt{\frac{\Sigma x^2 - \dfrac{(\Sigma x)^2}{n}}{n - 1}}$$

$$s = \sqrt{\frac{163 - \dfrac{(37)^2}{10}}{9}} = \sqrt{\frac{26.10}{9}} = \sqrt{2.90} = 1.7029.$$

In the present example of two species selected from Kibale, the 95% confidence limits and the percentage precision are given in Table 4-2. For illustration, the first value for the 95% confidence limits in the table was obtained by using the following formula:

$$\text{95\% confidence limits} = t_{0.05\,(n-1)} \times \frac{s}{\sqrt{n}},$$

where t = the critical values of Student's t-distribution obtained from two-tailed t table (used when dealing with small samples of fewer than 100) found in any standard statistical textbook (e.g., Sokal and Rohlf, 1969), n = the number of censuses, $n - 1$ = the degrees of freedom, and s = the standard deviation of the mean number of groups per census. Thus, the 95% confidence limits are:

$$= 2.26 \times \frac{1.7029}{\sqrt{10}}$$

$$= 2.26 \times \frac{1.7029}{3.16}$$

$$= 2.26 \times .538$$

$$= 1.218.$$

The 95% confidence limits are computed cumulatively in units of 10; thus, they were computed for each species for the first 10 censuses, then the first 10 and second 10 censuses were combined for the next computation and so on until the final computation included all 44 censuses.

$$\text{The \% precision} = \frac{\text{95\% confidence limits}}{\text{Mean number of groups seen for that unit of census}} \times 100$$

$$= \frac{1.218}{3.7} \times 100$$

$$= 32.9\%.$$

The results are graphed in Figure 4-4 and clearly show that for both species precision began to level off after the first 20–30 censuses.

To account for seasonal variation, one should conduct censuses uniformly throughout the year, preferably during every month. The number of censuses per month will again depend on the variability of the results. In most cases it will not be possible to conduct enough samples every month to demonstrate statistically significant differences between months, unless the differences are very pronounced.

How many censuses are required to make comparisons with other areas or with the same transect in different time periods? Through modification of a formula presented in Sokal and Rohlf (1969), Janson and Terborgh (in press) suggest that the minimum sample (N) necessary to distinguish with 95% confidence a given

TABLE 4-2 Estimates of Precision for 44 Censuses of Red Colobus and Redtails Along the Same Transect

Species	Census Number	95% Confidence Limits	Mean Number Groups	% Precision
Red colobus	1-10	1.218	3.7	32.9
	1-20	0.844	4.3	19.9
	1-30	0.654	4.0	16.5
	1-40	0.570	3.7	15.3
	1-44	0.532	3.8	14.0
Redtails	1-10	1.237	3.1	39.9
	1-20	0.816	3.3	25.1
	1-30	0.594	3.1	19.0
	1-40	0.501	2.8	17.7
	1-44	0.463	2.8	16.7

degree of difference between two means is roughly approximated by

$$N = \left(\frac{4 \times \text{C.V.}}{\text{degree of difference between means}}\right)^2 + 1,$$

where C.V. = coefficient of variation, which is the standard deviation divided by the mean ($s/\bar{x}$). For example (following Janson and Terborgh), suppose we want to be able to detect at least a 25% change in the red colobus population at Kibale. From the 44 censuses we calculate a C.V. of the mean number of red colobus groups seen per census, which is 0.46; thus, the minimum sample size required would be

$$\left(\frac{4 \times 0.46}{0.25}\right)^2 + 1 = 55 \text{ groups of red colobus,}$$

which would indicate 15–20 censuses. Janson and Terborgh suggest, however, that because the data are usually not normally distributed, the samples should be at least 10–20% larger than predicted from their formulas.

ESTIMATING DENSITIES BY USING DIFFERENT STRIP WIDTHS

The main problem in estimating group densities from line transect samples is determining the size of the area sampled. The length of the transect can be easily measured, but how does one determine the width of the strip sampled? This will be affected by the perceptiveness of the observer, visibility and audibility in the

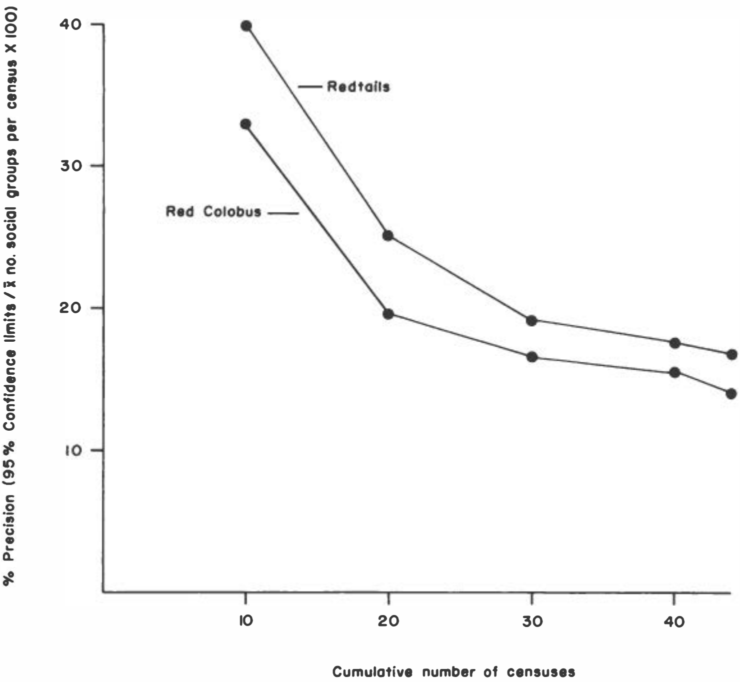


FIGURE 4-4 Precision of estimated mean number of social groups per census as a function of number of censuses completed. Vertical axis is the 95% confidence limits expressed as the percentage of the mean number of groups per census, i.e., 95% confidence limits divided by the estimated mean number of social groups per census times 100. This is a measure of precision, and as this percentage decreases the precision increases. The horizontal axis is the cumulative number of censuses completed. Data were collected during 44 censuses along one 4-km transect in mature forest (compartment 30) of the Kibale Forest, Uganda, during 1970–1972. Adapted from Struhsaker, 1975.

habitat censused, and detectability of the animals. Animal detectability can, in turn, be affected by group size, group spread, frequency of vocalization, activity at the time of census, sound made in movement through the vegetation, and the height of vegetation most frequently used.

Several methods for determining strip width are reviewed by Caughley (1977), Janson and Terborgh (in press), and Robinette *et al*. (1974). (K. M. Green discusses the subject in an unpublished report; to borrow a copy, write to the National Zoological Park, Washington, D.C.). Selected methods are tested here by comparing census results with the known group densities obtained from detailed, long-term studies of individual groups (see below).

There are two basic approaches to determining strip width: *Transect-to-animal distance* is the estimated perpendicular distance from the line transect to the first animal of each group seen. *Observer-to-animal distance* is the estimated distance between the observer and the first animal of each group seen.

Both of these estimates give some indication of visibility and detectability. The first method, however, gives an estimate of width regardless of the actual detection distance from the observer, whereas the second method is based on the actual detection distance (see Figure 4-5).

Transect-to-Animal Distance

Mean Perpendicular Distance Several formulas use the mean perpendicular distance of all first sightings to calculate the width of the transect. The methods indicated in Table 4-3 were tested with the red colobus census data (Struhsaker, 1975), but were rejected because of unacceptably high overestimates of group density. On the basis of detailed studies of individual groups, the red colobus density in the cenused area of the Kibale Forest was estimated at 6 groups per km^2.

Maximum Perpendicular Distance In this formula, the maximum perpendicular distance of all first sightings of a particular species is used to estimate transect width (unpublished report by K. M. Green). This means that all groups detected will be within this distance. In order to cover both sides of the transect, this maximum distance is doubled and then multiplied by the transect length to give the area censused. The number of groups seen is divided by the area to give the density.

Example: 44 censuses along a single 4-km transect was *176 km*.

(1) Maximum perpendicular distance from transect to a red colobus group was 110 m or *0.11 km*.

(2) During all 44 censuses a total of *168* sightings of red colobus groups were made.

$$\text{(3)}\quad \text{Density} = \frac{\begin{array}{c}\text{number of}\\ \text{groups sighted}\end{array}}{\text{area censused}} = \frac{\begin{array}{c}\text{sum of sightings on}\\ \text{different or repeat}\\ \text{transects}\end{array}}{\begin{array}{c}\text{2 sides}\\ \text{of}\\ \text{transect}\end{array}\left\{\begin{array}{c}\text{length} \times \text{width}\\ \text{of 1 side of}\\ \text{transect in km}\end{array}\right\}}$$

$$= \frac{168}{2(176 \times 0.11)}$$

$$= 4.34 \text{ groups/km}^2.$$

This figure of 4.34 groups/km^2 is an underestimate of 27.7%. The direction and magnitude of error were similar for redtails at Kibale, but for blue monkeys at Kibale this method overestimated by around 22%.

Maximum Reliable Transect-to-Animal Perpendicular Distance

A more critical method was first set forth by Kelker (1945) and modified by several others (see Robinette *et al.*, 1974, and Janson and Terborgh, in press). In this approach, one plots the frequency distribution of all estimates of the perpendicular distance between the transect and the first animal seen. On inspecting this frequency distribution, one attempts to determine the distance within which all groups were probably detected but beyond which some were missed. This maximum reliable distance is most readily determined when the frequency distribution curve shows an obvious plateau or asymptote that is followed by a sharp drop in

Comparison of distance from animal to 1) Observer 8 2) Transect

Animal	Distance to observer	Distance to transect
A¹	100	100
A²	100	90
A³	100	70
A⁴	100	30
A⁵	100	0

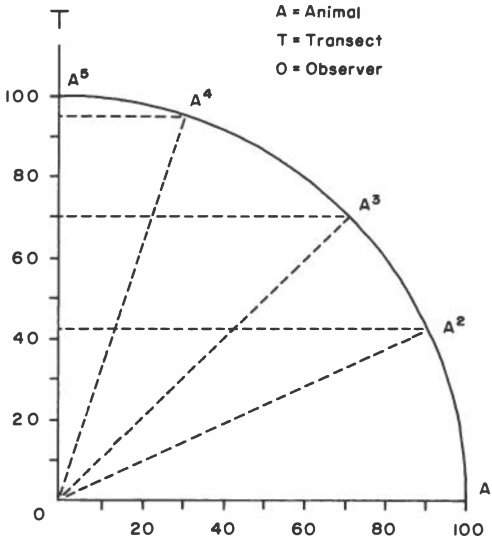


FIGURE 4-5 Diagram illustrating distinction between animal-to-observer and animal-to-transect distances.

frequency. The maximum reliable distance or cutoff point is where the curve begins its sharp drop. In cases where the frequency distribution of transect-to-animal distances does not show a clear plateau and sharp decline, one is faced with the problem of deciding the maximum reliable distance. In such cases it may be advisable to compute density estimates for more than one possible maximum reliable distance and to present the range of resulting density estimates. Take, for example, the case of the red colobus census data. Figure 4-6 suggests at least two possible cutoff points of maximum reliable transect-to-animal distances: 40 m and 60 m. With these distances, Kelker's method allows us to estimate group density as follows:

(1) Length of censuses: *176* km (44 censuses along the same 4-km transect).

(2) Width of transect: 80 m or *0.08* km (40 m × 2, both sides of transect).

(3) Total number of red colobus groups seen within 40 m of transect: *138* (from Figure 4-6).

(4) Density: 138/176 × 0.08 = *9.8 groups/km^2*.

This value represents an overestimate of 63.3%. If one uses 60 m as the maximum reliable transect-to-animal distance, the estimate becomes 156 groups/176 × 0.12 = 7.39 groups/km^2 or an overestimate of 23.3%.

Janson and Terborgh (in press) applied a modification of this method to their raw data from Manu, Peru, and found that it gave enormous overestimates, usually of several hundred percent. Only with a number of correction factors derived from their detailed studies of specific groups could this method give reasonable estimates.

A fundamental difficulty with the transect-to-animal distance is that many sightings will be made of animals directly over the trail and ahead of the observer. In such instances, the distance from trail to animal will be zero (see Figure 4-5). In the 44 censuses at Kibale, Uganda, referred to above, nearly 40% of the 166 sightings of red colobus were over the census transect and were scored as zero meters from the trail, although usually they were more than 20 m from the observer. Consequently, methods employing transect-to-animal distances will usually overestimate

TABLE 4-3 Rejected Methods of Estimating Group Density of Red Colobus Monkeys

Method	Source	Estimated Number of Groups per km^2	Overestimate (%)
Leopold *et al.* (1951)	Robinette *et al.* (1974)	22.0	266.7
Eberhardt (1968)	Caughley (1977)	33.5	458.0
Emlen (1971)	Emlen (1971)	21.0	250.0

TABLE 4-4 Estimates of Distances Between Observer and Animal When First Animal was Sighted, Together with Number of Initial Sightings, Regardless of Perpendicular Distance from Transect[a, b]

Estimated distances (m)	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	
Number of initial sightings at these distances:										
Red colobus monkeys	—	8	16	8	13	3	4	—	3	(Total: 55)
Redtail monkeys	—	8	10	8	3	1	—	2	2	(Total: 34)
Blue monkeys	—	5	7	3	5	—	3	—	1	(Total: 24)

[a] Data from 17 censuses along same 4-km route in mature forest in Kibale Forest, Uganda, beginning in 1974 and ending in 1976. Only social groups were considered—not solitary animals.

[b] Source: T. T. Struhsaker, unpublished data.

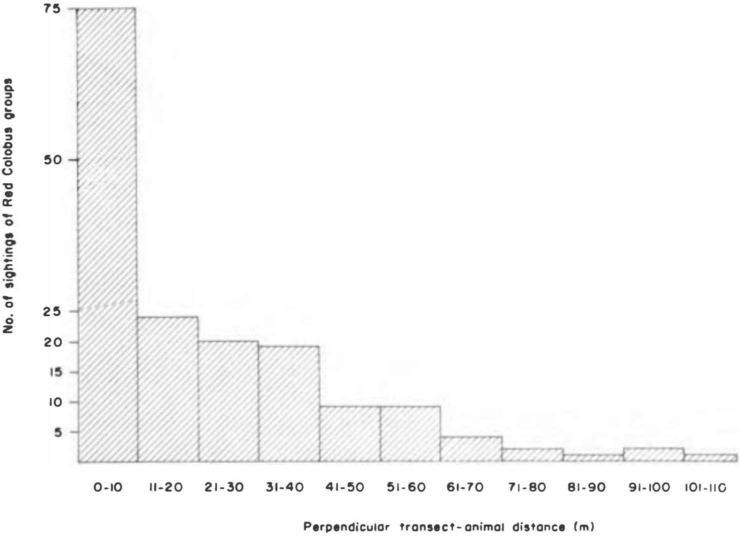


FIGURE 4-6 Frequency distribution of initial perpendicular animal-to-transect distance. Data are from the same 44 censuses that are dealt with in Figure 4-4. Red colobus sightings total 166.

the density because they underestimate the size of the area censused.

Observer-to-Animal Distance

Estimates of the initial distance between the observer and the first animal seen overcome the problem of zero distance inherent in the transect-to-animal method, although Janson and Terborgh (in press) discuss some of the theoretical difficulties.

Mean Distance The King method (in Robinette *et al.*, 1974) is based on the mean value of such estimates. By applying King's method to data from 17 censuses made in Kibale, Uganda, during 1974 and 1976 (when observer-to-animal distances were recorded; see Table 4-4) one finds that it tends to overestimate by a substantial factor: 80% for red colobus, 85% for redtails, and nearly twice this for blue monkeys. Similar gross overestimates resulted when Janson and Terborgh (in press) applied this method to their raw data from Peru.

Maximum Distance Applying the maximum distance (90 m) of all sightings of red colobus groups during the same 17 censuses to the basic formula gives: 55 sightings/68 km (i.e., 4-km transect × 17) × (2 × 0.09 km, the width) = 4.49 groups/km^2 or an underestimate of about 25%. The same method applied to the redtail data gave an underestimate of 30.5%, but for blue monkeys it yielded an overestimate of about 2–17.4%.

Maximum Reliable Sighting Distance More accurate estimates were obtained by inspecting the frequency distribution of observer-to-animal distances and, as with the Kelker method, determining the cutoff distance or maximum reliable sighting distance within which all animals were probably observed, but some missed (e.g., Ghiglieri, 1979). As discussed above, there may be a problem in determining the cutoff point, and it may be necessary to use more than one distance and to compute more than one density estimate. In any case, when this method was applied to the data from Kibale, Uganda (Table 4-4), the density estimates were generally closer to those from the detailed studies than to any of the other line transect analyses.

For the red colobus, the cutoff point would appear to be 50 m. Applying the basic formula: 45 sightings within 50 m/(length = 17 × 4 km) × (width = 2 × 0.05 km) = *6.6 groups/km*^{2}. This represents an overestimate of only 10% when compared with the estimate of 6 groups/km^2 from detailed studies of specific groups. A similar analysis for redtail monkeys in the same series of censuses gave an overestimate of 20% when 40 m was used as the maximum reliable sighting distance and 6.5% when 50 m was used. In contrast, estimates for blue monkeys were too high. With a 50-m cutoff, the results gave an overestimate of 47–67%, and with a 70-m cutoff an overestimate of 21–45%. It would tentatively appear that this method is most useful for primate species of generally high densities. For species of low density, it tends to overestimate.

Summary

In summary, it would seem that the observer-to-animal distance, at least for the Kibale data, gives more accurate estimates in general than the transect-to-animal distance; that the mean distance in both methods tends to grossly overestimate; that the maximum distance tends to underestimate except for species of low density; and that the maximum reliable sighting distance, depending on the species and how one determines the cutoff point, gives the most accurate density estimate.

NONLINEAR DENSITY PLOT METHOD

When time and resources are limited and information from interviews has confirmed that the species of interest is not selectively hunted, the first tasks in visiting a new area are to conduct a preliminary exploration of the region, making notes on vegetation height and quality and on soils and general topography. During the initial encounters with primates, attempts should be made to estimate group size, to estimate the distance from which the group was detected, and to determine what the animals were doing when detected.

After a few days of the initial survey, select a troop and attempt to study it through an entire day. In this way one can begin to focus on the number of animals in a group and the approximate size of its daily foraging range. Of course, in so short a time it is not possible to estimate the entire home range of group or to obtain a very accurate idea of the mean group size, unless the sample is very large. However, this approach provides sufficient data to permit one to estimate densities if the data are not normally distributed. By contrast, so far as methods described earlier in this section, it has been assumed that the data are normally distributed.

The data set approaches a Poisson distribution if the standard deviation approximates or exceeds the value of the mean. This simply means that the number of replicate samples (transects walked) is insufficient to generate a normal distribution of the variable that one is trying to measure: primate density.

One need not despair if this circumstance occurs. For example, if the species of interest has a mean group size approximating the size that has been noted in other areas, and if the preliminary investigation indicates that its daily range-use pattern approaches the value for the ranging of the same species studied in another habitat, then the following technique may be used with confidence. Remember, however, that the method assumes that there is more accurate knowledge of the density of the species in question for another area and that there is reason to believe that the physical conditions of the new area are similar to those of the reference area.

Even though high standard deviations are found in the analysis of the data, transect census data will positively covary with the real density. The preliminary data are thus a useful indicator of relative abundance. The number of transect samples may be increased or reanalyzed according to the following procedure: Set each transect length so that for a known detection width one will cover an area equal to 0.5 the average home range of the species in question. Each transect will then be treated as a single plot. Express the result of each transect as either the presence or absence of a group or subgroup. Run transects until at least 10 samples are available.

Since the transects are randomly placed in the habitat, one can use a Poisson distribution for estimating the real density of groups per unit area from the percentage frequency of groups per sampling unit or plot. The proportion of plots with no groups will be $1 - f = e^{-\bar{x}}$ (Caughley, 1977), where f is the mean frequency of sightings per plot and the proportion of plots containing one or more groups will be $f = 1 - e^{-\bar{x}}$. The value of $-\bar{x}$ can be found by using a table of exponentials. The relationship between the frequency of sightings and density can also be approximated from Figure 4-7. The transformed data can then be expressed as groups per unit area, which can be converted to individuals per unit area by multiplying by the mean group size.

In the example provided in Table 4-5, the average home range of howler monkeys determined independently by following troops at the Smithsonian Tropical Research Institute, Panama, was found to be 10.5 ha, or 0.10 km^2, in 1973. A plot with a transect width of 50 m (a detection or strip width of 25 m) and a length of

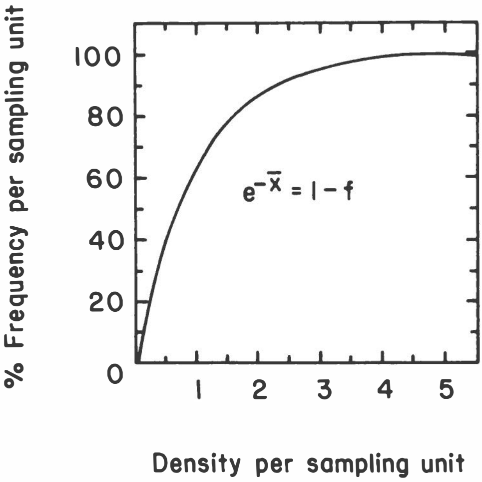


FIGURE 4-7 Nonlinear relationship between frequency of sightings and density in plots that are one-half the average home range of the species studied. From Caughley, 1977.

1,000 m gave an area one-half the average home range of these monkeys, or 0.05 km^2. Groups were sighted with a frequency (f) of 10 sightings per 18 transects, or $f = 0.55$. The proportion of transects with no troops was $(1 - f) = 0.45$. A table of exponentials was used to find the value of $-\bar{x}$ for $1 - f$ of 0.45—0.8 group per plot. By multiplying by the mean group size (10) and converting the density estimate for the 0.05-km^2 plot to whole numbers (20 plots/km^2), the density was estimated to $0.8 \times 10 \times 20 = 160$ howlers/km^2. This density estimate was higher than that determined from direct counts of groups or individuals. Note that the standard deviation, s, approximates the mean in Table 4-5, indicating that the data set follows a Poisson rather than a normal distribution.

The density estimates calculated by the plot method for 1973 were also higher than the overall estimate of 95 howlers/km^2 during this year (crude densities) for the entire island. This is expected because the above transect was made in the central part of the island, which supported the highest number of howlers, and may be considered an estimate of the ecological density (see discussion, Chapter 8).

This method was studied further in Venezuela and was found to generate density estimates comparable with those estimated from detailed studies (Eisenberg, 1979).

QUADRAT CENSUSES

This method involves covering a predefined area (the quadrat) and counting all the groups within that area at one time. It is most applicable to open habitats and areas with natural boundaries, such as islands and forest patches where the animals are necessarily confined. This method has seldom been used in censusing forest primates. Janson and Terborgh (in press) have used a method termed "synchronous sightings," which is essentially a combination of the line transect and quadrat methods.

Two or preferably more observers start at a baseline and each follows different equidistant and parallel transects through the quadrat. To ensure maximum coverage in a forest habitat, it would seem that observers should walk in parallel at about 100-to 150-m intervals, or at smaller intervals when censusing inconspicuous species. When groups are encountered the same data are recorded as in line transects. The data are combined by plotting all sightings on a common map and then trying to distinguish different groups. This will allow an estimate of the total number of groups present in the predefined area, which in turn allows an estimate of density. This method was used in censusing forest populations of rhesus monkeys in northern India (Southwick *et al.*, 1961).

In addition to requiring several observers, transects, and reasonable maps of the study area, this method requires some knowledge of the characteristics of each species. For instance, in order to distinguish between groups and to avoid duplicate counting, one should have some idea of the distance over which social groups of the different species can be spread and their rate of travel. A widely spaced group may be considered two groups by two observers if they see opposite edges of the group, even though the distance between them may be more than 100 m. A fast-moving group counted by one observer may be counted again, if another observer happens to see it later. The crucial factors are the time elapsed between the sightings and knowledge of how fast the species can travel.

A major deficiency of this method is that it fails to resolve the problem of individuals or groups living partly in the sample quadrat and partly outside it. (This causes no difficulty where quad-

TABLE 4-5 Use of the Nonlinear Density Plot Method to Estimate the Density of *Alouatta palliata* in Panama[a]

	Conditions: Transect length = 1 km; transect width = 50 m		
Plot Number	Animal Counts	Group Counts	Frequency of Plots with Sightings
1	7	2	1
2	3	1	1
3	0	0	0
4	0	0	0
5	3	1	1
6	4	1	1
7	2	1	1
8	0	0	0
9	3	1	1
10	0	0	0
11	0	0	0
12	5	1	1
13	0	0	0
14	4	1	1
15	0	0	0
16	5	1	1
17	3	1	1
18	0	0	0
Total number of animals per 0.90 km^2	39	11	10
Mean number of animals per 0.05 km^2	2.167	0.611	—
s	±2.256	±0.608	—
Estimated density of animals per km^2	43	122	160

[a] Data from J. F. Eisenberg (1974, unpublished).

rats consist of distinct forest patches.) It is also probably inadequate for relatively cryptic species (Janson and Terborgh, in press).

Modification of the block or quadrat sampling method may be used for both small and large census areas. Figure 4-8 shows the process of dividing the census area, which may be a province, state, or country, into convenient sample units. Next, representa-

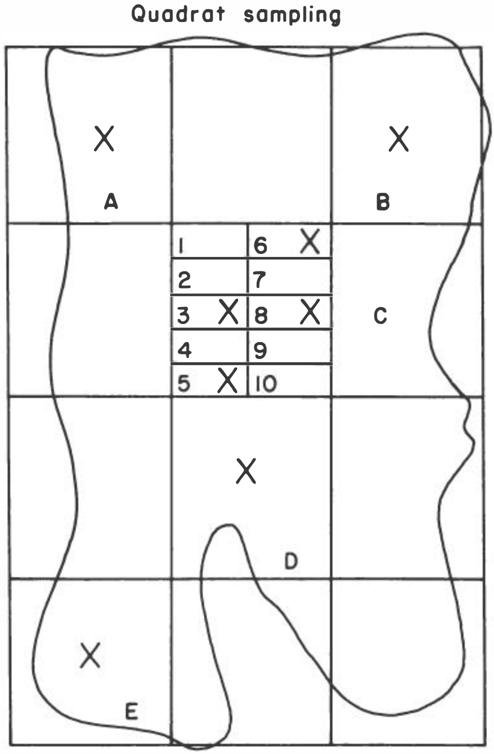


FIGURE 4-8 Quadrat sampling. Grids are drawn on maps of very large areas to subdivide the areas into quadrats until the sample quadrats represent about 15% of the study area. Each choice of quadrat is made randomly. In the illustration, four quadrats (e.g., Nos. 3, 5, 6, 8) are chosen randomly in each of the five sampling units, A–E, giving a total of 20 quadrats to be surveyed in detail.

tive sample units are selected randomly. Five sample quadrats (A–E) are shown in the example. Within each sample unit, subunits are selected on a random basis (e.g., Nos. 3, 5, 6, 8). One tries to choose a sample space equal to about 15% of the total area surveyed. In this figure, the sampling space consists of 4 of 10 randomly chosen subunits in each of the 5 sample quadrats. All potential monkey habitats contained in those subunits are censused. Calculations for population estimates using the quadrat method are shown in Table 4-6.

SPECIALIZED CENSUS METHODS

FIXED-POINT COUNT

In this method the observer remains at one point and records all primate groups seen or heard. It seems best suited for large, conspicuous, diurnal primates that give loud calls at predictable times of the day. Few primate studies have used this method (e.g., Chivers, 1969, 1974; Green, 1978a; Pollock, 1975). Unless the terrain is very steep and the lookout point is well positioned,

TABLE 4-6 Estimates of Population Based on a Random Sample of Four Quadrats as Illustrated in Figure 4-8

Variable											Total
Quadrat number	1	2	3	4	5	6	7	8	9	10	10
Sample quadrats			3		5	6		8			4
Number of groups/sample quadrat			14		9	10		9			42
Number of animals			140		90	99		91			420

Mean number of groups/subunit or sample quadrat $= \frac{42 \text{ groups}}{4 \text{ quadrats}} = 10.5$ groups

Estimated number of groups in 10-quadrat sample grid = 10.5 groups × 10 quadrats
= 105 groups

Estimated population = 105 groups × 10 animals/group
= 1,050 animals

this method has limited use for enumerating primates by sight alone. Counting the number of sources of loud calls assumes that each source represents a social group and that all groups call. Until further refinements have been made in this method, it is best used to determine relative abundance only, rather than to extrapolate estimates of absolute density.

TRAP, MARK, AND RELEASE

Mark-recapture techniques have been used extensively in population studies of small mammals (particularly rodents), birds, and fish (see Overton, 1971, and Caughley, 1977, for review of analytical methods). In such studies, one makes use of the proportion of marked-to-unmarked individuals in a series of catches in order to determine population size and density. This method is often inappropriate for estimating primate densities, particularly for arboreal species, because it can be harmful to the animals, time-consuming, and expensive.

Although several studies of primates have involved capturing by means of traps and immobilizing darts, marking, and releasing (e.g., Brockelman and Kobayashi, 1971; Dawson, 1977; Fogden, 1974; Neyman, 1977; Scott *et al.*, 1976a), this method has not been used to estimate densities. In studies of nocturnal or otherwise secretive species (e.g., Charles-Dominique, 1977; Thorington *et al.*, 1976), censusing by direct observation may be inadequate. In such cases, marking in combination with radio tracking may be the only way of estimating densities and home range size. Methods for marking such species are included in Chapter 5.

Small primates, such as marmosets, may actually be live-trapped and marked with a suitable tag. Other primates, such as howler monkeys (Thorington *et al.*, 1979), have been successfully darted and marked for long-term studies. When marking individuals for easy visual recognition, one can conduct censuses that give an estimate of the population density. Suppose you have marked 30 monkeys, and after a week you conduct a transect census through the same forest. During the transect you count 110 monkeys of the species under study and of these, 25 are marked.

The "Lincoln Index" is used to determine a rough estimate of the population size:

$$\frac{\text{No. marked animals seen}}{\text{Total no. animals seen}} = \frac{\text{Total no. marked animals}}{\text{Total population of animals}}$$

$$\frac{25}{110} = \frac{30}{X}$$

$$X = 132$$

The above calculation assumes that the 30 marked animals are from randomly selected groups. If, for example, all 30 animals were from one large primate troop, the application of the index would be invalid. The Lincoln Index was developed for species that are not grouped into large groups of mixed-sexed adults, but instead tend to have single individuals uniformly distributed in space. Thus, the application of the method assumes that you have selected animals randomly from within the area that you wish to census.

The method assumes that there is no loss of marked animals from the survey area and no immigration of unmarked animals into the survey area; that the means of marking is permanent; and that there is no differential observability between marked and unmarked animals. These conditions are not often met in practice (Caughley, 1977).

NEST COUNTS

Few primates build nests and only four species build nests large enough to be readily counted: gorillas, orangutans, and two species of chimpanzees. Several studies have used nest counts to estimate population densities of great apes (Ghiglieri, 1979; Kano, 1972; MacKinnon, 1974a; Schaller, 1961, 1963; Yoshiba, 1964). The field method consists of counting the nests in a predefined area, usually a transect of known length and fixed width. The total number of nests divided by the area searched gives nest density. However, in order to extrapolate primate density, it is necessary to refine the formula to take into account the age of the nests and the fact that some animals do not make nests (e.g., infants). Observer efficiency is also an important factor and can be estimated by recounting nests along segments of the transect soon after the original census (Ghiglieri, 1979).

In his study of chimpanzees in the Kibale Forest, Uganda, Ghiglieri (1979) derived the following formula: No. nest-building animals/km^2 = no. nests/area sampled in km^2 × 1/mean nest life span × 1/observer efficiency × total no. animals/total no. nest builders (excluding infants). The last factor depends on having some detailed information on the population age structure based on a detailed study of at least a portion of the study population. This formula can be further refined by computing a weighted mean nest life span that takes into account differences in nest life span. Life spans differ according to the kinds of trees or other vegetation in which the nests are built.

According to Ghiglieri (1979), in order to gain a representative sample of chimpanzee nest density for an area of 4–5 km^2 it was necessary to enumerate at least 9 km of transect that was 20 m wide. Furthermore, since the chimpanzees' use of certain parts of the forest was extremely variable and often at very irregular time intervals, Ghiglieri recommended that each transect be sampled at intervals of 4–6 months. The main advantage of the nest-enumeration technique is that it allows a single observer to collect in 3 or 4 days a sample that will give a fairly reliable index of animal density. Prior knowledge of nest life span and other factors mentioned above are necessary for greatest accuracy.

LONG-TERM MONITORING OF SPECIFIC GROUPS

This method is the most accurate for determining densities; however, it is also the most time-consuming. It requires an extensive network or grid of trails, detailed maps of the study area, and numerous observations and counts of specific social groups, preferably for several days of each month for at least 1 year. One usually has time to study only one group intensively, but in order to ensure greater accuracy it is advisable to follow one or two others. Each group must be individually recognizable.

How long must one observe a group before it can be confidently stated that the home range is known? This, of course, will depend on the species and the habitat. Species with large home ranges will usually take a longer time to cover their whole range than those with smaller ranges. Therefore, in order to determine sample size, one must monitor the data as the study progresses. Monthly samples (to cover seasonality) of 5–10 days with 10–12 h of observation for each day are recommended. One plots on a map at regular time intervals the location of the group (or preferably individuals in the group). By dividing the map of the study area into a grid of 0.25-ha quadrats, one is able to calculate the accumulation of new quadrats for each sample and to plot a cumulative range curve against study time (Figure 4-9). As the study progresses, the group will continue to enter new quadrats until the curve begins to level off. When a plateau or asymptote is reached, one can be fairly confident that the entire home range is known. In extremely seasonal habitats, however, one might anticipate a cumulative area curve consisting of several steps (e.g., Altmann and Altmann, 1970, Figure 37). Because a long step might be confused with an asymptote, caution should be taken in such situations.

Figure 4-9 clearly shows major interspecific differences within the same study plot. A group of 15 mangabeys at the Kanyawara study site in the Kibale Forest had an enourmous home range—some 400 ha. After more than 1,200 h of observation during 12 mo of study, the group was still entering new areas with no sign of approaching an asymptote. In contrast, the smaller redtail monkey, living in the same area in groups of 35 members, visited its entire home range of some 28 ha after about 370 h of observation during 10 monthly samples spread over a 12-mo period. Fifty percent of its range was visited within the first 63 h of observation. Waser (1976) emphasizes that the shape of the cumulative area curve is influenced by the choice of the quadrat size: the larger the quadrat, the sooner the leveling off of the curve.

To estimate densities it is critical to know not only the home range of the study group, but also the extent to which other con-

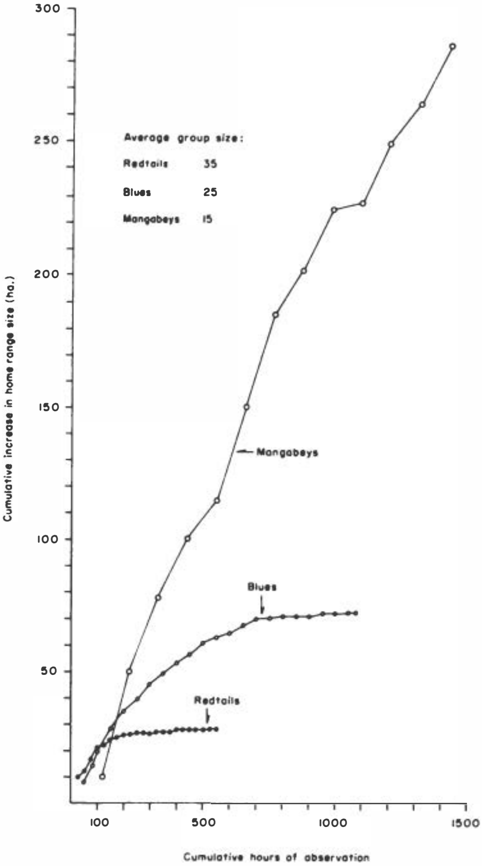
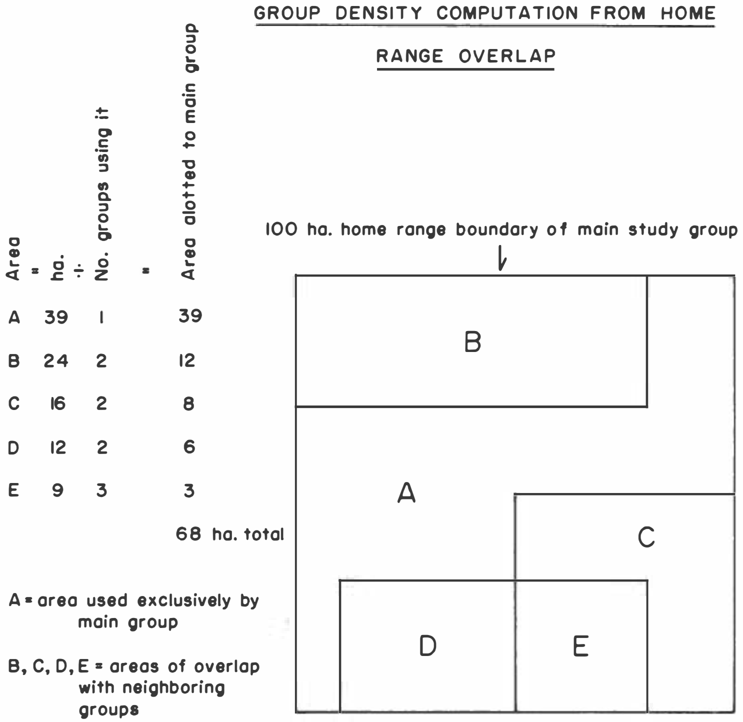


FIGURE 4-9 Cumulative increase in home range size as function of hours of observation. Each curve is for one social group. These three species are omnivorous. The home range of the mangabey group of 15 completely overlapped that of the blue (24 individuals) and redtail (35 individuals) groups, and the range of the blue group overlapped the redtail group. Home range increase was plotted in increments of 0.25-ha quadrats. Data are from compartment 30 of the Kibale Forest, Uganda. Data from Rudran, 1978; T. T. Struhsaker, unpublished; Waser, 1976.

specific groups share this home range. Parts of the home range used by more than one group must be apportioned according to the number of groups using them (Janson and Terborgh, in press). For example, if two groups share an area of 24 ha, each group is allocated half, or 12 ha. The group density per km^2 can be obtained by dividing 100 by the average home range of the groups in hectares (1 km^2 = 100 ha). This calculation gives a density of 8.3 groups/km^2. If three groups use this same 24 ha, then each is apportioned a third, or 8 ha (100 ha/km^2/12 ha/group), giving a density of 12.5 groups/km^2.

In reality, however, the situation is generally more complex. Usually the home range of the main study group is only partly shared, and the home ranges of neighboring groups are incompletely known. One can make a crude estimate of overlap by plotting the limits of incursion of these groups into the range of the main study group. In the schematic diagram in Figure 4-10, the main study group has a home range of 100 ha. Area A of 39 ha is not shared with any other group and is apportioned entirely to the main group. In areas B, C, and D, there is overlap with one other group per area. This area of overlap, totaling 52 ha, is therefore divided in half, giving a total of 26 ha to the main group. In area E, consisting of 9 ha, there is overlap between the main group and two other groups. Thus, the area is divided by 3 to give 3 ha to the main group. Summing these figures gives a total of 68 ha (39 + 26 + 3) to the main group, or a density of 1.47 groups/km^2. Partitioning areas of overlap between groups provides a more accurate estimate of density than the estimate of 1 group/km^2 obtained if overlap between neighboring groups is not taken into account.

Although this method involves an investment in time that is considerably greater than that required by any of the others described, the results are far more accurate and the kinds of additional data on the status of the population that can be collected are much greater. The most accurate counts of group size and composition are usually made during these studies. These counts are, of course, imperative for extrapolation from estimates of group density to estimates of numerical density, while composition of age and sex classes gives an indication of the status of the population in terms of fecundity and survivorship.



Area	= ha.	÷ No. groups using it	= Area alotted to main group
A	39	1	39
B	24	2	12
C	16	2	8
D	12	2	6
E	9	3	3
			68 ha. total

FIGURE 4-10 Group density computation from home range overlap.

SUMMARY OF IMPORTANT CENSUS METHODS FOR DIURNAL PRIMATES

When time to cover large areas is limited and replication of censuses along the same route is not plausible, emphasis should be placed on obtaining indices of relative abundance of social groups. These indices are usually expressed as numbers of groups seen per kilometer of transect and per hour of searching. Some indication of visibility, such as distance between the first animal seen and the transect or observer (or both), permits more realistic comparison of data between sites and habitats.

If time allows, many replications should be made along the same line transects throughout the year. Determination of sample size is outlined above. Comparative data from the Kibale Forest, Uganda, demonstrate that the method of *maximum reliable sighting distance* gives results most consistent with detailed, long-term studies of specific groups, especially for species of high density that are frequently seen. In order to verify this conclusion, however, there is clearly a great need for more case studies comparing these various methods with detailed group studies of a variety of species in different habitats.

The most accurate method of estimating primate densities is the detailed study of specific groups. It is also the method that gives the best data on group size and age/sex composition.

EXTRAPOLATION OF DENSITY ESTIMATES FROM CENSUS AREA TO OTHER AREAS

After determining estimates of density from the more accurate methods of repeated line transects and detailed studies, one would like to be able to extrapolate densities in similar habitats. This would permit population estimates to be made for areas much larger than the one studied. Unfortunately, such extrapolation has many shortcomings.

Within the same gross habitat type or even within the same forest, one can find large differences in primate densities. An example is provided by two study sites in the Kibale Forest, Uganda. These sites, which we will call *A* and *B*, differ significantly in primate densities although they are only about 10 km apart in the same continuous forest. At site *A*, blue monkeys are nearly 7 times more abundant than at site *B*; and at site *B*, mangabeys are about 1.5 times more abundant than at site *A* (T. T. Struhsaker, personal communication). Baboons were encountered on 10 occasions during 24 censuses at one site, but were not seen in any of the 44 censuses at the other site. Although the two sites differ in some of the predominant tree species, both are classified as medium-altitude tropical evergreen forests. This is usually the gross level of habitat classification that one must deal with when extrapolating densities from a small study area to a district or an entire country.

Even within the same small study area, one can find striking differences in primate densities. For example, at the Kanyawara study site in the Kibale Forest, within a linear distance of 2 km and in an area of 3 km^2, the density of black and white colobus ranges from 1.3 to 11.6 groups/km^2 (Oates, 1977, 1978; Struhsaker and Leland, 1979). Although the reason for this difference is not understood, subtle habitat differences linked to nutritional requirements may be involved (Oates, 1978).

When the forest is fragmented into relatively small blocks, such as in East Africa, northern Colombia, and India, differences in primate communities and densities of particular species between these forest patches can be very great. Even in large blocks of continuous forest, such as in La Macarena National Park in Colombia, one finds large differences in primate densities from one part of the forest to another (Klein and Klein, 1976; Struhsaker, 1974).

What this means in terms of estimating populations over large areas is that many study sites must be established to cover a wide variety of habitat types and separate habitat blocks. At present, there is no short and simple solution. Because those attempting to manage primates for conservation or utilization are eager to have the figures that best suit their purposes, it is important that any density estimate be as accurate as possible. Census methods, especially data analysis, still need much more study to improve their accuracy and general applicability. Extrapolation can be a dangerous guess.

5

Techniques for Aging and Sexing Primates

The amount of information that must be known about the individuals of a population depends on the questions being posed. Simple distributional or density estimates, for example, can omit information concerning the age and sex of the animals. If we wish to ascertain whether a species has a monogamous or polygamous social organization, distinctions between adults and nonadults and between adult males and adult females will suffice. But if we seek to understand the dynamics of population growth and patterns of mortality and natality, as in life-history analyses, knowledge of the age and sex of all individuals in a large population sample is indispensable.

Knowing a few easy-to-recognize "key" animals is useful for identification of a group for which most members are not identified. The greater the number identified, the better—because identifying a large number of individuals reduces the chances of counting the same individuals twice in a population census. Knowing the individual identities of animals is necessary for detailed studies involving individual life-history records; genealogical relationships among individuals in a group or population; and detailed behavioral, ecological, and genetic analyses. Methods for identifying and aging large numbers of primates individually from natural markings were developed by W. Dittus while studying a population of toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka. These methods, which have been refined over a period of 12 yr, are offered in this chapter in the hope that others may find them useful. The artificial marking techniques developed by R. W. Thorington and others are offered for use with those species and in those studies for which identification by natural markings is not feasible.

Primate species vary greatly in the ease, or difficulty, with which the age, sex, and identity of individuals can be ascertained. Difficulties arise because of cryptic genitalia, invariable individual morphologies, small body size, and nocturnal habits. Among forest-dwelling primates there is the added problem of restricted observability, especially among arboreal primates dwelling in tall, dense rain forests. In areas where primates are hunted, the investigator may have difficulty in getting close enough to his subjects to observe them, and habituation of the animals to the observer may be impossible or vary tedious and time-consuming.

The ease and reliability with which information concerning the age, sex, and identity of individuals can be obtained under natural conditions might affect the type of questions being posed and determination of the species and habitat to be studied. A pilot study to ascertain the feasibility of obtaining the information relevant to the research aims is a valuable investment, especially if these aims require data concerning the age and sex of a large sample of animals, as in demographic analyses.

A survey of morphological traits that are useful for aging, sexing, and identifying individuals belonging to all species of primates is beyond the scope of this chapter. Indeed, establishing a key for aging wild primates is impossible because accurate age data for most species under natural conditions are lacking. Instead, the aim of this chapter is to establish a methodology that can be adapted to a wide variety of primates. The following discussion provides guidelines for sexing and aging primates by different methods and with different degrees of accuracy.

SEXING

Among most sexually dimorphic primates, fully grown adult males may be distinguished from females by their larger body size, fuller musculature, larger canine teeth, and larger jaws and muzzle. Species vary in the expression of other secondary sexual characters. Adult male baboons, *Papio* and *Theropithecus*, develop long, thick mantles of hair around the shoulders. Adult male howler monkeys, *Alouatta*, have an enlarged hyoid and thick neck that may be accentuated by a beard. Adult male mandrils, *Mandrillus sphinx*, possess bright red and blue faces. Conspicuous colors of the testes or of the perineal skin may be found in adult males among several primates—for example, vervet monkeys, *Cercopithecus aethiops*; mandrills and drills, *M. sphinx* and *M. leucophaeus*; and gray langurs, *Presbytis entellus*. Adult females of chimpanzees, *Pan*, baboons, and many macaques periodically exhibit large, red tumescent swellings of the perineum. The color and degree of swelling vary with the monthly reproductive cycle. Adult females of many macaques have red faces. In some species of gibbons, *Hylobates*, sexual dimorphism is expressed by marked differences in fur color, and this may vary geographically (Fooden, 1969). Failing such conspicuous sex differences, the adult females in many primates are distinguishable by their elongate teats, which in males are undeveloped. Genitalia may be deceptive. The female spider monkey possesses a long, pendulous clitoris that is longer and more conspicuous than the male's penis.

Although size differences by sex in adults generally favor the male, the importance of assigning sex on the basis of genitalia rather than on size alone is underscored by the fact that the adult female may be slightly larger than the adult male in marmosets, *Callitrichidae*, and the black gibbon, *Hylobates concolor* (Ralls, 1976).

Distinguishing sex among infants and juveniles is difficult in some species because the genitalia or secondary sexual characters are insufficiently developed to be seen. Even congeneric species may differ in this regard; the genitalia of juveniles may be seen in the red howler monkey, *Alouatta seniculus*, but not in the mantled howler monkey, *A. palliata* (Thorington *et al.*, 1979).

In the Old World monkeys, the separation of the ischial callosities may aid sex identification. In the toque macaque, for example, the callosities are separated in the female but fused in the male. The difference is most marked in adults.

ESTIMATING RELATIVE AGE CLASSES FOR CENSUSES

Because of the limited time available during broad surveys and many transect censuses, investigators have used the size-scaling methods of early primate field studies to develop general age classifications and have assigned estimated chronological ages to these size classes on the basis of information from known-aged captive animals. In this method each animal is scaled against the largest animal in the group, usually an adult male, and is categorized as an adult, juvenile, or infant. Figure 5-1 illustrates the scaling technique for the arboreal howler monkey. With increased habituation, and thus improved visibility of the animals, investigators have subdivided relative-size classes into as many as eight classes, including adult males, adult females, subadult males, two or three juvenile classes, and often two infant classes.

Body proportions change dramatically with growth. As the head becomes relatively smaller and the hind limbs, especially the thighs, relatively larger, the weight moves posteriorly, changing the center of gravity and the locomotor and postural capacities of the animal. The thighs of climbing species are smaller than those of running species, and the tails, especially prehensile ones, are larger. Both of these differences can be seen in contrasting the howlers with baboons and macaques. Grand (in press) described the changes in body proportions between infant and adult male rhesus macaques, and these are diagramed in Figure 5-2. Changes in the mass of body regions are more significant than those in their lengths. During growth, the head in relation to body weight decreases rapidly, from 26% in the newborn infant to 12% at 10–15 mo to 8% in the adult female and 6% in the adult male. The transformation for howlers between the head of the newborn (20%) and that of the adult male (8%) is less extreme than that for macaques, but the change in proportion of the tail (10%–5.5%) is more extreme. An appreciation of the de-

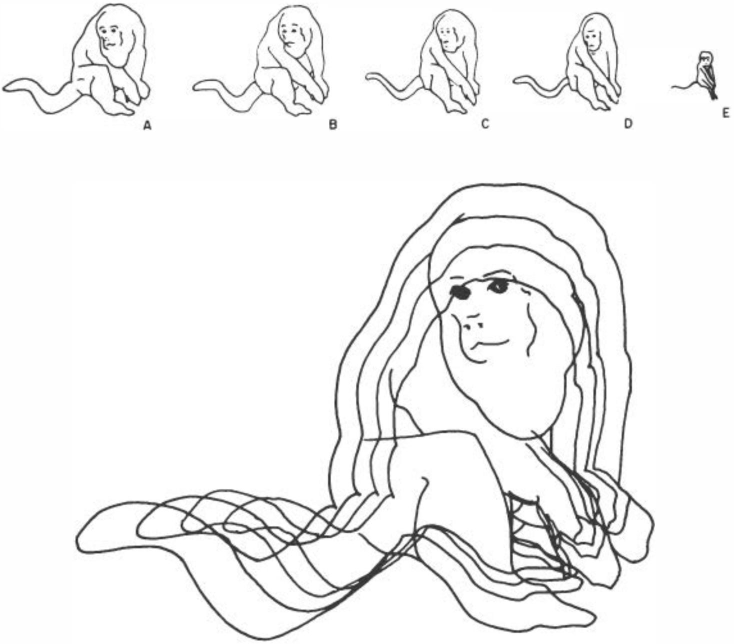


FIGURE 5-1 Age and sex classes of howler monkeys. *Top*: A = adult male, B = adult female, C = subadult, D = juvenile, E = infant. *Bottom*: Size classes are superimposed on each other as a first step in scaling animals for estimating relative ages. Greater refinement is achieved by considering changes in body proportions.

tails of these changes in body proportions over and above changes in stature greatly facilitates the aging and recognition of individual animals. Commonly recognized classes are characterized below.

ADULTS

Adults are fully grown and reproductively mature. In males, adulthood is indicated by the full development of the genitalia and of the secondary sexual characters. Usually they are larger than those of adult females. As a practical starting point, adult females have given birth to at least one infant and often may be

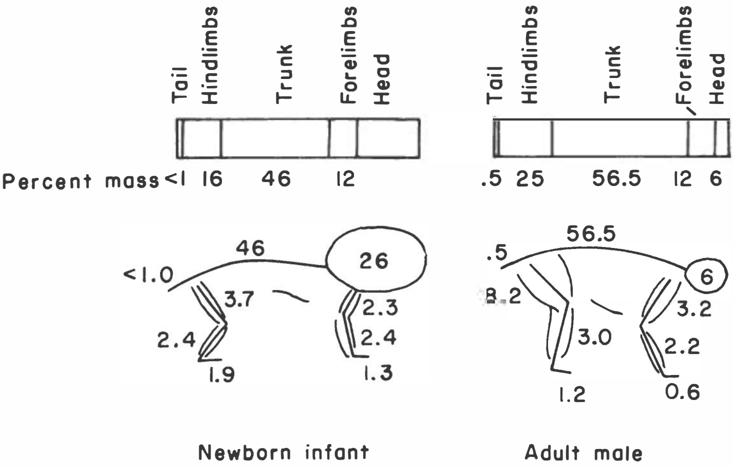


FIGURE 5-2 Changes in body proportions with age in macaques.

seen carrying one (see p. 89). They are distinguishable from large nulliparous juvenile females by their teats (but see comment on p. 95). In the latter the nipples are small and unprotruding as in males, whereas in adult females they are elongated and often pendulous as a consequence of having been suckled.

SUBADULT MALES

Subadult males are separately identified among sexually dimorphic species in which the adult males are larger than the adult females. They are intermediate in size between large juvenile males (or adult females) and adult males, and their secondary sexual characters are incompletely developed.

A few primatologists (e.g., Neville, 1972) working with howler monkeys, *Alouatta seniculus*, also recognize a subadult female class. These are juvenile females that have started to develop but have not yet achieved the body size and genital configuration typical of adult females. Most workers classify such females as juveniles and restrict use of the term "subadult" to males between the size of adult females and adult males.

JUVENILES

Juveniles are young animals that are usually weaned and not carried by the mother but are not yet reproductively mature. The upper size limit for juveniles corresponds to that of the average adult female, the lower limit to that of the largest infants. Several juveniles of varying sizes and ages usually occur in any social group. It has been common in field studies to recognize several classes with each class encompassing a range of sizes that is distinct from other such classes. Thus, small juveniles are known as "juveniles-1" and juveniles of the next larger size range are known as "juveniles-2" (see Figure 5-3 and Table 5-1). Generally not more than three juvenile size classes have been distinguished.

INFANTS

Infants are the smallest and youngest animals in a group. They are not yet weaned and are carried by the mother at least part of the time. The individual carrying an infant is not always its mother. For example, in tamarins, *Callitrichidae,* and squirrel monkeys, *Saimiri*, the fathers and other group members may carry infants; and in some colobines, juvenile females and adult

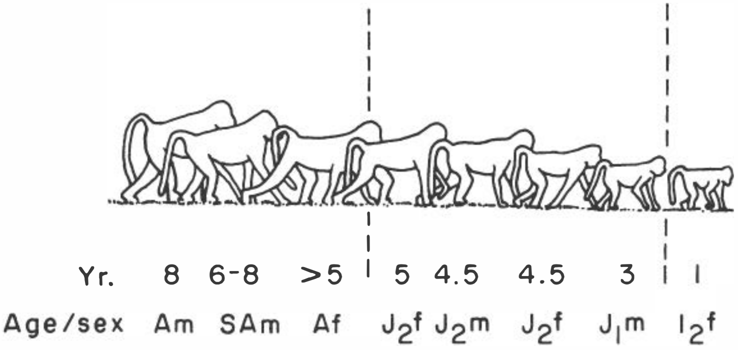


FIGURE 5-3 Age and sex classes of baboons. Diagram of baboons traveling on the ground helps to scale identified, known-aged individuals. Table 5-1 supplements the figure. Redrawn from Altmann and Altmann (1970) and personal communication (1979).

females other than the mothers may carry infants. In many primates the youngest infants are set apart from older animals by skin color or fur color (or both). The youngest infants are sometimes referred to as "infants-1," and those that have undergone a color change but are still being nursed and carried by their mothers are referred to as "infants-2." These color changes are illustrated in Figure 5-3 and Table 5-1 for baboons.

DIRECT MEASUREMENT OF CHRONOLOGICAL AGE

The most accurate measurement of age is direct, and the most convenient unit for measuring age is the year. The year is also a biologically meaningful unit of measurement for age because primates in most habitats are subject to seasonal environmental changes that directly influence seasonal variations in their food

TABLE 5-1 Physical Characteristics of Amboseli Baboons

		Estimates of Ages (years)[a]	
Class	Physical Characteristics	1963–1971	1979
Infant-1	Hair completely or partially black (natal coat). Black spots in tail and shoulders remain longest. Skin pink or red from skin vascularity; ears and nose retain pink longest.	0–1/2	0–2/3
Infant-2	Hair brown to cream-colored, often lighter (in Amboseli) than that of adults. Skin pigmented black, as in adults, except for pink scrotum.	1/2–1	2/3–2
Juvenile-1	Not sharply demarcated from previous class. Light hair retained. Face wrinkles disappear. Scrotum changes from pink to gray at 3–4 yr of age.	1–2	2–4

TABLE 5-1 (*continued*)

		Estimates of Ages (years)[a]	
Class	**Physical Characteristics**	**1963–1971**	**1979**
Juvenile-2	Not sharply demarcated from previous class. Hair often darker, as in adult. Males' testes descend at 5½–6 yr of age.	2–4	4–5 for females 4–6 for males
Adult female	Sexually mature; sexual skin swells periodically. Nipples buttonlike when nulliparous; elongated in more mature, multiparous females. First pregnancy at about 6 yr of age; full size reached at about 7 yr of age.	Over 4	Over 5
Subadult male	Development of secondary sexual characters: mantle, long canine teeth, large size, greater musculature than females. Scrotum (testes) larger than Juvenile-2. White streaks on muzzle. Canine ridges.	4–6	6–8
Adult male	Secondary sexual characteristics fully developed.	Over 6	Over 8

[a] Age estimates were revised as a result of increased field experience (see p. 95).
Source: Altmann and Altmann (1970) and personal communication (1979).

supply, reproductive and hormonal states, behavior, and survival.

Direct measurement of chronological age requires the identification of individuals at birth and the tracing of their identity through time. Since newborn infants may have few traits that set them apart as individuals, the identity of the mother is useful. By the age of weaning, the infant may have developed some of its own distinguishing features.

Although direct measurement of age is costly in human effort and time, it is valuable, if not essential, in any serious study dealing with life history or demographic processes. Ideally, one would like to assess the ages of all individuals in a population to the nearest year. Such accuracy is not always possible and may not be necessary. For example, if identified animals of known chronological age are first used to establish morphological criteria that correlate with age, then morphology might be used in turn to estimate indirectly the chronological age of animals whose birth days are unknown.

INDIRECT MEASUREMENT OF CHRONOLOGICAL AGE

Estimating chronological age from established morphological criteria is a compromise between relative and direct measurements of age and serves to establish chronological ages between and within relative age classes. Several changes take place in various parts of the body as individuals grow. If these changes occur in a regular sequence and show a high correlation with chronological age, they may be used as a basis for estimating age. Once the criteria for such estimates are established for a species, aging may be done without the long-term investment required by direct aging.

Among the criteria used for estimating ages in primates are changes in the number and sequence of erupted teeth, tooth wear, eye lens weight, allometric dimensions and weights of organs and skeletal segments, skin color, fur color, and body size (Gavan, 1953, 1971; Gavan and Hutchinson, 1973; Reed, 1973; Rosenthal, 1968; Stahl *et al.*, 1968; Wagenen and Catchpole, 1956). For the field worker who does not capture his subjects, the number and type of criteria are restricted to those external morphological traits that can be seen with the aid of binoculars. Examples include changes in the color of the skin and fur, size of the body or parts of the body, and the development of genitals and secondary sexual characters. Many observable morphological traits change gradually with age and are not useful for aging. Therefore, as an initial step in aging wild primates, one tries to find distinct morphological discontinuities or age markers that correlate well with a specific age. One such marker is the transition from the typically natal pelage to the adult skin and fur colors at 2–5 mo of age in many Old World primates. Other markers are the onset of reproduction, especially in females, and the end point of physical growth. Anchoring such events to the correct age requires an initial direct measurement through long-term observation.

Some of the physical characteristics that help define age and sex classes for a particular species are illustrated in Figure 5-3, which relates to baboons. Table 5-1, which supplements Figure 5-3, gives an idea of the continuing process by which age estimates are refined during field studies. During more than a decade of studying Amboseli baboons, Altmann and Altmann (1970 and personal communication, 1979) have been able to replace estimates that correspond only roughly to chronological age with improved estimates based on individuals of known ages within their study populations.

A method for obtaining weights of macaques under field conditions has been used by W. P. J. Dittus to augment observational techniques for estimating growth. This technique makes it possible to obtain more precise data on the growth of some species, thereby enabling an investigator to examine more closely the responses of individuals to variations with age and the food supply. By suspending a scale from a branch and placing food in a tray that is attached to the scale, it is possible to attract macaques to sit on the tray and so to weigh them. Weights can be read, with the aid of binoculars, from several meters away.

ESTIMATING CHRONOLOGICAL AGES OF INFANTS

In species in which changes from a natal pelage and skin color to an adult type occur, these changes can be used to age infants. The following morphological correlates of age are abstracted from a key that was drawn up for the toque macaque (W. P. J. Dittus, unpublished data). They illustrate the type of information that may be used for aging.

Day of Birth

Skin is pink and wrinkled. Natal coat is fine and uniformly dark brown. Eyes are open but squinted. Umbilical cord is attached; thick and flexible.

Day 2–3

Umbilical cord is generally thin, dry, and stiff or sometimes missing by the second day. By the third, it is usually missing, the eyes are wide open and alert, and the skin is less wrinkled and pink.

Week 1–3

Very slight melanin starts to occur on dorsal surfaces of hands, feet, and forelimbs during first week. By the third week, these areas are noticeably light gray. Otherwise the skin is white, but ears may flush in hot weather.

Week 5

Light gray melanin begins to appear at outer edges of pinnae.

Week 9–10

Gray hair follicles begin to appear on the bare white forehead as two small patches to the left and right of the midline. This is the beginning of the pretoque (see p. 111).

Month 4–5

Dorsal surface of hands and feet changes to black and acquires fur as in adults. Pretoque hair patches fuse across the midline and with the toque hair on the crown of the head. Adult-type pelage prevails.

Month 9–12

Pinnae are fully or almost fully pigmented black.

In the toque macaque, changes in the texture and color of the natal coat are variable between 2 and 5 mo of age and therefore are not very useful for aging within this age range. Useful age markers concern the onset of melanin deposits and the growth of hair on naked areas.

The transition from natal coat to adult pelage is variable also in the yellow baboon, *Papio cynocephalus*, and the deposition of dark pignent in the skin is correlated better with age. The following changes occur in infant yellow baboons (Altmann *et al.*, 1977).

At Birth

Skin is pink.

7 Mo

All infants have gray hands and feet, primarily gray paracollosal skin, a little gray pigmentation on a primarily pink muzzle, and pink ears.

12–15 Mo

Skin pigmentation is complete except for males' scrota, which remain pink until about the fourth year of life.

Most primate field studies are now of sufficient duration that similar keys might be established for infants of many species.

"Infancy" can be variously defined—the definition depending on purpose. In life-history studies the ability to identify infants about 1 yr old is useful. The size and morphology of 1-yr-old infants might be taken as the criteria defining the transition from infant to juvenile states.

ESTIMATING CHRONOLOGICAL AGES OF JUVENILES

The problem of aging juveniles is to assign chronological ages to a gradient of body sizes between 1-yr-old infants and adult females. Age estimates are aided if we know the duration of the juvenile phase (or the age at which it ends), the variation in body size or growth rate with age, and the factors that affect variations in growth. These topics, although interrelated, will be discussed in turn.

Duration of Juvenile Phase in Wild Populations

The onset of reproduction in females is thought of as marking the end of the juvenile phase, but "onset of reproduction" has been variously defined. It has been defined as the onset of menarchy or puberty, the time of first conception, the time of first pregnancy, and the time of first birth. The ages differ for these events. Under field conditions the time of first birth is the most practical because it is an obvious event that can be dated. It can also be anticipated because pregnant females in late term are usually conspicuous. If the period of gestation is known, the time of first conception can be estimated.

The duration of the female juvenile phase will generally be set by the age at which reproduction begins. In some cases a female may attain full growth but be infertile. This will be an exceptional event and can only be determined by long-term monitoring. The relationship between age and the onset of reproduction is worth closer examination. Human studies (Frisch and Revelle, 1970) suggested that menarchy occurs over a range of ages and heights but at attainment of an invariable critical body weight. Peng *et al*. (1973) found that the female Taiwan macaque, *Macaca cylcopsis*, cannot conceive unless she achieves a critical body weight in excess of 4 kg, and semen cannot be obtained from male Taiwan macaques weighing less than 5 kg. Similar critical body weights have been established for female (5 kg) and male (6 kg) rhesus *M. mulatta*; for female (6.5 kg) and male (5–8 kg) Japanese macaques, *M. fuscata* (Mori, 1979); and for male (4.3 kg) cynomolgus macaques, *M. fascicularis* (Hartman, 1932; Valeric *et al*., 1971, quoted in Peng *et al*., 1973). Female howler monkeys, *Alouatta caraya*, weighing less than 4 kg did not conceive, and Gilbert and Gillman (1960) provide evidence from the chacma baboon, *Papio ursinus*, that is consistent with the finding in other primates and human beings that females below a critical weight do not conceive. The typically heavier species have higher critical weights for conception.

If critical weight needs to be attained in order to reproduce, then any factor that may affect the rate of growth, such as food supply or social behavior, should influence the age at onset of reproduction or the duration of the juvenile phase. For example, under extreme food shortage, the physical growth of female Japanese macaques was delayed and their average age at first birth increased from 6.2 to 6.8 yr, some not experiencing first birth until the age of 9 yr (Mori, 1979).

Lacking long-term field data, primatologists have based their field estimates of age and of onset of reproduction on data from captive animals. However, captive primates usually receive liberal rations of well-balanced nutritious diets that maximize rates of growth and maturation. In nature, growth rates might be expected to be less because of variations in the availability of food. Indeed, newborn rhesus monkeys whose mothers were caught in the wild weighed 14–19% less than those whose mothers were raised in the laboratory (Valerio *et al.*, 1970). Recent long-term field studies in which the development of individuals was traced from birth to adulthood indicate that growth rate is slower than it was thought to be and that age at onset of reproduction is higher. For example, in his study of wild bonnet macaques, *Macaca radiata*, Simonds (1965) estimated the age of first birth in wild females to be the same as the age that had been established from studies of captive macaques: 3.5–4.5 yr. However, long-term field data for the slightly smaller toque macaque have shown that wild females of this closely related species do not experience their first birth until they are 5.5–6.5 yr old (Dittus, 1975, and unpublished data). Similarly, wild female baboons experience their first birth when about 6.5 yr old (Altmann *et al.*, 1977), which is 2 yr later than the corresponding age of those raised in captivity. In light of these long-term field records, Dittus (1975) and Altmann *et al.* (1977) advanced their original estimates of age among juveniles.

Thus, currently published estimates of age at onset of adulthood in wild primates are probably considerably underestimated, particularly among the *Cercopithecinae,* if they are based on extrapolations of age from captive primates rather than on observations of individuals in the field from birth to adulthood. Exceptions to this might be the published estimates of age for *Colobinae* or others that are difficult to raise in captivity.

Variations in the age at which the first birth in females occurs in a population may lead to uncertainty in determining age. To circumvent this difficulty, one may wish to distinguish between reproducing (primiparous and multiparous) females and those

TABLE 5-2 Weights and Sitting Heights of Captive Rhesus Macaques, *Macaca mulatta*, at Different Ages[a]

	Males		Females	
Age Range (yr)	Mean Weight (kg) ± SD	Mean Sitting Height (cm) ± SD	Mean Weight (kg) ± SD	Mean Sitting Height (cm) ± SD
0.00-0.03	0.48 ± 0.05	19.3 ± 1.0	0.44 ± 0.06	19.2 ± 0.9
0.46-0.54	1.50 ± 0.1	30.9 ± 1.1	1.30 ± 0.15	29.1 ± 1.3
0.96-1.04	2.20 ± 0.2	35.8 ± 1.4	1.90 ± 0.2	34.3 ± 1.7
1.46-1.59	3.00 ± 0.5	39.6 ± 1.6	2.50 ± 0.2	37.5 ± 1.1
1.92-2.08	3.50 ± 0.6	41.8 ± 2.1	2.90 ± 0.2	40.1 ± 1.1
2.92-3.17	5.10 ± 1.1	47.1 ± 3.0	4.20 ± 0.4	44.6 ± 1.3
3.83-4.17	7.40 ± 1.4	52.1 ± 3.2	5.20 ± 0.8	47.2 ± 1.3
4.83-5.17	9.70 ± 1.5	55.7 ± 2.5	5.70 ± 0.6	48.3 ± 1.7

[a] Data from Gavan and Hutchinson, 1973.

that are of the same age as the reproducing ones, but which are still nulliparous.

Habitat, Social Rank, and Season of Birth as Factors in Growth Differences

If body size is used to estimate chronological age, it is helpful to known how well age and body size correlate. Gavan and Hutchinson (1973) provide some of the best data for such an assessment in their study of growth rates in rhesus macaques, *Macaca mulatta*, raised under controlled colony conditions. Using animals of known ages, they measured the number of erupted teeth, the weight, and the sitting height (crown-to-rump length). A condensed version of some of their data is given in Table 5-2. Using such data, Gavan and Hutchinson arrived at several regression equations for estimating age. Following are examples of equations in which weight (W) is given in kg and sitting height (H) in cm:

$$\begin{aligned} \text{For males:}\quad & \text{Age} = 0.537 \times (W - 0.108) \\ & \text{Age} = (0.337 \times W) + [0.058 \times (H - 1.628)] \\ \text{For females:}\quad & \text{Age} = 0.921 \times (W - 0.646) \\ & \text{Age} = (1.021 \times W) + [0.021 \times (H - 0.152)] \end{aligned}$$

Testing these equations on a group of rhesus monkeys whose ages were known, the authors found their equations to have a maximum deviation of ±0.4 yr. But this degree of accuracy is valid only for rhesus raised under ideal conditions. In wild populations, growth rates are slower, but how do they vary?

Wild toque macaques, *Macaca sinica*, living in good habitats weigh more than those living in marginal habitats, and socially high-ranking animals, which enjoy priority of access to resources, grow faster than low-ranking ones (W. P. J. Dittus, unpublished data). Whether such relations exist among other wild primates is unknown, but it is likely that habitat quality and social rank cause greater variation in growth in any wild, food-limited population (where such exist) than in captive animals that have access to a superabundant and invariable food supply. One would also expect year-to-year variations in the natural food supply to accentuate or diminish size differences among growing animals born in different years. Primates subject to high year-to-year fluctuations in their food supply would be most affected.

The traditional method of assigning ages to size classes assumes a fairly close relationship between body size and age. In light of the above, such methods might be scrutinized.

Assigning ages to size classes is justified, however, where discontinuities in size distribution are apparent and are the result of a birth pulse. A well-defined birth season is one in which births in a population are fairly well synchronized, so that most individuals of a given birth season are fairly close in body size and may be recognized as belonging to a distinct age class or cohort. However, owing to the cumulative effects of differences in growth rates between individuals, these class distinctions become less demarcated with increasing age. The effects of a birth pulse are most useful, therefore, in distinguishing the 1-yr-old juveniles from the newly born infants and from the juveniles 2 yr old or older.

A breakdown of larger juveniles into distinct age classes presupposes an intimate knowledge of size differences by age. Given such knowledge of an average-sized juvenile of age "X," one might assume that in a large census sample the numbers of individuals wrongly underestimated and overestimated in age for any one age class would cancel one another. Such errors, however, will only partly cancel one another as illustrated by the following example.

Assume that the "true" age distribution in a hypothetical population is like that in row 1 of Table 5-3. Assume further that 75% in each age class are estimated correctly (row 3) but that there is uncertainty as to the correct age for the 25% remaining individuals in each age class (row 2). The latter do, however, definitely belong either to the age class under consideration or to one of the immediately adjoining age classes. If ages are assigned to the uncertain-aged individuals without bias into the age class in question or into one of the two adjoining classes, the numbers of uncertainly aged individuals are distributed evenly among adjoining classes as in rows 4–7. These "best-guess" age distributions (rows 4–7) are added to the known (row 3) to arrive at a final estimate of age distributions (row 8). The percentage of error be-

TABLE 5-3 Effect of Faulty Estimation of Ages and of Mutual Cancellation of Errors on Estimates of Age-Class Frequencies

		Number of Animals in a Hypothetical Population, by Age Classes (A, B, C, D)			
	Row Number	A	B	C	D
True age distribution	1	104	84	36	8
25% age uncertain	2	26	21	9	2
75% age correct	3	78	63	27	6
Number of individuals of uncertain age are assigned equally among adjoining age classes	4 (26 ÷ 2)	13	13		
	5 (21 ÷ 3)	7	7	7	
	6 (9 ÷ 3)		3	3	3
	7 (2 ÷ 2)			1	1
Estimated age distribution (sum of row 3 and rows 4–7)	8	98	86	38	10
% of error	9	6	2	6	25

tween the estimated (row 8) and true (row 1) age distributions is given in row 9.

Although errors in aging are generally reduced for each age class by adjustments such as those illustrated in Table 5-3, it is evident that errors do not wholly cancel one another. The error is greatest in age classes with low frequencies.

One way to reduce such errors is to combine two or more age classes and define the age limits of this combined class according to reliable age indicators. For example, in real census data, "young juveniles" might be readily distinguished as a distinct class as a result of a birth pulse and might be aged 1–2 yr old. "Old juveniles" might be those larger than "young juveniles" but smaller than adults; they would be 2–6 yr old.

Sex as a Factor in Growth Differences

Infant and juvenile males grow faster than their female peers among several primates studied in captivity—for example, rhesus

Macaca mulatta (Table 5-2), barbary macaques, *M. sylvana* (Roberts, 1978), squirrel monkeys, *Saimiri sciureus* (Kaak *et al.*, 1979)—and in the wild population of toque macaques, *M. sinica* (Dittus, 1977a). Species differ in the degree of sexual dimorphism in size. If growth rates by sex under natural conditions are unknown, an attempt to adjust age classifications on the basis of sex differences in growth may assume a degree of accuracy in age determination that under field conditions is unjustified. Among infants and young juveniles especially, growth differences by sex are slight, and the task of making accurate estimates is made more difficult by size differences resulting from differences in date of birth relative to peers of the same birth season or cohort. That is, infants born early in the birth season will be larger than those born late, although both are classified as belonging to the same age class (e.g., 0–1 yr old). Among older juveniles, adjustment of age classification according to growth differences by sex may be justified if the effects of sex on growth are consistent and can be distinguished from other effects, such as social rank, and if the growth differences by sex are great enough to influence age estimates within the size-age categories chosen. For example, the error in age classification owing to growth differences by sex will be greater if fine distinctions in age are attempted than if several size-age classes are combined into one class spanning several sizes or years.

Since growth differences by sex are cumulative, they will have their greatest effect among the oldest juveniles; therefore, they may need to be considered when establishing criteria for the upper limits of the juvenile period in males. In females, this is marked by the first birth and poses no problem. For demographic analyses, one wishes to identify males that are of the same age as the females at first birth.

Primiparous females often continue to grow for another year or so after their first birth until they reach full adult female size. In species where juvenile males grow faster than their female peers, a male the size of an average adult female may be fairly close in age to a smaller primipara at the time of her first birth. The degree of correspondence in these relationships needs to be established empirically for each species.

Since first birth seems to occur at a constant critical weight, the sizes of primipara may vary less than the sizes of the average adult females. Hence, the size of a primiparous female may be an easier anchor for aging males of the same size.

The age at which events such as first birth occur may vary according to the environmental conditions or according to whether the population is changing in size or is stable (Dittus, 1977a, 1980). Therefore, in using transitional stages such as first birth as indicators of age, one should be sure that the correlation between *stage* and *age* is established separately for each population under study.

Traits other than body size can be used to supplement such age estimates. For example, during the later stages of the juvenile phase, the genitalia begin to change. Altmann *et al.* (1977) report that among yellow baboons, *Papio cynocephalus*, the scrotum of juvenile males turns from pink to gray at 3–4 yr of age.

ESTIMATING CHRONOLOGICAL AGES OF SUBADULT MALES

The criteria defining the upper limit of the juvenile male phase also define the lower limit of the subadult male phase. Examples of morphological changes in males of known ages are provided from the two primates for which such data are available from wild populations.

Male toque macaques, *Macaca sinica*, by 5.5–6 yr of age are about the same size as multiparous adult females, and the canine teeth have erupted beyond the level of the incisors and molars. By the seventh year, the males are larger than adult females, and the testes have descended but are small. Males in their seventh and eighth year may appear lean owing to rapid skeletal growth that appears to have stretched their spare flesh. Full canine development, adult male size, and musculature are reached at over 8 yr of age.

Male yellow baboons, *Papio cynocephalus*, are the size of adult females by 5 yr of age, are larger than all adult females by 6 yr, experience descent of the testes at 5.5–6 yr, and acquire full adult male development at over 10 yr of age (Altmann *et al.*, 1977).

In the toque macaque, the average weight of adult males is 5.35 kg, the standard deviation is 0.70 kg, and the range is 4.0–7.7 kg ($N = 38$ males weighed). Much variation in the body size of adult males may be true also of other primates. Therefore, definition of the criteria for the transition from subadult to adult male could be problematic. In the toque macaque, some males in their prime (judged to be 10–15 yr old) weigh more than the "average" male owing to their well-developed musculature. Criteria for the transition to adulthood in males therefore might be taken as the attainment of canine teeth and body frame sizes, but not necessarily of body mass, as in prime males.

AGING ADULT ANIMALS

The onset of adulthood in males and females has been described in earlier sections. The end point of adulthood is defined by longevity or maximum life span of a species under natural conditions. It has been assumed generally that primates and other animals maintained in captivity live longer than their wild counterparts. Although conditions in captivity may improve the probability that more animals will live to old age, it is questionable whether the chronological limits of longevity per se are advanced significantly in captivity. Long-term field studies of the toque macaque suggest that a few individuals live to be at least 30 yr old, a figure that agrees with longevity records of this species in captivity. Table 5-4 lists the longevity of several primates living in captivity.

Age differences among adult primates seem to be registered best in the appearance of the skin and teeth. Therefore, it is more difficult to discern ages under field conditions in those species that are heavily furred and have deeply pigmented facial and other skin, since these conditions either hide or obscure changes in the skin with age. The experience of the investigator seems to be of little help in aging difficult species. Drs. Stuart and Jeanne Altmann have studied yellow baboons over many years and emphasize their inability (and that of others) to discern age differences consistently among adult yellow baboons (personal communication).

Although toque macaques may be exceptionally well suited for the identification of age-specific characters, adults were assigned ages only after the investigator had accumulated 3 yr of field contact with the macaques. Following Dittus' (1974, 1975) description of characters that vary with age among adults, Hrdy (1977, Hrdy and Hrdy, 1976) attempted to classify adult gray langurs, *Presbytis entellus*, which are much more difficult to age than macaques. As observers increase their attention to the details of age changes in the skin, pelage, teeth, skeleton, and behavior of adults, it should become possible to distinguish ages among adults even in some of those species that have previously been thought to lack age-specific characters. This may be expected because morphological changes are cumulative. Old age especially is marked by its own changes, such as weight loss, stiffness or lameness, and infrequent activity—factors that can be recognized despite cryptic skin areas.

The nature of the changes associated with aging vary with the species. Several changes are described here to illustrate characters that were observed in toque macaques and can be seen by comparing the photographs in Figures 5-4 and 5-5. Gradual changes in the wrinkling and color of the skin become evident between youth and old age. The facial and body skin of young adult animals usually is taut and smooth with few or no blemishes, whereas the facial skin of very old animals may appear pitted and creased, especially around the eyes and mouth. A loss of skin tonus may cause the lower lid to droop and produce "bags" under the eyes. The edges of the upper lips may be creased and drawn inward, giving a typically "toothless" appearance. Many small creases and wrinkles appear in the skin of the chest and abdomen, and loose folds of skin appear at the juncture of the limbs and trunk and under the chin. In the Cercopithecinae, the empty cheek pouches may hang as large, loose folds of skin. Hanging teats and mammae and abdominal stretch folds may become prominent in old females.

The degree of erythrization of the facial skin in some females also intensifies with age. The pale or slightly flushed complexion of young adult females may be intensified by middle age or old age to bright red and may deepen to bluish red in very old age. However, some young adult females also have bright red faces (but more even), and some old females have pale faces (but not unblemished), so that color is not a sole index of age. The number and size of pigment spots and the prominence of facial hair, especially around the mouth, increase with age in both sexes. The number of scars and cuts in the ears accumulate with age, although by itself the amount of scarring is not a reliable index of age.

TABLE 5-4 Maximum Life Spans for Selected Primates Maintained in Captivity

Species	Common Name	Sex	Age at Death (years)	Reference
Prosimians				
Daubentonia madagascariensis	Aye-aye		23	Jones, 1968
Microcebus coquereli	Coqueral's mouse lemur		15	Jones, 1962
Tarsius syrichta	Philippine tarsier	♀	12	Ulmer, 1960
Galago sp.	Galago		14[a]	Bowden and Jones, 1979
Lemur macacao	Black lemur		27	Jones, 1962
Lemur mongoz	Mongoose lemur		25	Jones, 1962
New World Monkeys				
Callithrix jacchus	Common marmoset		12	Napier and Napier, 1967
Saguinus sp.	Tamarin		12[a]	Bowden and Jones, 1979
Aotus trivirgatus	Night or owl monkey		17[a]	Bowden and Jones, 1979
Chiropotes satanas	Black saki		15	Jones, 1962
Saimiri sciureus	Squirrel monkey	♀	21	Hume, 1957
Cebus sp.	Capuchin		43[a]	Bowden and Jones, 1979
Ateles geoffroyi	Black-handed spider monkey		18	Jones, 1962
Ateles paniscus	Black spider monkey		20	Crandall, 1964

Old World Monkeys				
Cercopithecus aethiops	Vervet or green monkey		28[a]	Bowden and Jones, 1979
Cercopithecus diana	Diana monkey		31	Napier and Napier, 1967
Papio hamadryas	Hamadryas baboon		29	Jones, 1962
Papio ursinus	Chacma baboon		45	Flower, 1931
Macaca fascicularis (*iris*)	Crab-eating macaque	♂	38	Dathe, 1971
Macaca fuscata	Japanese macaque		33[a]	Bowden and Jones, 1979
Macaca mulatta	Rhesus macaque	♀	33[a]	Bowden and Jones, 1979
Macaca nemestrina	Pigtailed macaque		33[a]	Bowden and Jones, 1979
Macaca sinica	Toque macaque	♂	30+	Hill, 1974
Macaca speciosa	Stumptailed macaque		33[a]	Bowden and Jones, 1979
Presbytis entellus	Grey langur		22	Rabb, 1960
Presbytis cristata	Lutong	♀	29	Anon., 1974
Colobus polykomos	King colobus	♂	27+	Hill, 1975
Apes				
Hylobates lar	White-handed gibbon	♂	31	Jones, 1962
Gorilla gorilla	Gorilla	♂	40	Cutler, 1975
Pan troglodytes	Chimpanzee	♂	49[a]	Bowden and Jones, 1979
Pongo pygmaeus	Orangutan	♂	50	Cutler, 1975

[a] Mean of five oldest animals reported.

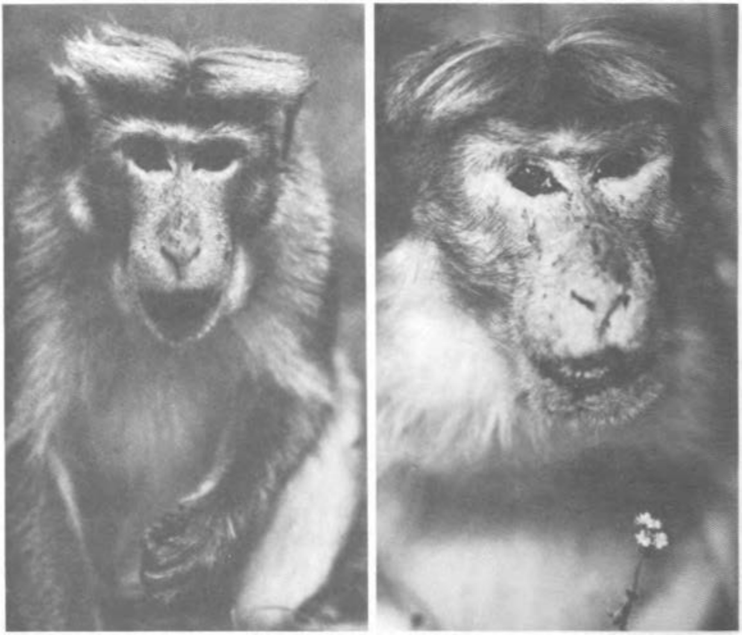


FIGURE 5-4 An adult male toque macaque, "Stumpy." *Left*, in December 1971 when middle-aged; *right*, in February 1980 when "senile." The number of red spots on the face has increased, and the facial skin has lost some of its tonus. Photograph courtesy of Wolfgang P. J. Dittus.

Changes in pelage are probably most evident in very old age. The pelage may become dull and without luster, and bald spots may appear, especially on the tail. Dunbar and Dunbar (1975) described changes in the length and color of the cape in adult male gelada baboons, *Theropithecus gelada*, that may be useful for distinguishing ages among them.

With increasing age the teeth become worn and discolored through tartarization. The canine teeth of adult males are especially useful for gauging these changes. The canines of adult male toque macaques in their prime (judged to 10–15 yr old) are fully erupted, sharply pointed, and clean ivory colored. With increasing age the canines become less pointed, shorter, and more stained.

By old age the canines may be worn to the level of the incisors, and the teeth in general are worn and stained yellow-brown. These changes, like those of the skin, are graded and may be useful for judging ages intermediate between youth and old age.

Very old animals often experience a loss in weight and appear scrawny. Lameness, gnarled fingers, stiffness and swelling of the joints (apparent arthritis), and difficulty in locomotion collectively are signs of very old age. When stiff fingers or awkwardly mended joints or bones are seen in young animals, they appear to be the result of injuries rather than a general syndrome of stiffness.

In the toque macaque the voice changes from infancy to adulthood, and very old adults may have a characteristically low-pitched, raspy, or quavery voice. Waser (1978) describes a similar "old voice" in an old female mangabey, *Cercocebus albigena*.

A summary of morphological traits observed in very old animals of several species is given in Table 5-5. The most useful characters for assessing ages intermediate between young adult and very old adult are those that change gradually and progres-

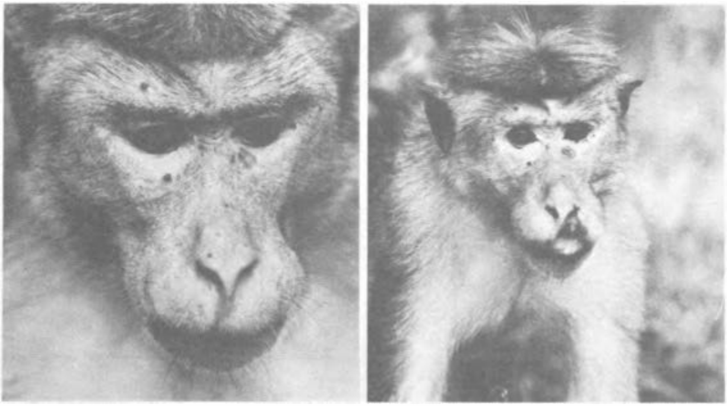


FIGURE 5-5 An adult male toque macaque, "Harris." *Left*, in December 1971 when middle-aged; *right*, in April 1975 after he had acquired a new cut on his upper lip. The red spot under the left eye has grown larger, and several new small red spots have appeared. Photograph courtesy of Wolfgang P. J. Dittus.

TABLE 5-5 Morphological and Behavioral Traits that are Typical of Old Age in Several Primates (X indicates that trait or change occurs.)

	Prosimians	New World Monkeys	Old World Monkeys						Apes		
Morphological and Behavioral Traits	Sifaka[a]	Capuchin[b]	Toque[c] Macaque	Rhesus Macaque[d]	Gelada[e] baboon	Chacma baboon[f]	Mangabey[g]	Gray langur[h]	Chimpanzee[i]	Orangutan[j]	Man[k]
Worn discolored teeth		X	X	X	X	X		X	X	X	X
Wrinkled and creased facial skin, loose "bags under the eyes"			X	X				X	X		
Hairy facial skin			X					X			X
Creased loose folds of body skin			X								X
Change in skin pigmentation			X	X	X						X
Change in pelage color and/or lustre	X	X	X	X	X	X			X		X

Hair loss, or bare patches of skin	X	X	X	X	X		X	X	X	X	X
Change in timbre of voice			X				X				X
Loss of weight, scrawniness	X	X	X	X	X			X	X		X
Accumulation of scars and injuries	X		X	X			X	X	X		X
Stiffness, or difficulty in locomotion		X	X	X				X			X
Lethargic or inactive			X				X				X

[a] Sifaka *Propithecus verreauxi* (Jolly, 1966).
[b] White-fronted capuchin *Cebus albifrons* (W. P. J. Dittus, personal observation).
[c] Toque macaque *Macaca sinica* (Dittus, 1974, 1975; W. P. J. Dittus, personal observation).
[d] Rhesus macaque *Macaca mulatta* (Wagenen, 1972; Southwick *et al.*, 1965).
[e] Gelada baboon *Theropithecus gelada* (Dunbar and Dunbar, 1975).
[f] Chacma baboon *Papio ursinus* (Saayman, 1970).
[g] Mangabey *Cercocebus albegina* (Waser, 1978).
[h] Gray langur *Presbytis entellus* (W. P. J. Dittus, personal observation; Hrdy, 1979).
[i] Chimpanzee *Pan troglodytes* (van Lawick-Goodall, 1971).
[j] Orangutan *Pongo pygmaeus* (MacKinnon, 1974a).
[k] Man (W. P. J. Dittus, personal observation).

sively with age—for example, the skin and the teeth. Although it is difficult to quantify these changes with age, they are very similar to those that occur in adult human beings.

It has been useful in the toque macaque to establish five adult age classes: young, young to middle aged, middle aged, old, and very old (or senile). Adult animals are assigned to one of the adult age classes based on the investigator's subjective appraisal of the animal's overall morphology or set of age traits as outlined above. As a rough approximation of the chronological ages that might correspond to each of the adult age classes, the following procedure is adopted. The "Young Adult Female" class is assigned a duration of 5 yr from the sixth to the tenth year of life inclusively (slightly revised since Dittus, 1975). The "Subadult Male" class (sixth and seventh years) plus the "Young Adult Male" class (eighth to tenth years) together span the same 5 yr as the "Young Adult Female." The remaining 20 adult years (eleventh to thirtieth years) are divided equally among the remaining four adult age classes for each sex, each class thus spanning 5 yr.

IDENTIFYING INDIVIDUAL PRIMATES BY NATURAL MARKINGS

Free-living primates can be identified individually if they possess recognizable natural or artificial markings that distinguish them from other individuals. Natural markings are discussed below. A discussion of artificial marking techniques begins on page 117.

Distinguishing individuals by their natural markings is by far the most common method used by field primatologists. Its success depends on the existence of morphological variations among the individuals in the population under study, on the experience and perseverance of the investigator in learning to recognize and record individual differences, and on good observation conditions.

The following guidelines for the establishment of keys for identifying individuals were developed from the study of toque macaques, *Macaca sinica*, at Polonnaruwa, where observation conditions are good and where 500 toque macaques have been individually identified by their natural markings. About 60 animals are added and lost annually. Each monkey is observed at least once a month as part of a regular census schedule. The guidelines are suggested as a general approach to the problem of identification and may have merit when applied to other species.

SELECTING AND DESCRIBING INDIVIDUALISTIC TRAITS

The most important aid to identification is knowing the kinds of differences to look for. A morphological trait that is to be useful for distinguishing individuals should have the following properties:

- Variable between individuals.
- Constant through time or changing slowly enough to permit a record of the change.
- Visible under normal working conditions.
- Recognizable by other investigators.

Some of the obvious traits that meet these criteria are sex, body size, missing limbs, healed scars, and presence or absence and size of canine teeth. Traits that are least useful for identification are those that change seasonally with the reproductive condition (e.g., color or size of perineal swellings in female baboons and some macaques) and those that change rapidly with maturation (e.g., color of pelage or skin among infants or the body size of subadult males).

The first task in identification therefore is the selection and compilation of a list of reliable "key traits." Such a list may include pelage color (among juveniles and adults); color of skin (face or other areas); length and configuration of head hair or mane; and distribution of pigment in ears, face, or elsewhere. The second task is to determine the extent of variation in the traits. The third is to devise a standard vocabulary for describing the variations in each of the key traits.

The following abridged list is an example from the toque macaque:

Pelage

The pelage (exclusive of the head hair) is described at two levels: first, the basic or overall coat color of light, medium, or dark brown; second, the tint or hue of the basic color. Thus, medium or dark brown furs can be tinted either orange, gray, or simply brown. Light-brown furs are more variable and may be tinted orange, golden, yellow, sandy beige, agouti, or gray. In addition to color the pelage varies in distribution of color and in luster.

Head Hair

Toque macaques and their closest relatives, the bonnet macaques, *Macaca radiata*, possess a whorl of hair that radiates symmetrically outward from a central spot on top of the crown. In the toque macaque, three growths of hair (toque, pretoque, and overtoque) interrelate to form very variable "hairdos," which may require lengthy though standardized description. The toque, which varies in color and especially in structure, is the most characteristic trait for some individuals, and it is useful for distinguishing young animals over 6 mo old.

Face Color

The face color of adult females can be described as follows: pale skin color, slight pink flush, light red, medium red, deep red, and deep red to slightly purple. The distribution of the color varies. The facial skin color of adult males and of juveniles of either sex may be pale, typical medium tones, beige, slightly flushed, or grayish. The lower lip may be unmelanized or melanized according to certain patterns.

Ears

The skin at the juncture of the pinnae and the head and also the tragus may be melanized totally or partially black, in varying patterns. Pigment patterns of juveniles change gradually.

Dermal Pigment

The skin on the ventral or inside surfaces of the body and upper limbs is sparsely haired so that the light-blue pigmented skin can be seen. In many animals the "ventrum" is entirely and evenly pigmented; in others, white depigmented areas occur. The configurations of these white patches are evident a few days after birth and remain constant (allowing for allometric growth) through life. These ventral patches therefore are extremely useful for distinguishing infants and juveniles that may otherwise appear similar.

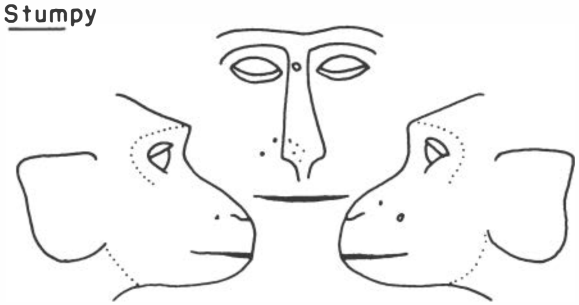
In addition to these traits and their variations, adult individuals especially vary in the number, size, and distribution of black, gray, brown, and red spots on the face. To some extent, the time of their appearance and their size are age related (spots become more numerous and larger with age), but the locations remain fixed for life. Adults are also frequently scarred.

RECORDING INDIVIDUAL IDENTIFICATIONS

Having recognized the nature and extent of morphological variation, one must decide how to record traits systematically in such a way that identification data are easily and quickly recorded, updated, and referred to under field conditions.

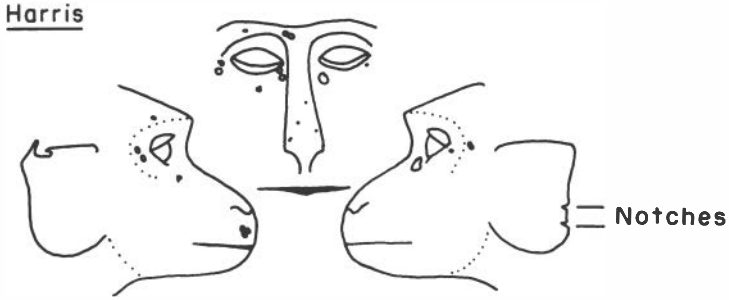
Contrary to what one might expect, photography is not the most useful tool, chiefly because of difficulties in obtaining close-up photographs of small subjects (e.g., monkey heads) from various angles or profiles. In addition, one must contend with poor or varying lighting conditions in the forest, moving animals, delays in film development time, and the sensitivity of film to outdoor tropical conditions. Photography is thus reduced to a supplemental method of recording.

The preferred procedure is to observe the animals with binoculars, to write descriptions of the animals (and prepare drawings) while the observer is still in the field, and to record the descriptions on identification cards. (See Appendix C and Figure 5-6.) Morphological traits that are not easily and quickly drawn are described. Such traits include pelage, toque structure, ears, face color, ventrum, and "other," which may refer to crippling, scarring, odd behavioral traits, and gait. Characters that do not lend themselves to concise description are usually easiest to draw. These relate to the size, color, configuration, and distribution of spots or scars. In the toque macaque, such spots occur mainly on the face. Therefore, left and right profiles and a frontal view of a standardized macaque face are printed on one side of identifica-



a.

Troop: B Stumpy Dec. 15, 1971
Adult male: middle-aged
Pelage: mid-to-dark brown
Toque: round; slightly projects beyond sides of head
and to brows, thus hiding the pretoque
Face color: normal beige; lip pigment thick and even
Ears: both intact; tragus black
Tail is cut; distal quarter missing
Ventrum: light blue except for small white patches
in left and right groins



b.

Troop: B Harris Dec. 15, 1971
Adult male: middle-aged
Pelage: mid-brown, tinted slightly orange
Toque: round overtoque strands project beyond sides
of head; pretoque small and V-shaped
Face color: flesh color, lip pigment slight dip
Ears: both cut; left tragus black, right blotched
Ventrum: no white patches; all even light blue

FIGURE 5-6 Sample identification cards (3" × 5") for the adult males whose photographs are seen in Figures 5-4 and 5-5. Red blotches are shown as circles, which are larger than actual size. Dark freckles are shown as dots. The sketch appears on one side of a card, the description on the other.

tion cards. The spots and scars are drawn on the faces at or near easily recognizable reference points, such as nostrils, lips, and corners of the eyes.

Facial spots and scars, especially small ones, are frequently conveyed more clearly in a drawing than in a photograph. However, photographs provide a better representation of a monkey's overall appearance or gestalt. As the sum total of a monkey's appearance is memorized, its gestalt becomes more important to an experienced monkey observer, and progressively less reliance is placed on key identification traits. Identification cards are nevertheless indispensable as mnemonic props because in making them an observer is required to learn to recognize individuals. Reliance on photographs alone may lead to unjustified confidence in one's identification ability. A combination of identification cards and photographs may be desirable, especially at the beginning of a study, as a check on one's accuracy in description.

Additional information that can be written on the cards includes the date of the description or redescription, the individual's social group, its identification code (name or number), its sex, and date of birth or estimated age. For young animals the mother's code may also be useful. The convenience of identification cards lies in the ease with which they are prepared and stored, and in their accessibility and reproducibility. The major investment in time occurs early—in learning the most useful traits and how to consistently recognize and describe their variations.

With modification of key traits the card system has been applied to the study of gray langurs, *Presbytis entellus*, at Polonnaruwa. As in the toque macaque, individual differences register best in the pelage color, configuration of the head hair, and in pigment patterns of the exposed skin. Gray langurs have darkly pigmented facial and body skin. Individual differences are manifested in small depigmented or "white" blotches of varying size and configuration that occur especially in the groin and inner upper thighs. In addition, the skin immediately above and lateral to the ischial callosities may vary in extent, configuration, and color. Wrinkles, scars, and overall facial gestalt help to distinguish individuals despite their generally all-black faces.

Investigators working with other species or under less favorable observation conditions have relied on different traits. A characteristic that has provided a ready means for distinguishing individual capuchins, *Cebus capucinus*, has been forehead hair patterns. The patterns described by Oppenheimer (1969) during his study in Panama are illustrated in Figure 5-7.

In tall closed-canopy forests the observation of primates is more limited, but investigators working in such habitats have found there a range of natural markings for recognizing individuals. In some cases it has not been possible to identify individual markings for all ages, and investigators have used marker individuals, location, and group affiliation to identify in-

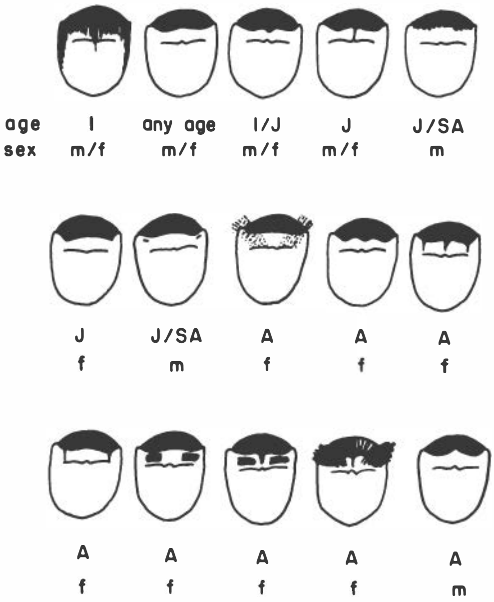


FIGURE 5-7 Forehead patterns of *Cebus capucinus*. The faces have been drawn to the same size without regard to age or sex class to emphasize the variability in hair patterns. Redrawn from Oppenheimer (1969). Symbols are: *I*, infant; *J*, juvenile; *SA*, subadult; *A*, adult; *m*, male; and *f*, female.

dividuals. The difficulties Struhsaker (1975) reported in identifying individual red colobus, *Colobus badius*, in Uganda are typical of those that have been faced by field workers in observing shy canopy primates. He reported:

> Among the red colobus, adult males were most easily distinguished as individuals. This was partly because they habituated faster and consequently, one could observe them for longer periods and thus pick out identifying marks. In addition, their appearance was more individualistic than that of the females. Invariably, I could pick out individual males on the basis of their facial and whisker characteristics. I did not need "natural" deformities such as ear notches or tail kinks to identify the males, because their faces all looked different. As an initial check on this means of identification I also kept notes on "natural" deformities. The most common natural mark was one or more stiff fingers. The digit number, combined with a notation of left versus right hand, provided a check against the identification based on facial appearance. Ear notches and tail kinks were notably absent from adult males, although some had tails that were 1/4 to 1/3 shorter than normal. In contrast, I found it quite difficult to identify adult females. For them I had to rely on tail kinks, whisker shape and extent of whisker development, and general tone of pelage coloration. Stiff fingers were not seen among the females, although some had pink tips on one or more digits.

IDENTIFYING INDIVIDUAL PRIMATES BY ARTIFICIAL MARKING TECHNIQUES

CAPTURING LIVE PRIMATES

Usually it is expensive and time-consuming to capture live primates. There is also a risk to the animal being captured. However, there are many benefits to an ecological study when animals are caught, so in each study the benefits, risks, and costs should be carefully considered before a capture program is initiated (Thorington, in press).

In using any technique for capturing primates, one should keep in mind the possibility of using decoy animals. A captured or tame primate will frequently attract others of the same species. A decoy can be placed in a separate compartment of a trap or in a cage where one wishes to dart or net animals. Since many primates are likely to be abusive toward a strange animal in the territory, it is important that a decoy be adequately protected. When used in a trap, decoys should be double-caged so they cannot be bitten.

Trapping

Trapping is the technique most commonly used for capturing primates (Dawson, 1977; Neyman, 1977). Many kinds of live traps are commercially available (e.g., Tomahawk Live Trap Co., Box 323, Tomahawk, Wisconsin 54487, USA), but in most tropical countries they can probably be made less expensively than they can be bought (Neyman, 1977). A cage with a guillotine door can easily be fitted with a tripping mechanism that will cause the door to fall when an animal takes the bait. Such traps are made and used in most parts of the world.

When several suitable live traps—big enough and strong enough—have been obtained, they should be placed where primates are seen high in the trees or on the ground, as appropriate. The trap should be "prebaited" with a suitable food. Prebaiting involves propping up the door of the trap so that it cannot be sprung, putting food in it, and thus using the trap as a feeding station. The objective is to accustom the animals to feeding there without concern. The advantage to the trapper is that he need not check the traps regularly at a time when the animals are most wary of them and least likely to be caught.

When the primates seem to be taking the bait the traps can be set. It is then important to check the traps regularly. Don't leave diurnal primates in the traps overnight or nocturnal primates during the day, and prevent them from being stressed by heat (especially in the sun), cold weather, or rain. You will probably catch other kinds of animals, like birds and rodents, in your traps. If released, many of these will not enter the traps again, but some may enter repeatedly and become expert at stealing the bait. These will need to be dealt with in other ways.

If the primates are social it may be possible to use a large trap to catch a whole troop or most members of one. Some persons have used a trap triggered by a string from a blind, in which case they could wait until several animals were in the trap before springing it.

Once the animals are in the trap the job is to get them out without traumatizing them or the investigator. It may be possible to chase small primates out of the trap into a cloth or string bag, but it is desirable to anesthetize larger primates before removing them from the trap. For this it may be necessary to have a stick with a syringe on the end, arranged so that the syringe injects the anesthetic when the animal is poked. Use a short needle and poke him in a nonvital area, like the muscles of the thigh or the back. The safest anesthetic for nonhuman primates seems to be Ketamine HCl (Domino, 1964; Martin, 1972). It is probable that 10 mg/kg is a safe dose or an underdose for all primates. For nervous animals it may be better to use a combination of Ketamine and Ace Promazine. Add enough Ace Promazine to the Ketamine bottle so that the animal will get 1 mg of Ace Promazine for every 9 mg of Ketamine.

Darting

Darting techniques are useful for capturing animals under many circumstances when trapping is difficult or impossible, such as trapping species that are trap-shy or spend most of their time high in the trees (Scott *et al.*, 1976a; Thorington, in press). These techniques are laborious, however, and there is more risk to the animal. A variety of darts and projecting weapons are available. Most commonly used are dartguns, blowguns, and crossbows. Dartguns are usually pumpguns or are powered by CO_2 cartridges. Generally, the CO_2 guns are preferable. A pumpgun must be pumped up between shots, which is a noisy and time-consuming procedure. If one misses his first shot, he cannot quickly and quietly take a second shot with a pumpgun.

To be accurate and effective a dartgun must fire straight; there must be an easy way to modify muzzle velocity so that one can shoot at animals at different distances; the darts must have dependable trajectories and must not tumble in flight; and the darts must not penetrate deeply but must discharge the anesthetic reliably. (Effective systems are sold by Pneu Dart, Inc., 406 Bridge Street, Williamsport, Pennsylvania 17701, USA, and by Telinject, Veterinärmedizinische Specialgeräte GmbH, Hohenzollernstrasse 92, D-6700 Ludwigshaffen am Rhein, Federal Republic of

Germany. Zoo veterinarians frequently have need of such equipment and may be able to advise you about its use.)

A blowgun is as good as the person using it. With practice, a person can become accurate and develop a good range. A blowgun is much quieter than a CO_2 gun. It must have the attributes named in the preceding paragraph. The critical factor is the dart, which must be very light. Darts can be made from tuberculin syringes with the plungers weighted so that they inject upon impact (Brockelman and Kobayashi, 1971; Dewey and Rudnick, 1973). Another kind of dart, which uses air pressure to inject the fluid, and a blowgun are also available from Telinject in Germany.

A crossbow can combine the accuracy and range of a CO_2 gun with the quietness of a blowgun. Most are a bit noisier than blowguns, however, and they do not allow one to modify the "muzzle velocity" easily when shooting at animals at different distances. With an increase in distance, one must unstring the bow, give the bowstring a few more twists, and restring it, but when darting distances are fairly constant, this would not be a problem. (Crossbows especially designed for capturing primates can be obtained from Mr. Thad Martin, Route 5, Box 65, Huntsville, Arkansas 72740, USA. They shoot tuberculin syringes on the end of short bolts. On impact, the momentum of the bolt pushes the plunger of the syringe, causing it to inject the anesthetic.)

The drug is a crucial part of the darting system. It should have a high ratio of lethal-to-effective dose. It must be concentrated enough to ensure that an effective dose will fit into a small dart. Sernylan, a phencyclidine, is such a drug, but it may be difficult to obtain. Ketamine is safer, but is is not so strong; two to four times as much fluid needs to be injected from the dart. These drugs do not work instantaneously, and the animal may flee the immediate area after it has been darted. If adequately dosed, however, the animal will stop in a minute or two. In many forest situations, one must follow the animal closely during this time or risk losing it.

When animals are darted in trees it is desirable to catch them, lest they injure themselves in the fall. A large animal is more likely to be injured in a fall than a small one—and the larger the animal, the harder the task of catching it. Two persons holding the corners of a blanket can catch a 10-kg monkey falling from a tall tree. If the forest floor is open so that persons can easily position themselves under the animal, a bigger "net" is desirable. If the understory is dense and positioning is difficult, a smaller net may be necessary. When the animal is being caught and while it is being maintained in captivity, it is important to follow humane practices.

Netting

Netting is one of many other techniques that has been used in capturing primates. It has been used successfully in capturing some of the smallest primates and some of the largest. Large terrestrial primates, like gorillas and chimpanzees, have been chased into lines of strong nets, where they have been physically overcome. This would appear to be hazardous for both the apes and the people involved.

At the small end, bird nets have been used to capture tarsiers (Fogden, 1974). Presumably, mist nets of appropriate size could be used to capture a variety of species of primates that regularly leap from one tree to another. It is probable that mist nets would be most effective for capturing small nocturnal primates, like tarsiers and bushbabies, but it is possible that they could be used effectively for animals like talapoins, squirrel monkeys, and marmosets.

MARKING LIVE PRIMATES

In some studies it is desirable to have animals individually marked so that they can be recognized from a distance or when they are recaptured. A variety of systems has been used, no one of which seems to be best in all circumstances (Thorington *et al.*, 1979). Investigators frequently use redundant identifications as a precaution against the loss of one of them.

If the animals do not need to be identified individually at a distance, they may be marked with ear notches, with ear tags, or with tattoos. If the animals do need to be identified at a distance, they may be marked by clipping and dyeing hair, using collars and freeze branding.

Ear Notches and Ear Tags

To make ear notches one needs only a pair of scissors. By notching the pinnae of the two ears in different ways one can make a variety of distinctly different patterns by which individuals can be recognized. Under some circumstances these notches will be distinguishable at a distance. The only problem with ear notches is that animals sometimes notch their own ears or their neighbors' in fights. Before deciding to use a system of ear notches, look at some of your animals and determine if there are many that already have notched ears from natural causes. If so, it is probably not a good system for that species.

Ear tags are easily applied and are unambiguous marks. They can frequently be seen at a distance, although the number itself cannot be read. The only problem is that animals will occasionally pull them out. Some investigators have reduced this problem by placing one ear tag in each ear on the theory that it would be unlikely for an animal to lose both tags. Ear tags can be used for individual recognition at a distance. The simplest system is to use several tags on each animal. A small number of individuals can be coded by the number of tags they have in each ear. Another system is to paint the ear tags. An enamel paint will last sometimes for several years, and while it does the individuals can be recognized by their color codes (Thorington *et al.*, 1979). Similarly, a small bit of plastic surveyor's tape may be looped through the tag, and the color of the tape may be used to distinguish individuals. For a species that is hard to sex in the field, a useful trick is to tag the right ear of one sex and the left ear of the other. In this way one can quickly ascertain the sex of individuals at a distance. (Monel self-piercing ear tags can be purchased from the Gey Band and Tag Co., P.O. Box 363, Norristown, Pennsylvania 19404, USA, or the National Band and Tag Co., 721 York Street, Newport, Kentucky 41071, USA.)

Tattoos

To tattoo an animal one must make small holes in the skin and rub a permanent ink into the holes. This can be done crudely with a needle and india ink. More desirably, one can obtain a tattoo kit for small animals, consisting of a set of small numbers and letters, a pair of applicator pliers, and some tattoo ink. (A small-animal tattoo kit is available from Nasco, 901 Janesville Avenue, Fort Atkinson, Wisconsin 53538, USA.) The numbers or letters desired are put in place in the applicator. One holds up a flap of the animal's skin, squeezes the skin between the jaws of the applicator, which makes the chosen pattern of perforations in the skin, and then rubs the ink into the holes. It is best to tattoo a relatively hairless place that is lightly pigmented. The skin under the arm or in the axila is frequently good. In macaques the chest or sternal area is often light in color and sporadically furred, making it ideal for tattooing. If the skin is light in color one can use a black tattoo ink. If it is dark one should use green or white ink.

Clipping and Dyeing Hair

For temporary marks that can be seen at a distance, one can simply cut the animal's hair in unusual patterns. Bands of hair can be shaved off the tail, for example, to provide a distinctive code, or patches of hair can be removed from other areas. One can also use hair dyes or bleaches. Nyanzol is a particularly good dye for this purpose. (It is available from Nyanza, Inc., 49 Blanchard Street, Lawrence, Massachusetts 01842, USA.) It is mixed with equal parts of hydrogen peroxide and water and painted on the animal to make dark patches in the hair (Fitzwater, 1943). Such dyes will last until the animal next molts its hair. It should not be overlooked that such dyes can therefore be used to determine when animals molt their hair in the wild.

Collars

For more permanent marking that can be distinguished at a distance, collars and freeze brands seem to be the most successful. Leather collars are suitable in some circumstances (Scott *et al.*, 1976a), but they should be held together with rivets rather than with stitching if they are to survive for long periods of time. Collars can also be made of ball chain. They can be cut to size easily, and they may survive better than leather collars on animals that have claws. Ball-chain collars made of nickel-coated brass will not last as long as ball-chain collars of stainless steel. Use the thickest gauge ball chain that seems reasonable for the size of the animal being studied if you wish to obtain a "maximum life span" for the collar. Collars should not be too tight around the neck, but they should not be so loose that an animal can get its forearm caught in the collar. Both kinds of collars can be coded for recognition of individuals. Round, numbered metal or plastic disks can be hung from the collar; the numbers should be large enough to be read with binoculars at a distance. Plastic disks can be color-coded. The ball-chain collars can have colored beads on them, arranged so that each animal has its own color pattern. If four beads are used one can usually see two adjacent ones easily; it is frequently difficult to see all four. Thus, it is best to use only one or two colors, alternating the colors when there are two. The animal can then be recognized whenever two adjacent beads are seen.

Freeze Branding

Freeze branding is accomplished by freezing the skin for a short period of time. This kills the melanocytes in the skin and causes the hair to subsequently grow in white. By freezing selectively one can give each animal a distinctive pattern of white patches—white bands on the tail, for example. When liquid nitrogen is available one can do the freezing with a piece of metal that has been cooled to the temperature of the liquid nitrogen. The metal should be attached to a wooden handle. Do not try to hold one end of the metal piece while freezing the other end. The metal may be cooled in a bath of dry ice in alcohol if liquid nitrogen is not available. Another way to freeze the skin is to use a spray of Freon (Lazarus and Rowe, 1975), frequently available in radio stores under the name of "Component Cooler." Be careful to spray only the desired area. It is usually best to use a mask over the area being sprayed so that only a small part of the animal is frozen. For thin-skinned, small primates, the skin freezes in about 10 s; for big, thick-skinned monkeys, it takes about 30 s. Freeze branding does not hurt at the time it is done, but it does hurt later. In the interest of animal welfare, use as little skin as possible in branding. Since freeze brands are not distinctive until the new hair grows in, it is best to combine this technique with a more temporary one, like cutting the hair distinctively or dyeing it.

TOOTH CASTS AND AGING

Tooth casts provide a permanent record of the teeth of the animals. They can be studied after the animals have been released, and they can be studied in greater detail than is possible in the live animal. From tooth casts one can estimate the ages of the animals, obtain dental measurements, and study dental anomalies and orthodontic problems. It is argued that asymmetries indicate stress (Siegel and Doyle, 1975a,b). Dental asymmetries can easily be studied on tooth casts and could be used to study nutritional stress during development. Discrete and metric variations of teeth have strong genetic components. Thus, tooth casts can be used to determine how closely related different troops or populations of animals are, and from them inferences can be made about the amount of genetic exchange between troops or populations (Froehlich and Thorington, in press).

To make tooth casts one needs plastic to make dental trays of the right size and shape, alginate for obtaining the molds, and dental stone to make the casts. Since these supplies are used by many dentists, they can be bought at any dental supply store or directly from dentists.

The dental trays must be shaped to the dental arcades of the animals being studied, but they must be slightly larger. The upper tray can extend straight across the rear molars, but the lower tray must be U-shaped so as to leave room for the tongue. If one has access to skulls of the species, one can pad the teeth with wet paper and then form the plastic over this before it hardens. Be sure to make the tray deep enough for the canines. If you do not have access to skulls, you will have to make your first casts without a permanent tray. Make temporary trays of cardboard, which you can shape to the animal you catch. When you have a cast of the teeth you can use it to make a permanent tray. If you are catching animals of different ages, you will need trays of different sizes. With heavy paper or cardboard you should be able to make a tray for any dental arcade you encounter. The trays should have holes in them so that the alginate will ooze through, thereby fixing the mold to the tray. The tray then serves to hold the flexible aliginate rigidly in the shape in which it sets.

To make a mold of the teeth, mix the alginate with water; you will probably find instructions on the container. Use a spatula for mixing, then transfer the alginate to the dental tray. Put the tray in the mouth of the animal, pressing the alginate firmly over the teeth. Hold it in place until the alginate sets, then carefully pop it loose from the teeth. Immediately examine the impression in the alginate. Be sure that you have good impressions of all the tooth crowns. Air bubbles in the alginate can obscure important details. If the animal's tongue is in the wrong place, a whole tooth row can be concealed. If the animal's teeth were not clean, you may have a beautiful impression of a leaf or of a piece of fruit, rather than what you are seeking. If you have a good impression, set the mold aside wrapped in damp paper or cloth until you have time to make the cast. If the mold dries, all is lost. It is better to keep it in water than to risk having it dry out.

The cast is made from the dental stone. Mix the powdered stone with water until it is a paste in consistency; follow the instructions on the box. Then carefully fill up the mold with it. You will find it easier to avoid air bubbles if you first immerse the mold in water, pull it out, and shake off the excess water before filling it with the dental stone. The dental stone will displace or mix with the water deep in the cusps, whereas it will not mix with air bubbles that get trapped in the cusps in the mold. Be sure to build up a good thickness of dental stone above the teeth, for this will be the base of the cast when you turn it out. If the base of the cast is weak, the cast will be easily broken. Let the dental stone set and dry, but you will have an easier time removing it from the mold if you do not allow the mold to dry. When the stone has set fairly hard, you can immerse the cast and the mold in water for an hour or two before removing the cast from the mold. If you separate them under water, you may be able to pour a second cast in the same mold. With practice you will be able to pull a cast from a mold without damaging either, even though there may be long canines to worry about. Have some glue available so that you can glue any broken canines back onto the cast right away. Be sure to number your cast as soon as possible, either by scratching the number into the base as the dental stone hardens, or by writing with india ink on the cast as soon as it hardens. Note the animal number and the date so that you will not confuse the cast with any you may make later of the same animal, if you recapture it.

New dental materials for tooth casts are becoming available. Molding compounds like silicone rubber provide a more detailed mold than does alginate. In fact, the detail provided by some is good enough for studies with the scanning electron microscope. These materials have the disadvantage of not mixing with water the way alginate does. Therefore, the teeth must be dry when the impression is obtained or the detail is lost. They have the advantage that the mold is permanent and will not dry out and lose its shape as alginate does. Therefore, one does not need to make the casts as quickly from the silicone mold as one must from the alginate mold. The casts may be made from dental stone with alginate molds, or for more detail the casts can be made with an epoxy plastic.

Because most dentists know and use these procedures, it is generally easy to get a demonstration of tooth-casting techniques. It is also relatively easy to obtain the necessary supplies in tropical countries as well as in Europe and North America. You will need the following materials or substitutes for them: plastic for dental trays (e.g., "Coe" tray plastic), alginate for the molds, dental stone for the casts, "flexibowls" for mixing alginate and dental stone, spatulas, a toothbrush, glue, and small plastic bags for keeping the molds damp before casting. (For epoxy casts one can obtain the molding material Xantopran from Unitek Corporation, 2724 South Peck Road, Monrovia, California 91016, USA.) A recommended epoxy for the casts is Ciba-Geigy Araldite Epoxy 6005 with hardener #956. It is desirable to store the molds in zip-lock plastic bags. For cleaning and drying the animal's teeth it is useful to have a small portable water-pick and canned Freon or dust-free air. In making the casts it is useful to have a vibrator to remove the bubbles from the epoxy.

6

Habitat Use

Mammals do not make uniform use of their habitats. They tend to be very selective of their times of activity and their spatial use of habitat. This selectivity is a very important aspect of their ecology, and thus it continues to be studied frequently. Little more than a watch, pencil, and notebook is needed. The basic paper on sampling methods is by Altmann (1974). Additional comments are given in Clutton-Brock (1977, Appendix 1).

TIME BUDGETS

Two techniques are commonly used in primate field studies. In one, called the focal animal technique, the investigator focuses on a single animal for extended periods. He records the activity of that animal for a period of time, then switches to another animal and records its activities for another period. The second technique is to scan the troop of primates at set intervals and record what each visible animal is doing at that time. This is the scan technique. In using either technique it is convenient to decide beforehand on the categories of activity to be recorded: feeding, climbing, resting, sleeping, and so on. These categories can be as detailed as desired and should reflect the full range of activities being studied.

When using the focal animal technique one should consider carefully beforehand how to analyze and present the data. In some studies, frequency is most useful (the number of figs consumed by a monkey or the number of interactions between animals). Continuous recording may be essential to obtain data on the duration of events—how long animals feed in fig trees or how much time during the day they spend foraging for insects. A sampling system can be used readily. For example, one can record every 2 min the major activities of the animal in the previous 2 min, tabulate the number of 2-min periods each hour in which different activities occurred, and use these data as estimates of frequency or of time spent in these activities, whichever is appropriate.

When using the scan technique one can make instantaneous observations (what each animal is doing the moment you look at it) or timed observations (look at each animal for 5 or 10 s, then record what it was doing). When scanning it is important to look at as many animals in a troop as possible and to be alert for biases. It is always likely that some activities will be recorded infrequently, only because it is more difficult to see the animals then. There may also be bias attributable to the shyness of certain individuals (e.g., females with newborn young).

Among social animals it is generally the case that males, females, and juveniles use their time differently, so it is desirable that the data be collected separately for each class of animal. In scanning this also enables one to determine if one class of animals is harder to see than another and hence is being underrepresented in the samples. When using the focal animal technique, randomize the choice of the animal and be sure not to watch just animals that are most easily observed. One should also check for other biases to make sure that adult males are not observed only on sunny days and females on rainy days or juveniles only when the troop is feeding on flowers. The shorter the study the greater the likelihood that some biases like these will occur, even though the selection of animals is randomized.

In many cases, primates' shyness makes it impossible to study them routinely. One can still use a scan technique, but the scan takes place when animals are first encountered, before they detect the observer. If one records the time, where they are, and what they are doing each time they are encountered, it is possible to gradually build up a good profile of their activities. However, if the encounter occurs at the same place or at the same time of day, the data will present a biased view of their total pattern of activity. Thus, it is desirable to establish a series of transects, along established roads, trails, or waterways where necessary, and in other areas where possible. Off-trail transects can be followed easily, even at night, if they are laid out with a white string. One can proceed along these transects at different times of day or night collecting data whenever one encounters primates. If the transects are arranged in a grid, data will show spatial as well as temporal use of the habitat.

USE OF SPACE

DAILY RANGING

How animals use space within their habitat can be studied in several ways. It is useful to know how far animals travel daily and over how large an area they range. This is best done by following the animals regularly, directly measuring the length of their path—either with a measuring tape or by pacing off the distance—and by plotting their movements on a map (Richard, 1979). The home range is the area the animals cover in all their activities. The longer one watches animals, the larger their home range proves to be, but after a certain number of hours of observation one usually knows most of the home range. There may be seasonal variation or changes in the home range, so it is frequently informative to compute the number of hectares used by the animals each month and to compare the areas used in different seasons.

The use of the home range is uneven. Frequently a core area is used much more often than are peripheral parts of the home range. This may be studied by dividing the home range into quadrats and recording how long the animals spend in each quadrat. For large primates the quadrats can probably be 1 ha (i.e., 100 m on a side). For small monkeys and prosimians it may be desirable to use smaller quadrats, perhaps 1/4 ha in size (Rudran, 1978). Even shy monkeys can be studied this way. Rather than recording the length of time they spend in each quadrat, one can record the number of times they are encountered in each quadrat (Rodman, 1978). With enough data of either type one can calculate the percentage of time the animals spend in each quadrat of their home range. These data can be compared with the types of resources found in each quadrat. Seasonal changes can also be documented.

HEIGHT AND SUBSTRATE

Another aspect of habitat use in a forest is the height above the ground at which the animals are found (Rodman, 1978; Sussman, 1972). This can be estimated with a rangefinder, with the viewfinder of a camera, or by eye. In any case one should regularly check his estimates against known heights. Heights may be classified according to a system appropriate for the habitat. For example, in high forest the classes might be 0–5 m, 5–10 m, 10–20 m, 20–30 m, and more than 30 m. In analyzing the height data it is useful to categorize the heights of the different parts of the forest. In some areas the tallest trees may be only 20 m in height, whereas in other areas the first branches may be higher than 20 m. This information should be included with the analyses of the heights at which the monkeys feed, rest, sleep, or travel. It is also important to test whether the presence of the observer affects the height of the animals. Check to see if the animals are at the same height when first encountered and 5 min later.

More refined studies of habitat use are becoming common. For example, it is of interest in some studies to record the sizes of the branches on which the primates move and feed (Fleagle, 1978) or the angles that they make to the horizontal (Rose, 1978). One makes these estimates from the ground, and with practice one can become quite accurate. Again, measurements are in classes. Angles are expressed in a range of degrees (e.g., 0–30°, 30–60°, 60–90°). Diameters are expressed in centimeters (e.g., 0–1 cm for twigs, 1–3 cm for small branches, 3–10 cm for large branches, 10–20 cm, and so on). The size estimates can be facilitated by comparing the size of the branch with the size of the fingers, feet, and body of the primate being observed.

FEEDING ECOLOGY

The foods of primates can be studied in several ways. The most obvious way is to watch what they are feeding on. This is highly effective for fruit and leaf eaters if the observer knows the plants as well as the animals do. If he does not, the observer can still label the plant and return to it later to obtain samples for identification. Identifying insects that a monkey is popping into its mouth is more difficult, but it is sometimes possible to identify insects by the sounds they make (as in the case of cicadas), or to see fragments of insects that are dropped when insects that are being picked up are too small to be identified. It is undesirable to kill wild primates, but if dead animals are available, one can examine the stomach contents (Charles-Dominique, 1972; Fooden, 1965). These can be studied fresh or they can be fixed in 10% formalin or 70% alcohol. The stomach contents can be sorted, and fragments of leaves, fruits, seeds, and insects can be identified. It is sometimes possible to sort and weigh the components of the diet. Stomach contents can also be obtained from a captured anesthetized animal by inserting a tube down its throat into its stomach. Water is injected down the tube into the stomach, then sucked out again (G. G. Montgomery, personal communication). The sample can then be strained from the water. Be sure that the tube goes down the esophagus into the stomach and not down the trachea into the lungs. With the outer end of the tube held to one's ear, one can hear or feel the animal's breath if the other end of the tube is in the trachea. Be careful, because the animal will die very quickly if water is injected into the trachea or lungs.

An astute naturalist can learn a great deal about the foods of animals just by examining the signs they leave behind. These include partially eaten flowers, fruits, and leaves. Feces can be collected and examined for plant and insect fragments, seeds, and other evidence of foods eaten. They can also be examined for parasites and parasite eggs, which may be clues to insect feeding. The feces can be preserved in formalin or alcohol, but it should be noted that many parasitologists do not like formalin preservation of worms.

Feeding studies have gradually become more detailed. It is commonly expected now that the investigator will record the species, the parts of a plant or animal that are eaten, and the phytophase or stage of each food item (Glander, 1978). Are the fruits ripe or green? Is it just the base of the flower that is being devoured? Is it just the abdomen of the beetle that is favored? Are only small caterpillars eaten? These are some of the detailed questions that may be asked in feeding studies. Frequently, a much longer list of plant parts is discriminated, including those phenophases listed in Chapter 3 and such items as petioles, bark, tubers, and resin.

Finally, the amount of each food item consumed can be estimated in various ways, the preferred way depending largely on the nature of observation conditions. Direct or indirect sampling measures are used, depending on whether visual contact can be maintained with individuals throughout the observation period. Ideally one might wish to know how much of each type of food an animal consumes throughout a day. This requires estimation of the number of items consumed and their weights. To estimate the number of items consumed, an animal is followed and the type and number of food items brought into the mouth are recorded for each minute of observation. The schedule followed depends on the amount and type of information required. Loss of information is minimized if one identified animal is followed from dawn to dusk and different individuals are followed on consecutive days for several days each month. In this way it is possible to accumulate a series of feeding-day profiles and a record of seasonal variation in the amounts of each food item consumed.

Occasionally, continuous observation of a feeding animal is not possible, as when its back is turned to the observer or when it is hidden in the foliage. However, the amount of food consumed can be extrapolated if one knows the type of food being consumed, the time the animal spends in feeding, and the rate at which the food is ingested.

The size of food items taken must be known in order to estimate the weight of comparable samples. For most food items (e.g., fruits, flowers, petioles) that are brought into the mouth singly, the size is self-evident. When several food items, such as a bunch of leaves, are brought to the mouth with a handpicking motion, the number of leaves per bunch is estimated. Similarly, the size of "bites" from large food items may require estimation.

To obtain accurate weights, food items should be collected in the field and placed into plastic bags to reduce the evaporation of moisture. Multiplication of the average weight of single or "bite-sized" food items by the number consumed yields the weight of each food item consumed per observation period. Once collected, food items may be analyzed for moisture content or nutritional content. The former involves simply drying the items slowly in an oven. The difference between the "wet" and "dry" weights yields the weight of water in the food items. Nutritional analyses require elaborate laboratory procedures that will not be considered here. Hladik (1977) described methods for collecting and preparing food items in the field for nutritional analyses.

The food intake in terms of both quantity and quality may ultimately be correlated with the energy demands of foraging movements and energy needs for reproduction. Attempts to calculate energy expended and food intake on a seasonal basis have been undertaken with *Alouatta*, *Ateles*, and *Papio* (Altmann, 1974; Coehlo *et al.*, 1979).

The relationship between food selection and plant defense mechanisms involving secondary compounds is an active area of current research. Some authors are relating food preferences by species and season to the avoidance of toxic secondary compounds such as tannins, saponins, and alkaloids. The problems encountered by folivorous primates in feeding on potentially toxic compounds in leaves are shared by other arboreal mammals including marsupials and edentates (see McKey *et al.*, 1978; Montgomery, 1978).

7

Primate Population Analysis

Population analysis is a technique for describing quantitatively the (1) size and structure of a population in terms of the numbers of animals of different age and sex and (2) changes in population size and structure due to births, deaths, emigration, and aging.

Estimates or measures of such numerical attributes of a population are referred to as vital statistics. They include the birthrate, death rate, population growth rate, and others. Vital statistics describe the dynamics of a population, or its demography.

The vital statistics of a population are a function of the genetic makeup of a species and of environmental influences. Therefore, they are useful for making comparisons of species, or of populations of the same species in different environments, or of the same population at different times. Knowledge of the vital statistics of a species, especially as they change under different environmental conditions, is fundamental to understanding its strategy for living. Apart from the value of such data for theoretical considerations concerning the evolution of behavioral-ecological phenomena, knowledge of a population's demographic behavior is essential in the applied fields of wildlife management and conservation.

DATA REQUIREMENTS

The raw data required for population analysis are animals, in sufficient numbers, of each age and sex. In studies of many species, especially game animals, "kill records" or trapping records have been used as raw data. For primates, such data are rare. Instead, free-living animals are usually censused by an observer who classifies them according to established aging or sexing criteria.

The data in population analysis must meet two requirements that are often difficult to fulfill. First, the data must represent a true sample of the population from which it was drawn. The second requirement is that the census data must be accurately classified by age and sex. Errors in estimates of vital statistics that can arise from faulty age classification are discussed in Chapter 5.

Changes in a population can be monitored by making an annual census of animals of all ages by sex and by making a series of annual censuses to find newborn infants.

BIRTHS AND FECUNDITY

The purpose of censusing for births is to obtain information on the distribution of births in time, the sex ratio at birth, and the rates of birth and fecundity.

BIRTH SEASONS

Theoretically, births can be distributed in time according to either of two models. In a birth pulse model, all births in the population for the entire year occur on the same day and on the same date every year. In a birth flow model, births occur at the same rate every day throughout the year. No population fits either model exactly, but any population will resemble one more than the other. Modern human populations closely fit the birth flow model, whereas most animal populations reproduce seasonally and come closer to the birth pulse model, which is illustrated later in this chapter. The determination of the mean or median birth day and the standard deviation of the birthdates should replace the imprecise descriptions of birth seasons based on the overall spread and peak periods of births, because these statistics allow more accurate division of the population into age classes. Caughley (1977) suggests that populations whose season of birth has a standard deviation of less than 30 days can be described by the birth pulse model.

To define the season of births one must sample a population for the presence of newborn infants during a period of at least 1 yr. Mortality among newborn infants can be high. Therefore, to reduce the error of not counting infants that were born and died in the interval between successive censuses, one should make the census interval as short as possible. Since pregnant females are conspicuous in some primates, the censusing effort can be focused on specific individuals until all adult females in a troop have recently given birth or can be seen nursing infants.

In a birth census it is important to detect all births and estimate birthdates as accurately as possible. This will depend on the interval between censuses and the accuracy of age estimates based on infant morphology. When a birthdate is uncertain it should be estimated within absolute confidence limits, that is, a range of dates between which the birth is certain to have occurred.

The frequency of births throughout a year or study period is tabulated by dividing the year or study period into equal periods. The period should not be less than either the interval between birth censuses, or the birthdate with the largest confidence limits as defined above. This prevents the tabulation from appearing to be more precise than it actually is. For most primates a period of 14 or 28 days is a convenient interval for analysis. If the birth season is brief and if the census data are very accurate, 7-day periods may be more appropriate.

The method of analysis as outlined by Caughley (1977, pp. 72–74) is given in Table 7-1 and is illustrated with data from 150 births that occurred in the population of toque monkeys, *Macaca sinica*, at Polonnaruwa, Sri Lanka, between 1968 and 1972 (W. P. J. Dittus, unpublished). The same data are plotted as a histogram in Figure 7-1.

TABLE 7-1 Estimating Averages and Standard Deviations of Birth Season in a Population of Toque Monkeys at Polonnaruwa, Sri Lanka

Date	Period Limits (days)	Period Code x	No. Births f	fx	fx^2
June 25–July 22	0–28	1	0	0	0
July 23–Aug 19	29–56	2	2	4	8
Aug 20–Sep 16	57–84	3	6	18	54
Sep 17–Oct 15	85–113	4	6	24	96
Oct 16–Nov 12	114–141	5	4	20	100
Nov 13–Dec 10	142–169	6	8	48	288
Dec 11–Jan 7	170–197	7	25	175	1,225
Jan 8–Feb 4	198–225	8	55	440	3,520
Feb 5–Mar 4	226–253	9	20	180	1,620
Mar 5–Apr 1	254–281	10	13	130	1,300
Apr 2–Apr 29	282–309	11	9	99	1,089
Apr 30–May 27	310–337	12	2	24	0.288
May 28–Jun 24	338–365	13	0	0	0
Totals			150	1,162	9,588

Source: W. P. J. Dittus, unpublished data, 1968–1972.

The mean date of birth and its standard deviation are first calculated in terms of the period codes and then converted to their real values in days or dates.

$$\text{Mean date, Mn} = \frac{\Sigma fx}{\Sigma f} = \frac{1{,}162}{150} = 7.75 \text{ periods,}$$

where

f = the number of births during a period, and x = the period code
= 7.75 periods × 28 days per period
= 217 days after midpoint of period 1 (June 25–July 22)
= July 8 + 217 days
= February 10.

Grouping the data into intervals of constant width (each equal to one unit in coded form) results in a slight overestimate of the variance. This is corrected by using Sheppard's correction for grouping (Snedecor and Cochran, 1967)—that is, by subtracting 1/12.

$$\text{Variance, } s^2 = \frac{\Sigma fx^2 - (\Sigma fx)^2/\Sigma f}{\Sigma f - 1} - \tfrac{1}{12}$$

$$= \frac{9{,}588 - (1{,}162)^2/150}{149} - \tfrac{1}{12}$$

$$= 3.85 \text{ periods}$$

Most birth seasons are skewed in the positive direction—that is, the frequency of births rises steeply to a peak and then descends in a long tail to the right. In such asymetrical distributions

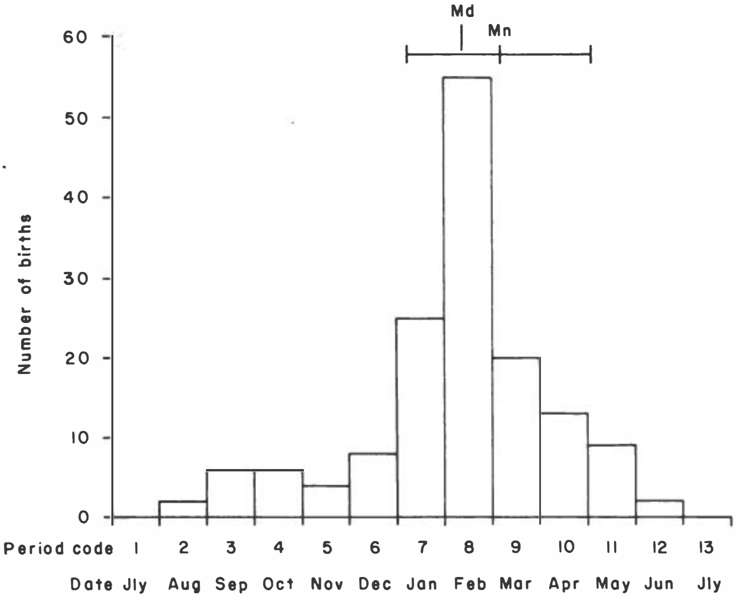


FIGURE 7-1 Distribution of births in toque monkeys at Polonnaruwa, Sri Lanka, from 1968 to 1972. The mean birthdate (*Mn*), the median birthdate (*Md*), and the standard deviation are shown on the bar above the histogram. Source: W. P. J. Dittus, unpublished data.

the median date of birth is a better indicator of the average birth day of all infants.

The median birthdate is the day when half the infants have been born—in this case, the day when $150/2 = 75$ infants have been born. The median birthdate is located in two steps. First, the median birth period is found by cumulatively summing the frequencies of births (f) until the median birth is located. In this example the median birth number, 75, falls within the median birth period from January 8 to February 4.

Second, the median birthdate is calculated as follows (after Snedecor and Cochran, 1967):

$$\text{Standard deviation, } s = \sqrt{\text{variance}} = \sqrt{3.85} = 1.96 \text{ periods}$$

$$= 1.96 \text{ periods} \times 28 \text{ days per period}$$

$$= 55 \text{ days}$$

$$\text{Standard error, } s/\sqrt{\Sigma f} = 55 \text{ days}/\sqrt{150} = 4.5 \text{ days}$$

$$\text{Median, Md} = L + \frac{g(C)}{f},$$

where

L = lower limit (in days) of the period in which the median lies
= 198 days
g = serial number of the median birth minus the cumulative frequency of births up to the upper limit of the period preceding the median period
= $75 - 51 = 24$
C = period interval = 28 days
f = frequency of births in the period containing the median = 55.

Thus,

Md = $198 + 24(28)/55 = 210$ days from the start of period 1
= June 25 + 210 days
= January 21.

The mode of a birth season may be of interest in comparisons of birth periods or for comparisons with some environmental event. The modal period is the period with the highest frequency of births. In this example it is January 8 to February 4. An approximate mode is calculated as follows (after Stanley, 1963):

$$\text{Mode} = L + \frac{fa(C)}{fa + fb},$$

where

L = lower limit of modal period = 198 days
f_a = frequency of births in the period following the modal = 20 births
f_b = frequency of births in the period preceding the model = 25 births
C = period interval = 28 days.

Thus,

$$\begin{aligned} \text{mode} &= 198 + 20(28)/20 + 25 = 210 \text{ days} \\ &= 210 \text{ days from start of period 1 on June 25} \\ &= \text{January 21.} \end{aligned}$$

By chance the major mode = median in this sample from the toque monkey.

Another method for obtaining birth season statistics involves probit analysis. This method is especially useful when regular census work is not possible, because it requires no constant sample size or regular interval between samplings, nor does the beginning or end of the birth season have to be sampled. It is an indirect method that relies on estimating the birth distribution from the cumulative proportion of births that have occurred up to each day of observation. This method is most accurate, however, when births are normally distributed and when there are no infant deaths during the sampling period or birth season. The latter constraint may be negligible when birth seasons are brief, but it is limiting when the birth season exends over several months during which infant mortality may be high. See Caughley (1977) or Caughley and Caughley (1974) for an outline of the method.

TESTING SEX RATIO AT BIRTH WITH THE BINOMIAL TEST

Owing to differential mortality by sex among young infants, a census taken several months following the birth season may produce an estimate different from the true sex ratio at birth. It is desirable, therefore, to census as close to the birthdate as possible.

Most primate and other vertebrate populations have an equal sex ratio at birth. The significance of a digression from a 1:1 ratio can be tested by using a binomial test. The toque monkeys at Polonnaruwa were sampled, and 208 females and 211 males were counted among 419 animals. The equation for the binomial test is

$$z = \frac{(x + 0.5) - NP}{\sqrt{NPQ}},$$

where

x = the smaller number of observed births (208)
N = the total number of observed births (419)
P = the proportion of births expected in one category or sex
$Q = 1 - P$ = the proportion of births expected in the other sex.

Since, according to our null-hypothesis the expected proportion of births of one sex is one-half $P = Q = 0.5$ and

$$z = \frac{(208 + 0.5) - (419)(0.5)}{\sqrt{(419)(0.5)(0.5)}} = \frac{208.5 - 209.5}{\sqrt{104.75}} = \frac{-1}{10.23}$$

$$z = -0.1.$$

The probability associated with the value of z is obtained from a table of probabilities for z as is found in most statistics texts, for example Sokal and Rohlf (1969) or Siegel (1956). In the above example, $p = 0.4602$ for a one-tailed test and 0.9204 for a two-tailed test. That is, the probability that a digression from a 1:1 sex ratio as large as the one observed in this example could have arisen by chance alone is 0.9204. For samples over 25, a significant ($p \leq$

0.05) deviation from a 1:1 sex ratio is obtained whenever $z \geqq 1.96$. For sample sizes less than 25, a different binomial formula and table of probabilities are applied as outlined in the texts *op. cit.*

BIRTHRATES AND FECUNDITY

Natality, or birthrate, is the number of infants produced in 1 yr by a population. It can be expressed on the basis of the population as a whole (the crude birthrate), or on a subset of the population—for example, birthrate per adult female. The term "fecundity" is generally used to convey differences in natality between females of different ages. In analysis it is often convenient to consider the female segment of the population only, or at least separately from the male segment. Hence the statistic symbolized by "m_x" is defined as age-specific fecundity and refers to the average number of *female* infants ($\bar{m}$) born to females of the age class "x."

The raw data required for calculating birthrates are: (1) numbers of infants born per year and (2) the total number of animals in that part of the population (total, segment, or female age class) for which the birthrate is expressed. Since the birthrate in primates is conveniently measured per annum, the observation period should span at least 1 yr. Adult females are generally easy to recognize and count in a census, and birthrate is most reliably expressed per adult female. As in collecting other birth data, frequent censusing reduces the likelihood of missing infants that died shortly after birth.

The choice of the three methods for estimating birthrate and fecundity rate described below depends on the duration of the observation period and on the degree of refinement in the raw data.

Method 1 is an estimate based on known births in 1 yr. If the observation period spans only 1 yr and females are individually identified, the birthrate is estimated as follows:

$$\text{Birthrate, } b = I_t/F_t,$$

where I_t = total number of infants born in 1 yr and F_t = total number of females observed throughout 1 yr. If females are classified according to different age classes (x), then the birthrate can be expressed specific to an age class (b_x):

$$\text{Age-specific birthrate, } b_x = I_x/F_x,$$

where I_x = number of infants born to females of age class x and F_x = total number of females of age class x. Given a sex ratio at birth of 1:1, the age-specific fecundity is one-half of the birthrate, or:

$$\text{Age-specific fecundity, } m_x = I_x/2F_x.$$

Similar data from several years of observation can be treated in the same way for each year, and the results can be averaged over all years.

Method 2 is an estimate based on interbirth intervals. The interbirth interval in most of the larger primates exceeds 1 yr. Three conditions must be met to use the interbirth interval for calculating the birthrate. First, the observation period must be more than the interbirth interval, probably at least 2 yr for most primates. Second, the females must be individually identified so that a given female's second birth is correctly linked to her first for calculating the interbirth interval. Third, the dates of successive births must be known fairly accurately because the size of the error in estimating the interval will be the sum of the errors in estimates of both birth dates.

Under these conditions, the birthrate, $b = 1/t$, where t = interbirth interval.

Assuming that the interval (t_x) for females of age class x is known, then $m_x = 1/2t_x$.

Method 3 is an estimate based on female-years of observation. In most field studies the size of the census sample increases with observation time, and the quality of the data generally improves with experience. Therefore data may vary in information content between years. Assume, for example, that the first two conditions outlined under Method 2 are fulfilled and that several identified females are known to have had infants but the birthdates are too vaguely known to accurately estimate interbirth intervals. The estimation of $\bar{m}_x$ from such data is given in Table 7-2 for middle-aged adult female toque monkeys.

Within each age class, x, the number of years of observation differed between females. The data can be expressed, however, in

TABLE 7-2 Estimating the Mean Fecundity for Middle-Aged (15–19 yr) Adult Female Toque Monkeys at Polonnaruwa on the Basis of Female-Years of Observation

Name of Adult Female	No. Infants Born to Female	No. Years Female was Observed	Mean Fecundity $\bar{m}_{15-19}$
Cres	4	4	
Fut	1	3	
Su	3	3	
Nar	2	2	
Zip	1	2	
Halo	2	2	
Total	13	16	$\frac{13}{2(16)} = 0.406$

Source: W. P. J. Dittus, unpublished data.

female-years. For example, 3 female-years represent 3 years of observation of one female.

As illustrated in Table 7-2, the age-specific fecundity is calculated from m_x = 1/2 the total number of infants that born to all females in age class x, divided by the sum of the female-years for all females in age class x.

The event of first birth may be used as a criterion for defining the age of primiparous females. To avoid circularity in analysis, one should base estimates of m_x for young adult females on at least 2 yr of observation after the first birth, or on the interbirth interval (Method 2).

The fecundity pattern of a population is generally displayed in Table 7-3, which is a fecundity table that lists the mean fecundity of females of each age class.

ESTIMATING RATES OF POPULATION GROWTH

PER-CAPITA RATE OF INCREASE

A simple measure of population growth is given by the per-capita rate or finite rate of increase, λ.

$$\lambda = \frac{N_{t+1}}{N_t},$$

where N_t = numbers in a population at time, t. For example, if population size at time zero were 450, $N_0 = 450$, and 1 yr later there are 622 individuals, $N_1 = 622$, then $\lambda = 622/450 = 1.38$. This value of lambda indicates that the population has grown at the rate of 1.38 per individual per year. When λ is greater than 1, the population has increased in the period t to $t + 1$; when λ is less than 1, the population size has decreased; and when $\lambda = 1$, the population size has remained constant.

OBSERVED EXPONENTIAL RATE OF INCREASE

Another measure of population growth is the observed exponential rate of increase, r. It is related to λ by $\lambda = e^r$, where e = base of natural (Naperian) logs = 2.7183. Thus, $\log_e \lambda = \log_e e^r = r$. From the example above, $e^r = \lambda = 1.38$; therefore, $r = \log_e 1.38 = 0.32$.

The expression of r in a population is $N_t = N_0 e^{rt}$. From this we see that if $r = 0$, then $N_t = N_0$, or the population is stable in size. Increasing populations have a positive r $(+r)$, whereas decreasing ones have a negative r $(-r)$.

TABLE 7-3 Estimating Mean Age-specific Birthrates (b_x) and Fecundity Rates ($\bar{m}_x$) of Females in the Population of Toque Monkeys at Polonnaruwa Between 1968 and 1972[a]

Age Class	Estimated Age (years)	Mean Birthrate b_x	Mean Fecundity $\bar{m}_x$
Infant and juvenile	0–4	0.000	0.000
Young adult	5–9	0.704	0.352
Young to middle-aged adult	10–14	0.724	0.362
Middle-aged adult	15–19	0.813	0.406
Old adult	20–24	0.885	0.442
Senile adult	25–29	0.286	0.143

Source: Dittus, 1975.

The observed exponential rate of increase is sometimes useful in calculations involving vital statistics and is often referred to in abbreviated form as the rate of population increase or the growth rate. It is generally used in place of λ. It is not the same as the innate or intrinsic rate of population increases, r_m, which is commonly quoted in ecology textbooks. The latter is primarily a theoretical construct that is measurable only, if at all, under specified or experimentally controlled conditions. The observed r calculated from λ cannot be used as an estimate of r_m.

ESTIMATING VITAL STATISTICS FROM A STABLE STANDING AGE DISTRIBUTION

CONSTRUCTION OF AGE-STRUCTURE TABLES

A standing age distribution is the number of animals of different age and sex observed at any one point in time. It is stable when the proportions of individuals at different ages remain constant through time. Age distributions are usually tabulated separately for each sex in age-structure tables, as illustrated in Table 7-4. In this table, most ages are grouped into classes and are tabulated according to the birth pulse model discussed under "Birth Seasons."

The importance of the censusing methods described earlier can now be understood in terms of the assumptions underlying the construction of an age-structure table, the accuracy of which depends on the adequacy of the sample of the population, the completeness and accuracy of the age and sex class identifications, and the accuracy of the estimate of the birth season. Sampling primate populations is relatively easy (compared with sampling herds of ungulates, for example) because most primates live in closed social groups of manageable sizes. A population sample is a set of these mutually exclusive troops. For estimating vital statistics, data on the age and sex structure of all troops must be combined in order to obtain a sample size sufficiently large for valid analysis.

Since the aim is to count all members of a population, care should be taken to identify all animals in each troop and to include any all-male groups and peripheral males in this tabula-

TABLE 7-4 Age Structure for the Population of Toque Monkeys at Polonnaruwa in 1971

Age Class	Estimated Age (years)	No. Females	No. Males
Infant	½–<1	21	30
Young juvenile	1	18	23
Old juvenile	2–4	36	60
Subadult	5–6	0	23
Young adult male	7–9	0	12
Young adult female	5–9	29	0
Young to middle-aged	10–14	26	16
Middle-aged	15–19	24	13
Old	20–24	20	6
Senile	25–29	11	1
Total		185	184

Source: After Dittus, 1975.

tion. The chances of noting peripheral males that may be temporarily absent from a troop are increased by visiting the same troop on different days during the count period. The completeness of counts within any troop can be enhanced by concentrating on one age and sex class at a time and by distinguishing between individuals even if this can only be done temporarily during a visit to the troop.

The timing of a count in relation to the birth season determines whether the ages of most individuals will be close to multiples of whole years or will have an added large fraction of a year. Since analysis by the birth pulse model has fewer constraints (because of the greater accuracy in assigning ages), it is advantageous to census close to the median or mean birth day of the population. These considerations assume, of course, that the average birth day of the population is the same every year and that the standard deviation from the average birth day is low. Individual troops may differ consistently in their average birth day from that of the population as a whole. The variance in birth days usually is less within a troop than for the entire population (W. P. J. Dittus, unpublished). If such information is available, the time of censusing a troop might be adjusted to coincide with its average birth day.

CONSTRUCTION OF A LIFE TABLE BASED ON THE BIRTH PULSE MODEL

A life table delineates the survivorship schedule of a population. The population is treated in an abstract fashion as though all animals in it were born simultaneously and their numbers were progressively depleted by mortality as they grow older. Such a group is called a cohort. Usually males and females are considered separate cohorts. The size of the cohort at its inception is 100% and is equal to the total number of births in the sample. One visualizes following the history of this cohort throughout life and recording the numbers still living at each birth day. These records would be equivalent to an age-structure table (but see limitations on p. 158), and the numbers alive at each age are the basis for calculating other statistics.

Vital statistics are most conveniently expressed as probabilities. The usual statistics given in a life table are as follows:

l_x = survivorship (or survival), or the probability at birth of surviving to the *exact* age x.
d_x = mortality, or the probability of dying *during* the age interval x to $x + 1$.
q_x = rate of mortality, or the proportion of animals alive at age x that will die before age $x + 1$.
p_x = rate of survival, or the proportion of animals alive at age x that will survive to age $x + 1$.

It is important to note that given any one statistic the others can be calculated; each statistic merely displays the same data in a different format. The statistics are related to one another as follows:

$$d_x = l_x - l_{x+1}$$

$$q_x = d_x/l_x$$

$$p_x = l_x - q_x.$$

Occasionally, life-table data are expressed on a per-1,000 or per-100 basis, the assumption being that the cohort started to-

TABLE 7-5 Life Table for Female Toque Monkeys

Age Class (years) x	No. Observed f_x	No. Ages per Age Class a_x	Average No. per Annum $\bar{f}_x = \frac{f_x}{a_x}$	Average Annual Survivorship to Age Class x $\bar{l}_x$	Total Mortality per Age Class d_x	Average Annual Mortality Between Age Class x and $x + 1$ $\bar{d}_x$	Average Annual Mortality Rate Between Age Class x and $x + 1$ $\bar{q}_x$
0	38	1	38	1.000	0.526	0.526	0.526
1	18	1	18	0.474	0.158	0.158	0.333
2–4	36	3	12	0.316	0.163	0.0543	0.172
5–9	29	5	5.8	0.153	0.016	0.0032	0.021
10–14	26	5	5.2	0.137	0.011	0.0022	0.016
15–19	24	5	4.8	0.126	0.021	0.0042	0.033
20–24	20	5	4.0	0.105	0.047	0.0094	0.090
25–29	11	5	2.2	0.058	0.058	0.0116	0.200
>29	0	∞	0	0	0	0	0
					$\Sigma d_x = 1.0$		

Source: After Dittus, 1975.

gether as 1,000 (or 100) animals and their numbers decreased through time. Instead of recording probabilities of survivorship, the life table would portray numbers still alive, or dead with increasing age. Converting the probabilities to such whole numbers involves simple multiplication—for example, 1,000 l_x, or 100 l_x, and so on. In this chapter all life-table statistics are expressed as probabilities because these are easier to work with in analysis.

The raw data for construction of a life table can be either the number dead per age class (death-based) or the number alive per age class (life-based). Most primate census data lend themselves best to life-based analysis, when the assumptions described under "Estimating Vital Statistics from Individual Life-History Records" are met (p. 163).

Transformation of raw data from an age-structure table to its hypothetical life-table equivalent requires two manipulations. First, unless the population's birth season conforms exactly to the theoretical birth pulse model and the census was taken on the day of all births for the population for that year, the number of infants born in that year or during the year preceding the census will be underestimated. This can be corrected for, however, by eliminating from the raw data the number of infants less than 1 yr old and substituting an estimate of the number that were born in the season preceding the census. This is calculated as the product of the number of adult females in the census and their average birthrate. In the example from the population of toque monkeys (Table 7-4), the number of adult females in the population was 110 and their average birthrate over 4 yr was 0.688 infants/adult female/year. The estimated number of infants born at the theoretical pulse prior to the census is $110 \times 0.688 = 76$ infants. The sex ratio at birth is 1:1; therefore, there are 38 infants of each sex (Table 7-5).

Life-table data are given in Table 7-5 for female toque monkeys. The number of females observed for each age class (f_x) is taken directly from the age-structure table (Table 7-5), except that the estimated number of female births (f_0) is substituted for the number of female infants recorded at the time of the census.

The second manipulation requires the transformation of the observed frequencies of females, f_x, to survivorship, l_x, on a per-total-number-born basis: $l_x = f_x/f_0$.

For example, for age class $x = 1$, in Table 7-5: $l_1 = 18/38 = 0.474$. If l_x values have been computed for each year of age, $x = 1$, $x = 2$, $x = 3$, and so on, the statistics d_x, q_x, and p_x can be derived directly for each year by using the formulas indicated above. The statistics are then tabulated for each year of life in a format similar to that in Table 7-5 to give a life table.

ESTIMATING VITAL STATISTICS FROM AVERAGED AGE CLASS FREQUENCIES

Theoretically, one would wish to have the observed frequencies of females, f_x, for each year of life. This requires that the ages of all animals in the census be estimated to the nearest year. Unfortunately, in most primate censuses such accuracy is elusive. Data are generally presented according to age classes whose limits are estimated with confidence. In Table 7-5, f_x is tabulated per age class, x, and an average $\bar{f}_x$ is computed to express f_x on a per-annum basis within each age class. These averages represent f_x at an age midway between the birth pulse limits or age limits of an age class. The procedure is equivalent to smoothing f_x between years. Thus,

$$\bar{f}_x = \frac{f_x}{a_x},$$

where a_x = number of birth pulses of ages (in years) encompassed by age class x. For example, from Table 7-5,

$$\bar{f}_{2\text{-}4} = \frac{f_{2\text{-}4}}{a_{2\text{-}4}} = \frac{36}{3} = 12.$$

The values of $\bar{f}_x$ are then transformed to the average number of survivors in each age class in the usual manner:

$$\bar{l}_x = \frac{\bar{f}_x}{f_0}.$$

For example, for the age class encompassing $x = 2, 3, 4$,

$$\bar{l}_{2\text{-}4} = \frac{12}{38} = 0.316.$$

To find $\bar{d}_x$ one first calculates d per age class or d_x

$$d_x = \bar{l}_x - \bar{l}_y,$$

where y is the age class next older to age class x; then, the annual average number of animals dying per age class x is

$$\bar{d}_x = \frac{d_x}{a_x}.$$

For the macaque data, for example,

$$d_{2\text{-}4} = \bar{l}_{2\text{-}4} - \bar{l}_{5\text{-}9} = 0.316 - 0.153 = 0.163$$

and

$$\bar{d}_{2\text{-}4} = \frac{d_{2\text{-}4}}{a_{2\text{-}4}} = \frac{0.163}{3} = 0.0543.$$

Note that the sum of all deaths $\Sigma_{x=0}^{\infty} dx$ or $\Sigma(\bar{d}_x)(a_x)$ is 1.000, the size of the cohort at birth. The standard notation $\Sigma_{x=0}^{\infty}$ represents the limits of the summation—in this case, the sum of values for x from 0 to infinity or the sum of all age classes. Following convention, the limits of the summation will not be shown when all age classes are summed.

Age-specific mortality, q_x, also is expressed as an average per annum for each age class:

$$\bar{q}_x = \frac{\bar{d}_x}{\bar{l}_x} \text{ and } \bar{p}_x = 1.000 - \bar{q}_x.$$

From Table 7-5, for example,

$$\bar{q}_{2\text{-}4} = \frac{\bar{d}_{2\text{-}4}}{\bar{l}_{2\text{-}4}} = \frac{0.0543}{0.316} = 0.172$$

and

$$\bar{p}_{2\text{-}4} = 1.000 - \bar{q}_{2\text{-}4} = 1.000 - 0.172 = 0.828.$$

To express $\bar{l}_x$, $\bar{d}_x$, $\bar{q}_x$, or $\bar{p}_x$ on the basis of the age class as a whole, one multiplies each statistic by the appropriate a_x. Using very old females (25–29 yr old) from Table 7-5 as an example, we find:

$$\begin{aligned} q_{25\text{-}29} &= (\bar{q}_{25\text{-}29})(a_{25\text{-}29}) \\ &= 0.200 \times 5 = 1.000. \end{aligned}$$

That is, all females of the age class $x = 25\text{–}29$ will, on the average, die before their 30th birthdays.

When $a_x = 1$, as for $x = 0$ and $x = 1$ in Table 7-5, then $\bar{l}_x = l_x$, $\bar{d}_x = d_x$, and so on.

Another statistic that is often displayed in life tables is e_x = mean expectation of life remaining for individuals at the start of an age x.

The statistic $e_x = (L_{x+n} + \ldots L_{x+2} + L_{x+1} + L_x)/l_x$, where L_x = average survivorship during the age interval x to $x + 1$:

$$L_x = \frac{l_x + l_{x+1}}{2}.$$

From Table 7-5, for example, $L_0 = l_0 + l_1/2 = 1.000 + 0.553/2 = 0.777$. The sum of L is obtained by starting with the oldest age class and adding from the bottom of the life table until the specified age class is reached, in this example—L_{25}. Because x varies between the limits from the specified age class to infinity rather than from 0 to infinity, the limits are shown as $\Sigma_{y=x}^{\infty} L_y$. The data shown in Table 7-6 are given to exemplify estimation of e_x for a portion of the life table only. Thus, for 25-yr-old female toque monkeys

$$e_{25} = \frac{(L_{29} + L_{28} + L_{27} + L_{26} + L_{25})}{l_x}$$

$$= \frac{0.029 + 0.058 + 0.058 + 0.058 + 0.058}{0.058}$$

and

$$e_{25} = \sum_{y=25}^{29} \frac{L_y}{l_{25}} = \frac{0.261}{0.058} = 4.5 \text{ yr.}$$

The average life expectancy for females in the senile age class is

$$\bar{e}_{25\text{-}29} = \frac{e_{25} + e_{26} + e_{27} + e_{28} + e_{29}}{a_{25\text{-}29}}$$

$$= \frac{4.5 + 3.5 + 2.5 + 1.5 + 0.5}{5}$$

$$= \frac{12.5}{5} = 2.5 \text{ yr.}$$

Or, a female of the age class $x = 25\text{–}29$ will, on the average, live another 2.5 yr.

The average life expectancies of individuals of different age classes are given in Table 7-7 for female toque monkeys. The life expectancy at birth, e_0, is the average life expectancy of the entire cohort; for the female toque monkey, $e_0 = 4.8$ yr. It is so low because of high mortality among infants and juveniles.

GRAPHIC REPRESENTATION OF LIFE TABLES

Vital statistics can be displayed graphically in a plot of age on the abscissa and the selected statistic on the ordinate. The most use-

TABLE 7-6 Estimating the Life Expectancy, e_x, for a Portion of a Life Table for Female Toque Monkeys

Age x	l_x	$\bar{L}_x$	$\Sigma\bar{L}_x$	$\bar{e}_x$
0–22		not tabulated		
23	0.105	0.105	0.448	4.3
24	0.105	0.0815	0.343	3.3
25	0.058	0.058	0.261	4.5
26	0.058	0.058	0.203	3.5
27	0.058	0.058	0.145	2.5
28	0.058	0.058	0.087	1.5
29	0.058	0.029	0.029	0.5
30	0.000			

Source: Adapted from Dittus, 1975.

ful schedules are survivorship (l_x) and age-specific mortality rate (q_x). The advantage of such graphs is that mortality rate and survivorship schedules can be easily assessed at a glance. Figures 7-2 and 7-3 show survivorship and mortality rate curves for male and female toque monkeys.

The survivorship curves appear in a stepwise fashion because statistics were computed as averages that apply to all ages within

TABLE 7-7 Average Life Expectancies for Female Toque Monkeys of Different Age Classes

Age Class (years)	Average Life Expectancy $\bar{e}_x$
0	4.8
1	8.6
2–4	10.7
5–9	16.6
10–14	13.0
15–19	9.3
20–24	5.2
25–29	2.5

Source: Adapted from Dittus, 1975.

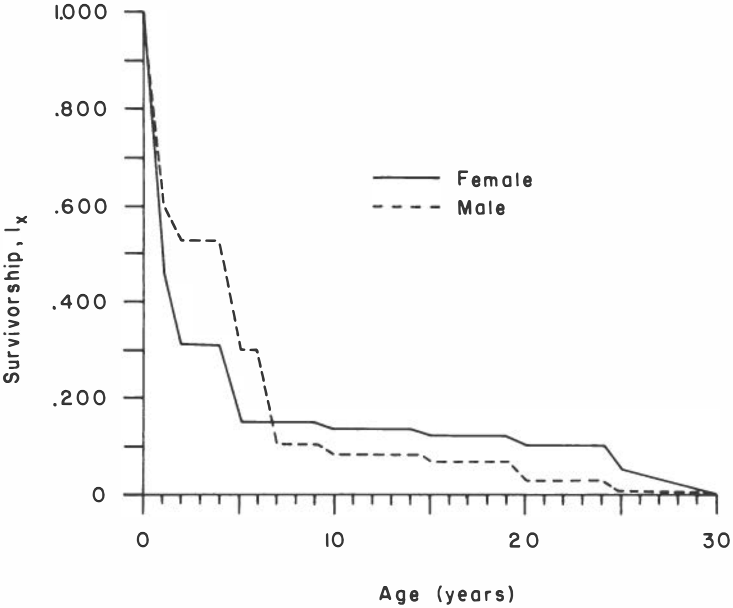


FIGURE 7-2 Survival curves for male and female toque monkeys at Polonnaruwa from 1968 to 1972. After Dittus, 1975.

any one age class. Theoretically, one would expect the transitions from one age to the next to be smoother than they appear here.

Other graphic representations include age pyramids for each sex, or histograms made by plotting l_x and d_x against age (see Eberhardt, 1968, for examples).

LIFE TABLES BASED ON THE BIRTH FLOW MODEL

The life-table calculations above assumed a birth pulse model. In a birth flow situation, the census data are divided into intervals of age x to $x + 1$ starting with age class 0.5–1.5. The cohort is assumed to begin at age 0.5 yr. To estimate the size of the cohort at age 0.5, one must know the mortality in the interval 0–0.5 yr. Given the cohort strength at birth, l_0 (as calculated from fecundity), mortality in the interval 0–0.5 can be estimated if the number of infants 6 mo old is known.

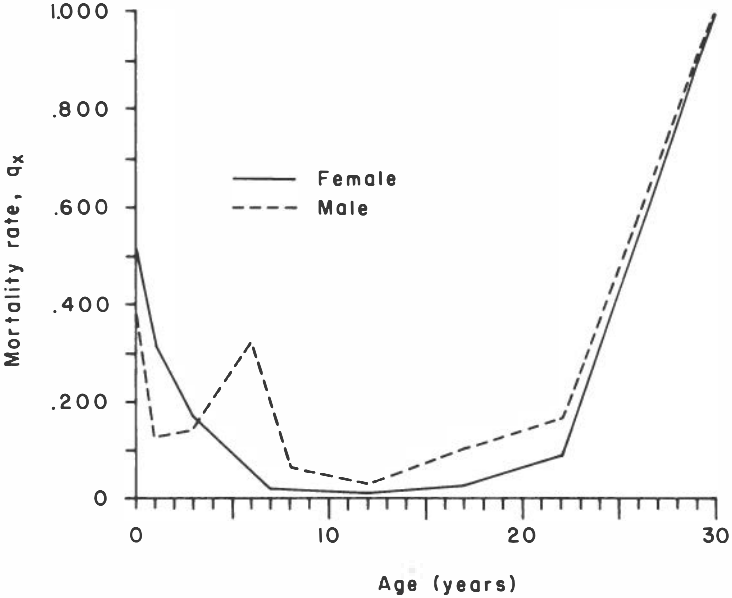


FIGURE 7-3 Age-specific mortality rate curves for male and female toque monkeys. After Dittus, 1975.

LIMITATIONS OF AGE DISTRIBUTION DATA FOR CALCULATING VITAL STATISTICS

The Effect of Age Distribution on Life-Table Estimates

The frequency distribution of ages in a population sample at the time of the census is known as a "standing age distribution" and is usually shown in an age-structure table. In estimating life-table statistics from such data, one assumes that the standing age distribution is equivalent to a "temporal age distribution" of a cohort. The latter is an abstract distribution of the number of survivors remaining each year from a group of animals that started life together and thereafter faced the same risks of death at each age, although these risks changed with successive years or ages.

In a real population, however, natality differences between years by themselves may influence the numbers recruited from 1 year (or age) to another. Also, at any point in time the ages of all animals in the population are not equal as is assumed in the imagined cohort model. Thus if the environment changes to the extent of altering the risks of death from one calendar year to another, not all animals in a real population would face the same risks of death in passing through a particular age.

The assumptions of a cohort model hold true only if the population sampled is a "stationary" one so that over many years the schedules of fecundity and survivorship have been constant and the exponential rate of population increase (r) has been zero. This can be shown as follows.

The standing age distribution, S_x, can be expressed as the number of animals in an age class relative to the number of newborn (Caughley, 1977). It is estimated from a census sample as $S_x = f_x/f_0$. It is related to survivorship l_x by $S_x = l_x e^{-rx}$, where r = rate of population increase. It is clear from this relationship that unless $r = 0$, the standing age distribution will differ from l_x. Therefore, S_x can be used to estimate l_x only in populations where r is and has been zero for some time. Or, intuitively, if r is constantly changing, the numbers recruited or dying at different ages are changing and are thereby altering the age distribution from year to year.

In a "stable age distribution" the survivorship and fecundity schedules have also been constant for some time so that the proportions of one age or age class to another are constant. Under these conditions r will also converge toward a constant value, but not necessarily $r = 0$. However, if the value of r is known and can be shown to have been constant for a long time then, from the relationship of r to S_x and l_x, l_x may be computed given S_x.

Estimation of life-table statistics from a standing age distribution is therefore restricted to only those populations whose mortality and fecundity schedules have been constant for two or three generations and whose rate of population increase (r) is known and has been constant for a long time.

Assessing Population Stability

Stable populations have stable age distributions. They are "stationary" when $r = 0$. But stable populations need not be stationary; they can have any r. Given any r, however, a population requires two or three generations to converge toward stability. Hence a good deal of information is needed about the history of a population before S_x can be used to estimate l_x. Any information indicative of the state of population growth (r) might be useful for rejecting or accepting S_x as a basis for estimating vital statistics.

Population growth rate (r) may be assessed directly or indirectly. A direct assessment requires that r be estimated at intervals over a period of two or three generations. Short-term estimates, as over a few years of a field study, are by themselves inadequate to predict whether long-term stability will occur.

Indirect assessments of population growth rate (r) deal with gauging the stability of the environment, which influences population growth. In a stable environment the seasonal changes are of the same kind and magnitude every year. Most primates are K-selected, and their numbers are attuned to the carrying capacity of their environments (see Chapter 8). A population inhabiting an environment that has been stable over a long period probably has an average annual $r = 0$ and a fairly stable and stationary age distribution.

The following conditions are indicative of long-term environmental stability:

- Forest and other vegetation types that are climax and undisturbed.
- Constant climatic regime. A climatic regime in which temperature and amount and seasonal distribution of rainfall follow the same pattern over many years would tend to induce predictable phenological and productivity patterns in the forest. Most primate populations are attuned to the predictable seasonal flux in resources.
- A balanced flora and fauna relative to environment type.

Unstable environments would tend to alter r so that populations inhabiting such areas probably do not have a stable age distribution. Unless an environmental change is of the same kind and magnitude over a long period of time, it is unlikely that any value of $r \neq 0$ would be constant for a long period. Conditions that are indicative of unstable environments or populations are as follows:

- Forests that have been disturbed recently, either through natural events, such as fire, cyclones, or changes in soil salinity, or through felling by people.
- Change in cultivation practices. The balance of populations in an area where they are partly or wholly dependent on agriculture would be changed by a change in long-established cultivation practices in the area, such as the introduction of a new crop or of the use of pesticides.
- Unnatural disease. For example, the introduction of yellow fever to South America resulted in a marked decline of howler monkey populations (Collias and Southwick, 1952).
- Hunting or trapping by man.
- Highly irregular climatic regimes.
- The introduction of human settlements.
- An impoverished flora and fauna relative to environmental conditions.

Data from several sources may assist in a final judgment about stability. For example, the population of toque monkeys at Polonnaruwa was judged to have had a fairly stable history based on forest ecology, a very constant long-term climatic regime, and short-term population stability.

Errors Due to Inaccurate Age Estimates

Probably the greatest source of error in estimating vital statistics is faulty age estimation. Since estimates of mortality are a function of $(l_x - l_{x+1})$, the ability to distinguish individuals aged x from those aged $x + 1$ is obviously crucial in determining the numbers in each age class. Indirect age estimates are often based on body-size differences (see Chapter 5).

The relationship between body size, age, and numbers of animals is shown in Figure 7-4. In this figure, *A* and *B* are physical growth curves for two cohorts having equal birthrates, sex ratios at birth, and survivorship schedules. The cumulative number of living individuals by age groups is the same for both cohorts. The

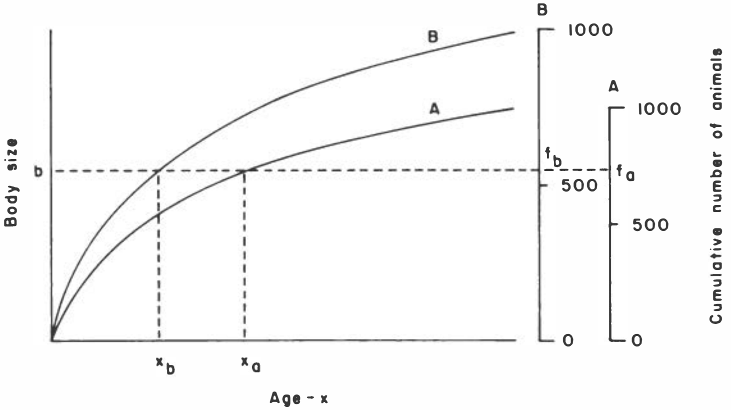


FIGURE 7-4 The relationship between growth in body size, age, and cumulative survivorship in two imaginary cohorts. The imaginary cohorts, *A* and *B*, have equal survivorship and sex ratios at birth, but they have different growth rates, with *B* growing faster than *A* (see text).

curves serve to illustrate the type of error that can arise in population analyses from faulty age estimation.

An error that might occur is estimating the ages of slow-growing animals (*A*) on the basis of the size of fast-growing ones (*B*). Assigning an age x_b to an *A* animal of size *b* would underestimate the true age, x_a, of *A*, and would overestimate the number of *A* animals, f_a, relative to their assigned age, x_b, and relative to the number of *B* animals, f_b, of the same age, x_b. In analysis, such an error would underestimate the mortality of *A* animals relative to their true ages and relative to *B* animals of the same age.

In primate studies this error may arise if the size-to-age relationships of fast-growing captive animals fed on nutritious diets are used to estimate the ages of equally sized but slower-growing wild animals. Similarly, male infants and juveniles often grow faster than their female age mates. Using the size-to-age relationship of one sex to estimate the ages of the other, or an average growth curve to estimate the ages of either, would tend to overestimate the mortality of the faster-growing males relative to their slower-growing female age mates.

When one does not have empirically derived growth curves for both sexes in a census population, it is advisable to use the same growth-age relationship to estimate the ages of both sexes, keeping in mind that if growth differences by sex occurred, the mortality of the faster-growing sex would tend to be underestimated among infants and juveniles.

In conclusion, the use of standing age distributions to estimate life-table functions should be approached with caution and should be used only when it is possible to approximate the conditions of stable age distribution, long-term zero population growth rate or known r, and accurate aging in the census.

Two alternative methods can be used to estimate vital statistics when no assumptions are required concerning the stability of the age distributions or the rate of population increase at any time. (The methods are given in the next two sections.) The first method involves identifying a large number of individuals and tracing their fates from birth. The second involves identifying only a set of troops and comparing their standing age distributions at yearly intervals.

ESTIMATING VITAL STATISTICS FROM INDIVIDUAL LIFE-HISTORY RECORDS

To estimate vital statistics from individual life-history records one must have, as raw data, (1) numbers of individuals that died in the age interval x to $x + 1$ or (2) numbers of individuals alive at age x.

The method used in obtaining both kinds of data is similar and requires that all individuals in the population be identified so that their fates can be traced and their birth days determined. From records of the age at death of individuals the number of deaths, f'_x, in each age interval x to $x + 1$ is obtained. From records of numbers living at census time, t, the number surviving, f_f, at age x is obtained. The accuracy of both age estimates will depend on the census interval. If an estimate to the nearest interval of 1 yr (x to $x + 1$) is sought, then each individual should be censused at least on every birth day. In practice, of course, any one census will sample many individuals whose birth days vary. Therefore several censuses are needed, especially during the birth seasons. In populations whose average birth days have a large variance, or whose birth schedule approximates the birth flow model, a regular census schedule at intervals of 1-3 mo is desirable.

When the original data are f'_x = number of deaths in each age interval x to $x + 1$, the following calculations are used to derive vital statistics (after Caughley, 1977, p. 91):

$$d_x = \frac{f'_x}{\Sigma f'_x}$$

$$l_x = 1.000 - \sum_{0}^{x-1} d_x$$

$$q_x = \frac{d_x}{l_x} \quad \text{and} \quad p_x = 1.000 - q_x.$$

When the original data are in the form of f_x = number of survivors at age x, the following calculations apply (same source):

$$l_x = \frac{f_x}{f_0}$$

$$d_x = l_x - l_{x+1}$$

and q_x and p_x are estimated in the same fashion as above.

The use of individual life-history records provides the most accurate estimates of life-table statistics; their main disadvantage is the large investment of time and effort needed for their application.

ESTIMATING VITAL STATISTICS FROM STANDING AGE DISTRIBUTIONS SAMPLED AT YEARLY INTERVALS

When a standing age distribution is obtained from the same population two or more times at intervals of 1 yr, any two successive samples may be used to calculate life-table statistics.

The number of survivors, f_x, at the time of the first sample is compared with the number still living, f_{x+1}, 1 yr later in age class $x + 1$. The difference $f_x - f_{x+1}$ is the number that died in the interval x to $x + 1$, or in the year between census dates. The following calculations are used to determine q_x for each age interval (from Caughley, 1977):

$$q_x = \frac{f_x(\text{at time } 0) - f_{x+1}(\text{at time } 1)}{f_x(\text{at time } 0)}.$$

This method has the following constraints:

- The same proportion of the population must be taken at any two samplings. In primate populations this condition is readily fulfilled by sampling the same *set* of troops each time. Hence, individual troops making up the sample must be identified. Sampling the same *number* of troops making up the sample does not meet the stated condition because troops vary in size and composition.
- Any two successive samples should be taken at the same time of year, preferably during the birth season, so that in a birth pulse population the ages of animals will be distributed near their birth days.
- Since most births are unlikely to occur on the day of sampling ($t = 0$), the estimate for the number of births, f_0, might be based on a series of birth censuses.
- The accuracy of estimates of f_x will reflect the accuracy of aging individuals.

DERIVING VITAL STATISTICS FROM FECUNDITY AND SURVIVORSHIP SCHEDULES

The rate at which individuals replace themselves depends on how well they survive and reproduce. Several important measures based on the relationship between fecundity and survivorship are considered below.

ESTIMATING NET REPRODUCTION RATE

The net reproductive rate, R_0, is the rate of population increase per generation. It is a special case of λ, where the time interval t

to $t + 1$ over which the population increase is measured is equal to one generation.

R_0 can also be defined as the average number of female offspring produced by a female during her entire lifetime (Wilson and Bossert, 1971). Thus defined, it is easy to visualize how R_0 would depend on the survivorship and fecundity of females. R_0 is calculated from fecundity and survivorship schedules as follows: $R_0 = \Sigma l_x m_x$.

In Table 7-8 the toque monkey data are used to illustrate the estimation of R_0. Since l_x and m_x are expressed as averages ($\bar{l}_x$ and $\bar{m}_x$) per annum within each age class, and we are interested in the sum of $l_x m_x$ for each year of life, the $\bar{l}_x$ and $\bar{m}_x$ must be multiplied by the number of ages, a_x, in each age class. For grouped data, $R_0 = \Sigma l_x m_x = \Sigma \bar{l}_x \bar{m}_x a_x$.

When $R_0 = 1$, the population is stationary per generation; when R_0 is less than 1, it is decreasing; and when R_0 is greater than 1, the population is increasing. If l_x is calculated with the assumption that $l_x = S_x$ and $r = 0$ (as in Table 7-9), then R_0 must $= 1$. Therefore, R_0 can be estimated from $l_x m_x$ only if the l_x schedule was calculated by methods not assuming $r = 0$.

TABLE 7-8 Calculation of Net Reproductive Rate, R_o, from Fecundity and Survivorship Schedules of Female Toque Monkeys

Age Class (years)	Age or Years per Age Class a_x	$\bar{l}_x$	$\bar{m}_x$*	$l_x m_x = a_x \bar{l}_x \bar{m}_x$
0	1	1.000	0.000	0.000
1	1	0.474	0.000	0.000
2–4	3	0.316	0.000	0.000
5–9	5	0.153	0.352	0.269
10–14	5	0.137	0.362	0.248
15–19	5	0.126	0.406	0.256
20–24	5	0.105	0.442	0.232
25–29	5	0.058	0.143	0.041
			$R_o = \Sigma l_x m_x =$	1.046

*The values of $\bar{m}_x$ (Table 7-3) are based on small sample sizes. If the average fecundity ($\bar{m}_x = 0.344$) for all females is based on a large sample size and is used to estimate R_o, then $R_o = 0.9959$.

Source: W. P. J. Dittus, unpublished data.

ESTIMATING MEAN GENERATION LENGTH

The mean generation length, $\bar{T}$, can be defined as the mean period elapsing between the birth of a mother and the birth of her offspring (Laughlin, 1965). This has also been called the mean cohort generation length.

In mammals such as primates, where a female gives birth to many offspring over a long period, the mean generation length might be more easily understood as the mean interval between the birth of a mother and the birth of a daughter that survives to reproduce herself. Stated in this way, it expresses the average age that a female must attain in order to replace herself once in the population. Of course, if the population is increasing, the mother will replace herself by more than a single daughter.

The formulas used for calculating mean generation length, $\bar{T}$, for populations with overlapping generations (after Caughley, 1977) are as follows. For a birth pulse population,

$$\bar{T} = \frac{\Sigma l_x e^{-rx} m_x x}{\Sigma l_x e^{-rx} m_x}$$

$$= \Sigma S_x m_x x.$$

And for a birth flow population,

$$\bar{T} = L_x e^{-r(x+1/2)} m_{x,\,x+1}(x + 1/2),$$

where $m_{x,x+1}$ is the fecundity between age x and age $x + 1$.

In a birth pulse population where ages are expressed in classes, $\bar{T} = \Sigma \bar{S}_x \bar{m}_x \bar{x} a_x$, where $\bar{x}$ = average age of age class x and a_x = number of birth pulses of ages in years encompassed by age class x and $\bar{S}_x = \bar{f}_x / f_0$.

ESTIMATING EXPONENTIAL RATE OF POPULATION INCREASE

The exponential rate of increase, r, may be estimated from $r = \log_e R_0/\bar{T}$. This estimate of r may be used only if in the derivation of l_x, which is used to compute R_0 and $\bar{T}$, it was not assumed that $r = 0$.

TABLE 7-9 Estimation of Reproductive Values, v_x, for Female Toque Monkeys at Polonnaruwa (1968–1972) when $r = 0$

Age	$\bar{l}_x$	$\bar{m}_x$	$l_x m_x = \bar{l}_x \bar{m}_x \bar{a}_x$	$\sum_{y=x}^{\infty} l_y m_y$	$\frac{1}{l_x}$	$\bar{v}_x = \frac{1}{l_x} \sum_{y=x}^{\infty} l_y m_y$
0	1.000	0.000	0.000	1.046	1.000	1.0
1	0.474	0.000	0.000	1.046	2.110	2.2
2–4	0.316	0.000	0.000	1.046	3.165	3.3
5–9	0.153	0.352	0.269	1.046	6.546	6.8
10–14	0.137	0.362	0.248	0.777	7.299	5.7
15–19	0.126	0.406	0.256	0.529	7.937	4.2
20–24	0.105	0.442	0.232	0.273	9.524	2.6
25–29	0.058	0.143	0.041	0.041	17.241	0.7
		$\Sigma l_x m_x =$	1.046			

ESTIMATING REPRODUCTIVE VALUE

The reproductive value, v_x, is an estimate of the number of female offspring that remain to be born to a female of age x. It is a unitary measure expressing how survivorship and fecundity interact to determine how many offspring a female is likely to produce before dying. Young adult females that are just beginning to reproduce have a long life expectancy and will produce more offspring before dying than will older females. Similarly, juvenile females and very old females with zero or low fecundity have low reproductive values. The "exact" v_x will of course be determined by how survivorship and fecundity interact.

Following Wilson and Bossert (1971), v_x is calculated for each age x as

$$v_x = \frac{e^{rx}}{l_x} \sum_{y=x}^{\infty} e^{-ry} l_y m_y,$$

where y = all the ages that a female has yet to pass through from age x to infinity (death).

Assume, as in the example from the toque monkey in Table 7-9, that $r = 0$. Then, the formula for the calculation of v_x simplifies to

$$v_x = \frac{1}{l_x} \sum_{y=x}^{\infty} l_y m_y .$$

To find $\Sigma_{y=x}^{\infty} l_x m_y$ for any age x, we first assign the sum of the $l_x m_x$ schedule to age 0. Thereafter, for each age (or age class) $\Sigma_{y=x}^{\infty} l_y m_y$ is computed by subtracting $l_x m_x$ of the preceding age from the $\Sigma_{y=x}^{\infty} l_y m_y$ of the preceding age. For example, from Table 7-9 $\Sigma_{y=x}^{\infty} l_y m_y$ of age class $x = 10\text{–}14$:

$$\sum_{y=x}^{\infty} l_y m_y = 1.046 - 0.269 = 0.777.$$

The average $\bar{v}_x$ per age class is the product of the reciprocal of $\bar{l}_x$ and $\Sigma_{y=x}^{\infty} l_y m_y$ appropriate to each age class. For female toque monkeys of age class $x = 10\text{–}14$, for example,

$$\bar{v}_{10\text{–}14} = \frac{1}{0.137} \times 0.777 = 5.7.$$

The values of $\bar{v}_x$ are plotted against age in Figure 7-5. At birth, $v_0 = 1$; the average female replaces herself once per generation in this population for which we have assumed $r = 0$.

For a more detailed discussion of the estimation of reproductive values, see Wilson and Bossert (1971).

Reproductive value is preeminently of genetic and evolutionary interest because it indexes the force of selection acting on behavioral and other traits that differ by age.

DISPERSAL

The process of dispersal whereby animals leave their natal group to live and reproduce elsewhere is of interest for two reasons. First, the disappearance of an individual through dispersal must be distinguished from its death if estimates of mortality are to be correct. Second, the rates at which individuals of different age and sex disperse are of interest in themselves from the point of view of genetic interchange between populations.

From the perspective of the biologist studying a population, movements of individuals can be considered at two levels: intra-

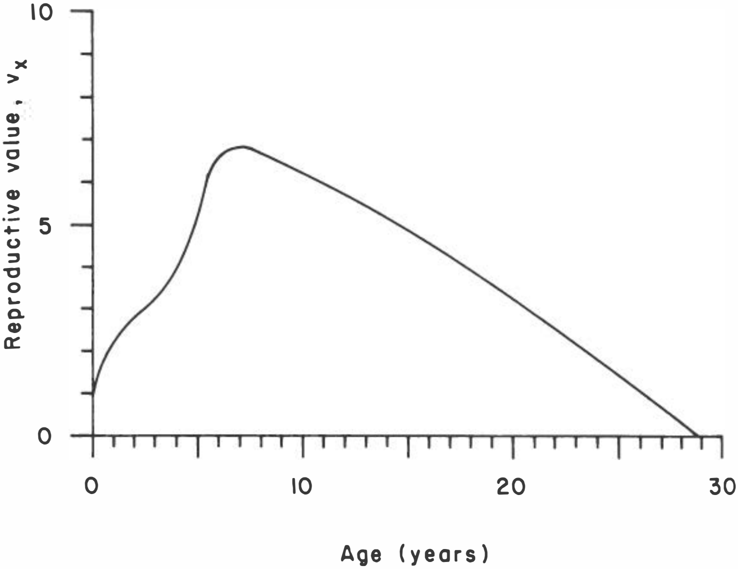


FIGURE 7-5 The reproductive values, v_x, of female toque monkeys at different ages. After Dittus, 1979.

population and interpopulation movements. Primatologists have referred to the former as intergroup transfer of individuals. The distinction between intra- and interpopulation movements is merely one of sampling convenience; biologically they are similar, except perhaps for the difference in the distances moved and the genetic implications this may have. For interpreting demographic events within the sample population, it is important to know rates of movement into and out of the population. For example, if a high proportion of males leaves the study population every year, and they are not replaced by an influx of an equal number of males, the mortality of males in the population might be overestimated.

Intrapopulation movements have little influence on the demographic sample and therefore have little bearing on estimates of life-table statistics. However, knowledge of such movements is important for correctly assessing interpopulation movements.

The best estimates of intra- and interpopulation movements are based on individual life-history records. With respect to any one social group or population, there are two kinds of movements: emigration and immigration. For analysis, a distinction between the following types is useful:

Type 1: In intrapopulation emigrations, an individual is known to have left one social group and has joined another within the sample population.

Type 2: Intrapopulation immigrations are the same as intrapopulation emigrations.

Type 3: In interpopulation emigrations, an individual is known to have left a group within the sample population and has joined a group outside the sample population.

Type 4: In interpopulation immigrations, a new individual not previously seen in the population appears in a census.

Type 5: Disappearances occur when a previously censused individual is no longer sighted and its fate is unknown.

Note that in these considerations the membership of the sample population is defined by the sum of the memberships of all the social groups in the population. With these distinctions in mind, estimates might be made of rates of transfer between social groups within a population and of those between populations.

ESTIMATING RATES OF TRANSFER BETWEEN SOCIAL GROUPS

The raw data for estimating rates of intergroup transfer are (1) number of individuals whose life histories are being traced, (2) duration for which their histories are being traced, and (3) the number of transfers each individual has made during the period of observation. Since there is a category of "unknown fates" (Type 5), the exact rates of movements cannot be estimated, but a minimum and maximum can be estimated.

To find rates, the minimum and maximum numbers are found first:

Minimum number of emigrations = total of Type 1 plus Type 3.
Maximum number of emigrations = total of Types 1, 3, and 5.

TABLE 7-10 Estimation of Minimum and Maximum Rates of Emigration for Toque Monkeys of Different Age and Sex at Polonnaruwa Between 1968 and 1972

Age-Sex Class	No. Monkey-Years of Observation	No. Emigrations		Rate of Emigration		Average Interval per Capita Between Emigrations (years)	
		Min.	Max.	Min.	Max.	Max.	Min.
Adult males	58.73	10	14	0.170	0.238	5.9	4.2
Adolescent males	24.19	7	12	0.289	0.500	3.5	2.0
Adult females	131.80	0	1	0	0.008	0	131.8
Infants and juveniles of either sex	> 100.0	0	0	0	0	0	0

Source: After Dittus, 1975.

Minimum number of immigrations = total of Type 2 plus Type 4.
Maximum number of immigrations = same as the minimum.

To calculate rates, one finds the total number of monkey-years of observations per individual, or for a class of individuals. Estimates of emigration are given in Table 7-10 for different age and sex classes of toque monkeys at Polonnaruwa. Rates are found by dividing the number of immigrations or emigrations by the number of monkey-years observed for a class or individual. An example taken from Table 7-10 shows that the minimum rate of emigration for adult male toque monkeys is 10 emigrations per 58.73 adult male monkey-years, which is 0.170 emigrations per monkey per year. The reciprocal of such rates gives the average interval of time between successive emigrations. Adult male toque monkeys, for example, emigrate maximally at an average of once every 1/0.170 = 5.9 yr.

ESTIMATING RATES OF MOVEMENT BETWEEN POPULATIONS

The dynamics of dispersal between populations is likely to be the same in kind as between social groups. Knowledge of the latter therefore is useful for predicting movements between populations. For example, from Table 7-10 it is highly unlikely that adult females or infants and young juveniles shift between populations because they appear not to leave their social groups.

If we consider a set of troops to constitute the sample population, the number of individuals moving into and out of the population is estimated as follows:

Minimum number of emigrations = total of Type 3.
Maximum number of emigrations = total of Type 3 plus Type 5.
Minimum number of immigrations = total of Type 4.
Maximum number of immigrations = same as the minimum.

These numbers are expressed as rates by dividing them by the total number of monkey-years of observation appropriate to the class in question.

Finding individuals that have left the population is probably the most difficult task in population analysis. Methods for assessing such movements accurately are beyond the scope of this chapter; see Caughley (1977) for general approaches to this problem.

An indirect assessment of the fate of animals that frequently disappear might be obtained by censusing populations adjacent to the study population. If an unusually high proportion of the age-sex class whose members frequently disappear shows up in an adjacent population, emigration from the sample population might be seriously suspected.

MORTALITY VERSUS EMIGRATION

Estimates of intrapopulation movement indicate which age and sex classes are subject to emigration. The disappearance of individuals of a class that does not emigrate can be safely assumed to have died. With some notable exceptions, female and young juvenile primates do not emigrate from their natal groups.* The males of many species, however, do emigrate from their natal groups as adolescents, and as adults they continue to shift between groups (Dittus, 1980). If estimates of mortality are based on individual life-history records, the disappearance of a male may be interpreted as either death or emigration.

In populations where it can be assumed that immigration and emigration are equal, mortality can be estimated independently of dispersal by applying methods based on standing age distributions. (See "Estimating Vital Statistics from a Stable Standing Age Distribution" and "Estimating Vital Statistics from Standing Age Distributions Sampled at Yearly Intervals," above.) The survivorship and mortality schedules of male toque monkeys (Figures 7-2 and 7-3) are based on such independent derivations.

In speculations concerning the fate of individuals it is generally considered "conservative" to attribute such losses to emigration. Whether this is conservative in the sense of being the "most likely" biological outcome or of projecting human values to

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*For the exceptions, see Chivers (1974)—siamang gibbons; Harcourt *et al.* (1976)—gorilla; Kawanaka and Nishida (1975) and van Lawick-Goodall (1973)—chimpanzee; and Marsh (1979) and Struhsaker and Leland (1979)—red colobus.

demographic events is open to question. If all males that disappeared from a population had merely emigrated and such emigration was common in other populations as well, then somewhere there must be a large reservoir of emigrated males. Such a population has yet to be found in primate demographic studies. Lone males and all-male groups must, of course, be incorporated into any valid demographic sample.

SUGGESTED READINGS

The following are excellent introductions to the study of animal populations: Caughley (1977), Eberhardt (1968), and Wilson and Bossert (1971). The book by Caughley is especially recommended as a clear and practical manual.

Some other important publications are: Andrewartha and Birch (1954), Caughley (1966, 1967), Deevey (1947), and Pielou (1969).

8

Determinants of Population Density and Growth

In the foregoing chapters, methods for measuring a variety of physical, floral, and faunal parameters of the habitat were discussed. In this chapter the relationships between some of these variables are discussed in light of their influence in determining population size in relation to environmental factors.

MEASURES OF POPULATION SIZE IN RELATION TO THE ENVIRONMENT

ESTIMATES OF DENSITY AND BIOMASS

In estimating the vital statistics of a population, knowledge of only the numbers of animals is relevant. Often, however, population size is expressed as a density, which is defined as the number of animals per unit area. Statements of density express an interest in the relationship between a population's numerical size and its environment.

Density is often converted to biomass by multiplying the number of individuals in the population by their average weight. Accurate estimates of biomass should take into account differences in the numbers of animals of different body sizes (or ages) in the population. Thus, expressed mathematically,

$$\text{Biomass} = \frac{\sum_{x=1}^{x=j} n_x \overline{W}_x}{A},$$

where n_x and $\overline{W}_x$ are the number and average weight, respectively, of individuals in age class x, there being a total of j age classes, occupying an area of size A. The weight of inert gut contents may be subtracted in estimates of mean weights.

The biomass of a species roughly represents the amount of resources or energy that it extracts from an environment. Since species vary in body size, such interspecific comparisons based on numbers alone would be inadequate. It is desirable to express densities in terms of biomass because it provides some measure of the importance or impact that a species has on an environment relative to other species. Comparisons of biomass can be made between different age classes within the same population (e.g., adults versus juveniles or males versus females) or between species, higher taxonomic groupings, or ecological groupings (e.g., folivorous versus frugivorous primates).

Different methods for estimating densities and their corresponding biomasses are in use. The following definitions are useful:

Crude density refers to the number of animals within a defined geographic area without regard to the suitability of the area for supporting the species in question. Estimates of crude density are useful only for reporting numbers of animals in a defined area, such as a game reserve or census plot. The area itself may encompass a diversity of habitats, some of which are totally unsuitable for the species in question.

Ecological density refers to the number of animals per unit area of suitable habitat. Estimates of ecological density may be higher than those of crude density if the latter incorporates areas not inhabited by the species of interest.

The most accurate method for estimating ecological density involves charting the actual area of land or home ranges that a set of troops or a population has been observed to be using. Usually this requires a long-term intensive survey of a relatively small area of land. Eisenberg (1979) reviewed density estimates for neotropical primates made by 24 different authors. For meaningful comparisons he found it useful to separate density estimates according to the method of data collection. For example, for each of the following species the first and second values from each pair of density estimates are based on the home range method and on a less intensive survey method, respectively: *Callithrix torquatus*, 20/km^2 and 15/km^2; *Cebus capucinus*, 130/km^2 and 70–90/km^2; *Alouatta palliata*, 60–80/km^2; *Alouatta seniculus*, 160/km^2 and 86/km^2. In each case the estimate of ecological density based on the home range method was greater than that based on a broader, less-intensive survey method. Probably the latter method involves the risks of underestimating the number of animals occupying a large area and of incorporating habitats of variable suitability.

Eisenberg (1979) called ecological densities based on the intensive home range method "K density," on the assumption that these densities are probably close to the mean equilibrium density (see below) for the species in question within the particular environment where the measurements were carried out.

It is evident from these considerations that the method used for estimating density should be clearly spelled out in reporting estimates of density.

MEAN EQUILIBRIUM DENSITY (K)

Figure 8-1 illustrates the pattern of changes in a hypothetical population having an annual birth pulse.

Observations of growing populations have indicated that they eventually reach an endpoint of no more growth. Although population density may fluctuate, the mean value of population density remains fairly constant through time. This value has been called the asymptotic density, or the mean equilibrium density, and has been designated by the symbol K.

K relates to the rate of population growth, r, and to any measure of population density, n, as follows. In growing populations, $r > 0$, $n < K$. In declining populations, $r < 0$, $n > K$. In

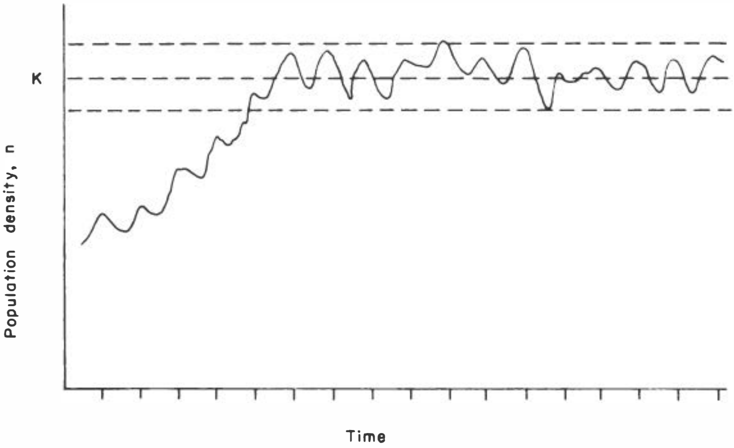

FIGURE 8-1 Changes in population density, *n*, in a hypothetical population having an annual birth pulse and increasing in density until it reaches its mean equilibrium density, *K*. The carrying capacity of the environment is defined by *K* rather than by the maximal (n_2) or minimal (n_1) values fluctuating about the mean *K*.

stationary populations at equilibrium, $r = 0$, $n = K$. It is evident that any measure of population density, n, is not necessarily equivalent to K. One may assume that $n = K$ only if the average population density over several years remains constant; or, if calculations based on other demographic parameters indicate that the rate of population growth, $r = 0$ for some time. The value of r is determined by the sum of the rates of birth (b) and immigration (im) minus the sum of the rates of death (d) and emigration (em); i.e., $r = (b + im) - (d + em)$; or, if $im = em$, $r = b - d$.

Since K is in part a function of environmental stability (see below), it is sometimes assumed that $n = K$ if all other evidence points to long-term environmental stability. Such an assumption is less satisfactory than estimates of $\bar{n}$ over several years.

THE CONCEPT OF CARRYING CAPACITY

The mean equilibrium density, K, varies both with the features of the species and of the environment. The fact that different values of K may be reached by the same species in different environments, or by the same population at different times, has emphasized the importance of the environment in determining K. As a result the focus of interest often is the environment itself, which may be discussed in terms of its "carrying capacity" with respect to a particular population, species, or group of species. Thus, carrying capacity is often used in an abstract sense in comparing the relative qualities of different environments. It must be recognized, however, that the many factors that determine the quality of the environment and, ultimately, the value of n or K are not always known or easy to measure. For example, the food supply has a major influence on population density. Yet it is doubtful whether absolute food availability can ever be measured, except perhaps in very simple environments. In contrast, the measure of K either in numbers of individuals or in biomass is fairly straightforward. For convenience, therefore, carrying capacity is defined in terms of K, or, as the maximum mean density of a species that an environment can support on a sustained basis without being degraded.

In such assessments, carrying capacity is represented by the actual *mean* equilibrium density, K, rather than by the temporary maximal or minimal fluctuations away from the mean, particularly if such fluctuations are short term, as result, for example, from an annual birth pulse (Figure 8-1). One should also be aware that predation or disease may depress population density, n, below its potential maximal K. Or, a rare environmental event, such as a severe drought, may temporarily depress K below its usual maximal value. On the other hand, an environmental change may be more permanent and alter the long-term carrying capacity for a particular species. Thus a change in n may indeed reflect a real change in K. One might suspect a change in carrying capacity especially if n changes over the long term. It is evident that the nature of such interrelationships is best understood through a close study of both the environment and the population and preferably over a long term.

Despite the limitations in measuring some environmental features, one can often gain a fairly good appreciation of the nature of ecological interrelationships from correlated changes among measures of different environmental factors. Whether or not one may assume that such correlations represent cause and effect events depends on the quality of the information.

Because of the complexity of the relationships that determine carrying capacity, one generally does not prove, but assumes, that a population's constant size may represent its mean equilibrium density with respect to the carrying capacity of the environment.

DETERMINANTS OF POPULATION SIZE

The causes and mechanisms responsible for changes in population size are of central interest in ecology. They may be approached at four levels: (1) measurement of the demographic processes underlying changes in population size or density, (2) identification and measurement of the environmental factors that may cause demographic changes, (3) measurement of annual fluctuations in food, and (4) identification and measurement of the behavioral and physiological mechanisms through which environmental factors affect demographic processes. The last two levels are discussed in detail later.

DEMOGRAPHIC PROCESSES

This method was discussed in Chapter 7, which deals with population analysis. In that chapter we identified the basic data required for measuring demographic events and formulated the manner in which demographic processes determine population growth rates (e.g., R_0).

ENVIRONMENTAL FACTORS

We have noted that many environmental factors influence population size and that the observable mean equilibrium density (K) for a species may vary between habitats or over time within the same population. Several of the physical and biological factors that ultimately influence densities of a population (or the carrying capacity of the habitat to support that population) are discussed below. A simplified hierarchy of interrelationships between these factors is given in Figure 8-2.

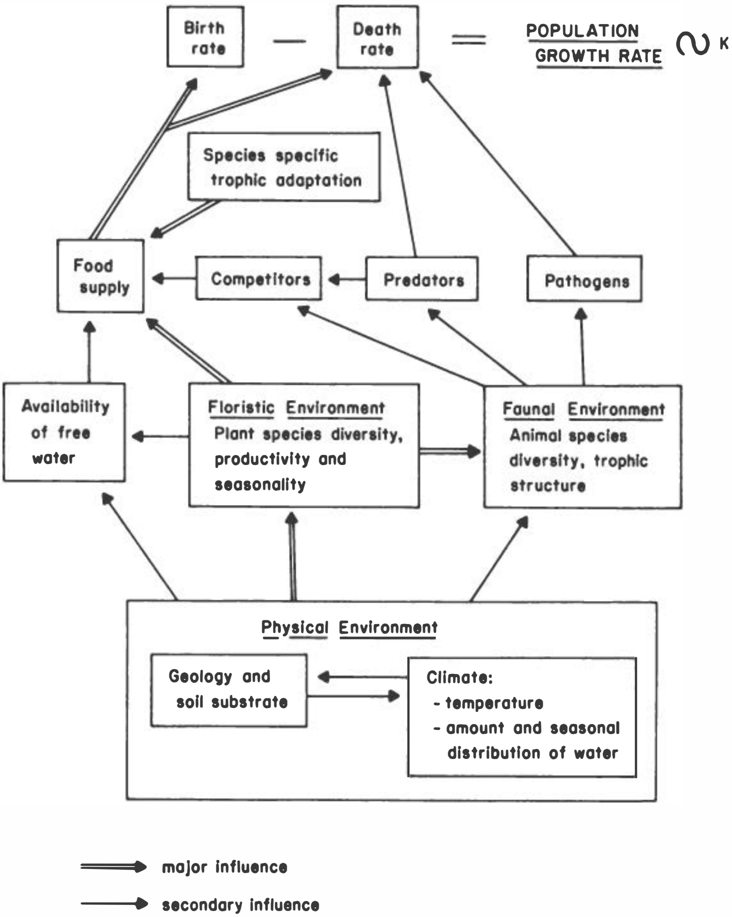

FIGURE 8-2 Interrelationships among physical and biological factors that influence the population growth rate and mean equilibrium density of a species.

Physical Factors

Basically, the physical environment determines the diversity and abundance of plant life, on which all animals ultimately depend. Therefore, information concerning the physical world is useful for making predictions concerning the biological communities one might expect in a specific area.

On a global scale the warm lowland and tropical regions support more diverse plant and animal communities than do the colder temperate or high montane areas. Areas of high rainfall that is evenly distributed throughout the year are richer in life than those of low or seasonal rainfall. On a local scale the location of oceans and mountain ranges in relation to prevailing wind currents affects temperature and rainfall patterns. For example, areas on the windward side of montane zones are generally drier and warmer than those on the leeward side.

The effect of physical parameters can be more subtle, as in the Amazon rain forests where areas subject to nutrient-rich flood waters support a greater diversity and abundance of life forms than do areas that are not flooded, despite minor differences in rainfall or temperature between these areas. Similarly, in areas of equivalent rainfall and temperature, porous soils support less life than those that retain water.

In classifying the world's vegetation into major types, such as savanna grassland, deciduous forest, semi-evergreen forest, and evergreen rain forest, Walter (1971) found the parameters of temperature, total rainfall, and the duration of drought in the annual cycle to be the most useful variables in predicting major vegetation types, despite variations in the taxonomic composition of the forest types.

Biological Factors

The density of a studied species may vary between habitats having similar physical characteristics but differing in species composition. A biological community is composed of the vegetation that gives structure to it and the fauna that directly or indirectly depends on it for food and shelter—the consumers, competitors, predators, and pathogens.

The type of vegetation will in large part determine its dependent animal populations. For example, stable savanna grasslands support large and diverse populations of grazers and predators that prey on these grazers, whereas tall rain forests support fewer terrestrial animals. Instead, tropical forests support a larger biomass of arboreal browsing folivores and frugivores (Eisenberg and Thorington, 1973). Moist semi-evergreen forests support a higher density of primates than semi-deciduous dry forests

(Eisenberg *et al.*, 1972), and even within small geographic areas, the diversity of the vegetation correlates with the diversity of primate species it supports (Struhsaker, 1975).

The food supply is a major factor influencing the size of primate populations (Dittus, 1977a, 1980). The amount of food that is available to a species is determined by a variety of factors, including the species' trophic adaptations, the diversity and productivity of the vegetation in the habitat, and competition from other animals. These factors are not wholly independent of one another but interrelate in a complex fashion. These relationships and how they might be measured are examined more closely in the next section.

The natural food supply for any primate is likely to fluctuate in abundance during the yearly cycle. Many vertebrates and invertebrates share the foods that are eaten by a particular primate species. If the food supply is limiting, competition from these animals is likely to have its greatest effect during the season of least food abundance. The extent of competition needs to be established empirically in each community.

Indirectly, the vegetation will also influence the occurrence of predators for primates. The influence of predation can be estimated by making a faunal list of potential predators in an area and then making a rough estimate of mortality from predation through long-term observation. The incidence of predation on a given primate species can also be assessed indirectly through examination of fecal scats of predators for remains of the primate of interest. Leopards, for example, exist primarily on prey species, such as deer, antelope, and pigs, that inhabit savanna and savanna woodlands. Although primates are not a major food item in the leopard's diet (Muckenhirn and Eisenberg, 1973), they nevertheless are subject to leopard predation in habitats that support the leopard's main prey animals. Most field studies of medium-to-large primates have indicated a low incidence of predation.

It is generally assumed that most populations of large vertebrates have become adapted or fairly resistant to the pathogens natural to their populations, and large-scale reductions in their populations through disease have been thought to be rare. The widespread episodic heavy mortality observed among South American howler monkeys, *Alouatta* sp. (Collias and Southwick, 1952), may represent an unstable relationship between *Alouatta* and the yellow fever virus that was introduced from Africa more than 200 yr ago. The case exemplifies how an introduced pathogen can decimate populations that have not fully adapted to its virulence. The proportion of mortality in natural populations that is attributable to pathogens can be assessed only through close studies directly addressing this problem. Morbidity and mortality statistics are unavailable for primate populations that may be affected by parasites and diseases such as yellow fever, malaria, tuberculosis, Lassa fever, and Marburg virus. Since resistance to disease may be in part a function of other factors, such as nutritional state, wounding, or age, its effect on mortality is not easily isolated from that of other factors (Freeland, 1976).

FOOD SUPPLY AS A MAJOR FACTOR DETERMINING POPULATION SIZE

Consideration of food supply in relation to population size involves three aspects: (1) the dietary intake of a species, (2) the diversity and productivity of food plants relative to the food items consumed, and (3) the manner in which food supply influences demographic parameters. Methods for estimating the diet were described under "Feeding Ecology" in Chapter 6. Methods for estimating the diversity, productivity, and phenology of plants were described in Chapter 3. In addition to the productivity of food plants in the habitat, the amount of food that is available to a primate population depends on the primate's trophic adaptations and the abundance of competitors that feed on or otherwise destroy the same foods.

TROPHIC ADAPTATIONS

Trophic adaptations include all those morphological and behavioral traits that allow a species to collect, chew, and digest food. Trophic adaptations should not be confused with "trophic level," which defines a species' role in the flow of energy within an ecological community. Prehensile tails and modifications of dentition and the digestive tract are examples of trophic adaptations.

Prehensile tails, for example, allow South American cebids to hang from sturdy branches in order to reach plant food items at the ends of flimsy twigs that they would not be able to reach otherwise. The long hooklike arms and hands of gibbons and siamangs serve a similar purpose (Grand, 1972, 1978).

Strong incisor teeth in savanna-dwelling baboons aid in the uprooting of tubers and roots, and modification of the molar teeth aid leaf-eating primates in chewing mature fibrous leaves (Kay, 1978). The most striking trophic adaptation may be the ruminantlike digestive system of leaf-eating primates. The foreguts (in the Colobinae) or the caecum (in the Indridae and Alouattinae) are highly specialized as fermentation chambers supporting symbiotic microbes that break down the tough cellulose in mature leaves (Bauchop, 1978). Since leaves are much more abundant than flowers and fruits, leaf-eating primates have available to them a much greater store of food than do non-leaf-eating primates. As a result, leaf-eating monkeys occur at much higher densities than non-leaf-eating primates sharing the same habitat (Eisenberg *et al.*, 1972; Struhsaker, 1975).

Estimation of a species' trophic adaptations therefore includes documentation of anatomical adaptations or specializations relevant to the acquisition, processing, and digestion of food; behaviors used in the acquisition and processing of various food items; and the diet.

RELATIONSHIP BETWEEN THE DIVERSITY AND PRODUCTIVITY OF FOOD PLANTS AND POPULATION SIZE

The diversity of primate species correlated positively with the diversity of tree species in the rain forests at Kibale, Uganda (Struhsaker, 1975), and New Indenau, Cameroun (Gartlan and Struhsaker, 1972). Conceivably, primate diversity is a function of the diversity of ecological niches. Thus, as floristic diversity decreases, the diversity of exploitable feeding niches decreases until at some point the carrying capacity of the habitat is reduced to zero for some species.

To a large extent, climatic and edaphic (or local ecological) factors determine both the diversity and productivity of a forest type; in an undisturbed forest, diversity and productivity are likely to be positively correlated. Thus, an attempt to distinguish the effects of each factor on the density or biomass of a particular species may be difficult. An example taken from Sri Lanka shows that all tree species found in the forests at Wilpattu are also found in those at Polonnaruwa, but not vice versa, so that the Wilpattu forests have a lower diversity (Table 8-1). Forest productivity is also lower at Wilpattu than at Polonnaruwa. The biomass of primate species found at Wilpattu is less than in the more diverse and productive forests at Polonnaruwa, as is predicted by this correlation. Such a correlation does not hold, however, for comparisons of primate biomass between the forests at Polonnaruwa and Horton Plains. Although forest diversity and productivity are greater at Horton Plains than at Polonnaruwa, the biomass of all three primate species there is considerably less. In such cases, knowledge of the nutritional requirements of the

TABLE 8-1 Differences in Biomass Among Species of Primates in Three Forest Habitats and Climatic Zones of Sri Lanka

	Wilpattu	Polonnaruwa	Horton Plains
Climate			
Average annual rainfall	1,200 mm	1,671 mm	2,000 mm
No. months drought per annum	4–5	2–4	none
Forest Type	arid scrub	semi-evergreen	montane cloud evergreen
Forest productivity in metric tons/ha/yr[a]	2	4.5	5
Tree species diversity[b]	low	moderate $H'(ln) = 2.97$[c]	moderately high
Primate Biomass (kg/km^2)[d,e]			
Macaca sinica	1	300	<40
Presbytis entellus	19	730	0
Presbytis senex	0	1,430	630

[a] Hladik and Hladik, 1972.
[b] Dittus, 1977b.
[c] See Chapter 3 for derivation of Shannon Index.
[d] Eisenberg *et al.*, 1972.
[e] Dittus, 1977c.

species in relation to the relative abundance of available foods in the different forest habitats may provide a clue for this apparent contradiction. For example, the macaque's preferred foods at Polonnaruwa are the fruits of seven species of fig trees (*Ficus*). In the montane forest at Horton Plains, figs are absent. Thus, despite the greater overall productivity of the montane forest, the productivity and diversity of the plants on which the macaques depend are less than at Polonnaruwa. This probably explains the lower biomass of macaques at Horton Plains. It is obvious from this example that a great deal of ecological information is required to draw conclusions concerning ecological relationships.

EFFECTS OF FOOD SUPPLY ON THE VITAL STATISTICS OF A POPULATION

The relationship between food supply and the demographic parameters that determine *K* density are illustrated by the following examples:

- Natural populations of vervet monkeys, *Cercopithecus aethiops*, and of yellow baboons, *Papio cynocephalus*, decreased in size by over 40% and 90%, respectively, as a result of the destruction of their natural food plants through edaphic changes in the Masai-Amboseli Game Reserve in Kenya (Hausfater, 1975; Struhsaker, 1973, 1976). The natural population of toque macaques, *Macaca sinica*, decreased by 15% as a result of a drought; but during the same drought period, the population increased by 60% in an area where artificial feeding occurred (Dittus, 1977a). Declines in the populations of vervet monkeys and toque macaques were attributed to an increase in mortality among juveniles, especially the youngest juveniles (Dittus, 1977a; Struhsaker, 1976). In Nepal, rhesus macaque, *M. mulatta*, populations are food-limited in relatively undisturbed habitats. Although natality declines at high densities, mortality increases in the juvenile and adult age classes (Southwick *et al.*, 1980).
- Populations of rhesus macaques, *Macaca mulatta*, and of Japanese macaques, *M. fuscata*, that have been provisioned with food by man have grown at annual rates of 16% (Koford, 1965) and 9% (Dittus, 1980, after Itani, 1975), respectively, and exist

at densities that are over 10–100 times higher than those in their natural habitats (Dittus, 1975). Compared with the wild nonprovisioned population of *M. sinica*, where $r = 0$, in the growing populations of *M. mulatta* and *M. fuscata*, the mortality among juveniles was less and the natality was greater (Dittus, 1975).

- The Koshima colony of Japanese macaques was heavily provisioned with food for many years and increased in size. Then artificial feeding was decreased, and the population declined. Comparisons of vital statistics from the period of food surplus and population growth with statistics from the period of food scarcity and population decline indicated the following changes: infant mortality increased from 15 to 68%; the average natality decreased from 66 to 32%; and the average age at first birth in females increased from 6.2 to 6.8 yr, and in some females first birth was delayed until the ninth year of life (Mori, 1979).

Together these data suggest that the food supply is of utmost importance in limiting the density of some if not all primate populations and that food supply has its effect on population growth rate by influencing mortality, natality, and age at onset of reproduction. These relationships have been examined in greater detail by Dittus (1977a, 1979, 1980), who presents evidence to suggest that social behavior, or competition for food and mates, in large part mediates mortality and natality in relation to the availability of limiting resources. In short, social behavior regulates the size and age-sex composition of many primate societies in relation to the food supply, in a fashion that maximizes the reproductive success of some of its members.

POPULATION REGULATION BY BEHAVIORAL AND PHYSIOLOGICAL MECHANISMS

This section deals with the manner in which environmental factors can influence the vital statistics in a primate population—its rates of mortality, fecundity, and maturation. A flow diagram (Figure 8-3) is presented to clarify important relationships between environmental factors and behavioral and physiological factors that ultimately influence demography. The various relationships are discussed in turn.

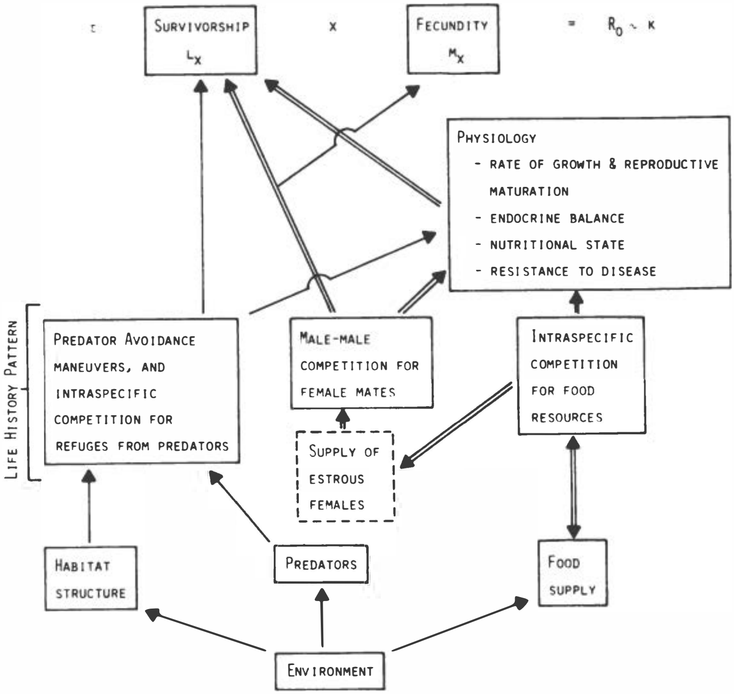

FIGURE 8-3 Flow diagram of hierarchical interrelationships among environmental, behavioral, and physiological factors that determine population growth rate and equilibrium density.

IDENTIFYING AND MEASURING INTRASPECIFIC COMPETITION FOR RESOURCES

Competition occurs when a number of individuals (or groups) utilize common resources that are in short supply or, regardless of whether the resources are in short supply, when animals (or groups) harm one another in utilizing the same resources (modified after Krebs, 1972).

Competition can be measured directly through observation and recording of behaviors. Prerequisites to such recording are good observation conditions and well-habituated animals that are not disturbed by the proximity of an observer.

The first step in measuring competitive behaviors is their identification. The investigator should familiarize himself with gestures of communication used by the primate under study.

In most primates, unequivocal competitive behaviors can be recognized in situations when (1) one individual removes food from the hands, mouth, or cheek pouches of another and consumes it while the exploited individual attempts to resist such robbing or (2) one individual displaces another engaged in feeding and consumes the abandoned food. Such displacements may involve the use of physical force, such as biting, hitting, or pushing; more frequently it involves only a threat gesture or simply an approach.

More subtle competitive behaviors involve the gradual encroachment and displacement of another individual from the vicinity of a desired resource. Displacements need not involve only food items or water; they may involve, for example, priority of access to a safe perch when scrambling to avoid a predator or an aggressive conspecific or when selecting secure sleeping perches.

Some competitive acts may involve more than two individuals, as in coalitions of two or more individuals against a target animal. Similarly, whole groups may defend their feeding territories against other conspecific groups, or a group may simply defend or avoid a particular feeding site in areas of home range overlap.

The type of hypothesis formulated concerning competitive behaviors will define the method used for its testing. As a general guide, the focal-animal sampling method, in which each individual in the social group is identified and followed for a fixed duration, is suggested as one that can be modified to suit many needs. The observation period will be determined by the total time it takes to collect a sample of behavioral frequencies that is sufficiently large to test the hypothesis statistically. A minimum of 10 h of direct observation per individual is suggested. For species with low interaction rates, such as langurs, a longer duration may be required.

For each minute of observation the subject animal's activity (e.g., feeding, resting, grooming) and behavioral interactions with others are recorded. One might also record food type consumed and distance to other animals (nearest neighbors). Since data are specific to identified individuals, frequencies or durations of behaviors, foods consumed or "competed for," and the like can be analyzed according to individual attributes such as age, sex, reproductive state, and genealogy. For further details concerning the collection and analysis of such data, see Dittus (1977a).

Socially dominant animals are those that have priority of access to food and other contested resources. Socially subordinate animals are ones that do not have such priority of access. In a detailed study of the effects of competitive behavior in the toque macaque, *Macaca sinica*, Dittus (1977a) showed that relative to socially subordinate animals, dominant ones have the following advantages:

- Dominant animals expend less time or energy in searching for food items because they frequently usurp food from subordinates who have expended time and energy in locating it.
- They feed at sites where food is most abundant and therefore feed at faster rates.
- They consume a greater proportion of foods that are high in caloric or nutritional content.
- They have a faster rate of growth or weight.

In addition, dominant mothers have a higher fecundity than subordinate ones, and their offspring survive better than those of subordinates (Dittus, 1979; Drickamer, 1974).

Dominance differs according to an individual's age, sex, and genealogy. Dittus (1977a) showed that mortality patterns by age and sex for toque macaques closely follow the differences by age and sex in successful food competition. Competition for resources was thought to be a major cause of mortality.

The general pattern of mortality in most mammals is one of high mortality early in youth and decreasing mortality toward adulthood. Mortality curves differ between the sexes in several species (Ralls *et al.*, 1980). Individuals that survive to reproductive age generally have a long life (Caughley, 1966).

Most primates appear to adhere to this pattern, and it is likely that food competition is a major factor in adjusting primate population density to the food supply (Dittus, 1980). When the food supply changes, food competition affects survivorship among infants, young juveniles, and old individuals the most

(Dittus, 1977a; Struhsaker, 1976). Such competition is exhibited within social groups but may also occur between them, as in intergroup dominance hierarchies or in territorial behavior.

MATE COMPETITION

The different reproductive roles of males and females subject them to different life histories. Although both males and females compete for food resources, males may also compete for mates. Mate competition occurs when males fight or otherwise vie over mating access to estrous females. The frequency of such behaviors can be documented through focal-animal sampling techniques similar to those outlined above. Primate studies that have investigated mate competition (Dittus, 1977a; Lindburg, 1971; Vandenbergh and Vessey, 1968; Wilson and Boelkins, 1970) indicate that males are frequently wounded and die as a result of wounds incurred in fights with other males.

The life history of young males may involve their emigration from the natal troop at adolescence. Such emigrant adolescent males attempt to attach themselves to other social groups. In these attempts they are frequently forced to assume a subordinate position peripheral to the troop. As a result of food competition and of fighting with other, often stronger, adult males over female mates, they are frequently wounded and die. Male mortality reaches a peak during the adolescent phase and decreases with the attainment of adulthood. In adulthood, males continue to transfer between social groups, albeit at a lower rate than during adolescence (Boelkins and Wilson, 1972; Dittus, 1975; Kawai and Yoshiba, 1968). Because of such emigrations and the intense mate competition in their adult lives, adult males suffer higher mortality than adult females. The latter generally do not fight for mates, nor do they emigrate from their natal troop (for exceptions, see Chapter 5).

Male-male competitive behavior in some species—for example, many colobines—may involve the killing of infants fathered by other males (Hrdy, 1974; Rudran, 1973b; Struhsaker, 1977; Sugiyama, 1967). Such infanticide has two benefits for males. First, females whose nursing infants die come into estrous sooner than if their infants had lived and continued to nurse. Therefore, such a female is "freed" to conceive the infant of the infanticidal male sooner than if her first infant had continued to live. That is, the male increases the number of infants he can sire, or he enhances his fitness (Hrdy, 1974; Struhsaker, 1977). Second, males generally practice infanticide only at the time of first taking over a troop and displacing the resident male from it. If food resources are limiting, the new male leader who kills the infants sired by the deposed male eliminates food competitors for himself and especially for his own young. Because his own offspring would be younger, and therefore subordinate to the infants of the deposed male leader, they would stand to lose the most in food competition with the older, dominant infants. The infanticidal male therefore enhances the survivorship of his own infants by eliminating the most likely food competitors for his own offspring (Dittus, 1979; Rudran, 1979).

Regardless of the source of mortality, be it resource competition, mate competition, or the outright killing of individuals as in infanticide, such behaviors have a direct effect on the vital statistics of the population and on its growth rate and density. To test whether such behaviors are truly regulatory would involve documenting behaviors and their different effects on demography under different environmental conditions or under different phases of population growth (Dittus, 1977a).

POPULATION REGULATION IN RELATION TO LIFE HISTORY

The regulatory factors or behaviors one might expect a primate species to exhibit are predisposed by its life history. Although food competition is likely to affect all age and sex classes in most primate species, mate competition, as outlined above, appears to be most prevalent among sexually dimorphic species where males are larger than females. With the exception of the study of the toque macaque that directly addressed the question of population regulation (Dittus, 1977a), documentation of such regulation is fragmentary. The evidence for population regulation in other primates has been reviewed (Dittus, 1980).

Among monomorphic species where male-male competition for mates is less prevalent, and where both males and females may emigrate from their natal troops, one might expect male mortality through mate competition to be minimal, and females might be subject to mortality resulting from troop transfer behaviors. Studies addressing these problems would be highly desirable, for only then can the phenomena underlying population regulation in primates be better understood.

PREDATION IN RELATION TO POPULATION REGULATION

Primates living in open savannal habitats are subject to predation from large mammalian predators. Both the body and canine teeth of adult males among savanna-living primates (e.g., baboons, *Papio* sp., *Theropithecus*, and patas monkeys, *Erythrocebus patas*) are believed to have evolved to their characteristic large size at least partly owing to their advantage in the defense against predators.

If the incidence of predation on a primate population is very high, its density might be kept lower than it would be in the absence of predation. Except for some primate populations that are hunted or trapped by man, such a population among the medium-to-large primates has yet to be discovered in undisturbed situations.

If refuges from predators, such as tall trees in open savannah, are scarce, they might constitute a limiting resource. Access to such refuges is likely to be determined by differences in social dominance relations so that the effect of predation on vital statistics would be determined at least in part by social behavior.

THE INFLUENCE OF BEHAVIOR ON PHYSIOLOGY THAT MEDIATES SURVIVORSHIP AND REPRODUCTIVE PERFORMANCE

Except for the outright killing of individuals, behavior exerts its influence on survivorship and fecundity through physiological changes. Physiological mechanisms are obviously involved in mediating behaviorally determined access to food into nutritional state and rates of growth and reproductive maturation. Social behavior also determines the hormonal balance of individuals. Laboratory and field experiments with other animals have indicated that behaviorally subordinate and harrassed individuals may die from stress. The typically lethal stress syndrome involves marked changes in the endocrine systems. Such mortality may occur quite independently of food deprivation. Starvation is simply an intense form of physiological stress. Generally, animals that are in poor physical condition because of nutritional and endocrine stress also have lower resistance to disease organisms and parasites. Thus, death or lowered reproductive performance may be mediated by a variety of endocrine changes that are brought about by behavior (see reviews by Christian, 1963, 1970).

9

Commentary

Transect censusing is useful for determining relative abundance when densities for censused areas are to be compared. Such comparisons are most useful when the censused areas are comparable in terms of forest type and patterns of human disturbance. Transect estimates of density most nearly reflect real density for those primate species that are relatively large (> 1 kg) and conspicuous in their activities. To date, the best transect estimates of density have been developed by experienced field workers working in a familiar habitat type who are well trained in observing and detecting the primate species indigenous to the area.

One must be careful to distinguish between a density *estimate* and the *actual* density for a given population in a designated region. Intensive studies in small sample plots are mandated for small primates and those primate species that are cryptic or nocturnal if the aim is a close approximation to actual density. Table 9-1 reflects current judgments concerning the appropriate census technique for a range of primate species. In light of these considerations, the following comments can fairly be made:

1. Transect length must be determined empirically. A transect line should be long enough to cross all habitat types in the census area. In the example used in this report (see p. 52), Struhsaker found that 4 km was large enough to enable an observer to encounter the primate species present in his forest.

2. In a broad survey it may not be possible to census more than once. When this is the case, the length of the transect line is determined by pacing during the census. For most censuses the transects should be repeated along a predetermined line.

3. The sample size must be determined empirically by calculating 95% confidence limits as data are collected. In the sample data used in this manual, Struhsaker found that 20–30 repeat transects were adequate. Spacing samples over an annual cycle is the only way to determine the effects of seasonal changes in habitat use.

4. Because detection distances vary with many habitat characteristics, especially foliage density, the transect width must be determined empirically in each habitat. Two distances are measured: the observer-to-animal, or sighting, distance and the transect line-to-animal distance, or perpendicular distance. The total strip width may then be calculated on the basis of a fixed or variable strip width for each method. The maximum reliable detection distance is the most commonly used type of variable strip width.

5. The application of line-transect census methods to forest primates is sufficiently recent that there is no best method, other than inspection of graphed or tabulated data. Examples of three useful methods are given. Much of the theory for census methods has been developed on the basis of surveys of animals in a two-dimensional space; it is assumed that the animals do not move in response to the observer before being detected. Forest primates must be censused in a three-dimensional space; they are often detected by sound before they are sighted; and they often move from their original positions before being detected. Three standardized studies are available that compare the accuracy of census methods for forest primates with density estimates determined from detailed studies.

Struhsaker (see Chapter 4, this volume) found that an empirical inspection of the frequency distribution of sighting distances with a cutoff distance for reliable detectability (50 m in this example) was the most accurate census method for making density estimates for a common species in his study forest.

Density estimates based on perpendicular distance estimates were inadequate under Struhsaker's survey conditions because many sightings made over the trail (a zero distance) resulted in an overestimation of the population.

In contrast, density estimates based on sighting distances proved to be less adequate than perpendicular distance estimates under Janson and Terborgh's (in press) survey conditions because they overestimated population densities based on detailed studies of their target species.

Eisenberg (see p. 65) describes a nonlinear density plot method that requires prior information on home range size and mean group size. This method also provided density estimates comparable with those estimated for a common species from a detailed study.

6. Records of all individuals actually counted provide a known minimum. It is often useful to record a separate estimate of the number of additional animals in the vicinity (range of group size).

For density calculations it is best to estimate densities of groups (excluding sightings of single animals that may be separated from groups or may be transients).

Detailed counts of group size should be made at a time separate from standardized transect periods when the groups can be followed. The best group counts are obtained when the animals leave or enter sleeping trees or when they cross a restricted or open area during a progression. Total population densities should be calculated by multiplying the number of groups by the average number of individuals counted in several groups.

Duplicate counts of the same groups (due to group movements or multiple observers) can be avoided by knowing the travel rate of the species and by identifying groups by individually distinct size/sex compositions or distinct individuals.

7. Most census methods have depended on age and sex classes that are scaled by size to the largest adult. Observers often subdivided the immature categories beyond the basic age classes of infant, juvenile, subadult male, adult female, and adult male.

TABLE 9-1 Suggested Census Methods for Selected Primates[a]

Species	Habitat Type	Transect	Point Census	Quadrat	Intensive Study of Selected Areas	References
Lemuridae						
Microcebus murinus	Forest			++	++	Martin, 1972
Lorisidae and Galagidae						
Loris tardigradus	Forest				++	Petter and Hladik, 1970
Galago demidovii	Forest			+	++	Charles-Dominique, 1972a,b
Callithricidae						
Saguinus o. oedipus	Forest				++	Neyman, 1977
S.o. geoffroyi	Forest	+		+	++	Dawson, 1977
Cebuella pygmaea	Forest			+	++	Soini, 1978

Cebidae						
Aotus trivirgatus	Savanna	+				Rathbun, 1980
Aotus trivirgatus	Forest				++	Thorington *et al.*, 1976
Cebus apella	Forest	+			++	Janson and Terborgh, in press
Alouatta seniculus	Savanna	++				Eisenberg, 1979
A. seniculus	Forest	+				Green, 1978a
Ateles belzebuth	Forest	+	++			Green, 1978a
Cercopithecidae						
Macaca mulatta	Cultivated land	++		+		Southwick *et al.*, 1965
M. fascicularis	Forest	+				Crockett and Wilson, 1980
Cercopithecus sp.	Forest	+			++	Struhsaker (Table 4-4, this volume)

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[a] + = useful method; ++ = preferred method.

These size classes have been roughly correlated with age classes on the basis of information from captive animals. These techniques have been satisfactory for general comparisons of the status of a species in different parts of its range.

Using recent field data of known individuals, Dittus (see Chapter 5, this volume) showed that aging techniques can be further refined by taking into account the fact that captive individuals grow and mature faster than wild individuals, and the size classes may be expected to vary between sexes, places, and years, reflecting the nutritional status of those populations. The more precise the age classifications, the more accurate the life tables and the understanding of population dynamics.

8. Transect census methods provide density estimates of a general nature that are useful when comparisons based on an order-of-magnitude difference are useful. The accuracy of censusing is improved with standardization and an increased characterization of habitat productivity and seasonality.

Long-term studies provide increasingly accurate data on densities and additional data on such topics as home ranges and overlap between neighboring groups, seasonal changes in habitat use and diet, and records of groups with known age and sex compositions.

9. So far as possible, habitat should be characterized by a description of the vegetation profile, and the description should include notes on the distribution of water and a gross classification of drainage and soil type. In more intensive surveys, vegetation should be analyzed to gain an understanding of the relative abundance and dominance of woody plant species.

10. In longer-term studies, seasonal changes in rainfall and temperature should be recorded, and the findings should be augmented by phenological studies of the trees because ultimately the carrying capacity of the habitat is related to plant productivity. In long-term studies of primates, some method for individual recognition must be devised that utilizes either natural or artificial markings. Chronological age can be estimated by empirically verifying growth patterns of known individuals or by indirectly estimating age by morphological changes or tooth wear.

11. In order to understand carrying capacity for different species, long-term studies concentrated on feeding ecology and

use of space must be undertaken. There is reason to believe that many primate species are food-limited in their natural habitats.

12. Before controlled cropping can be undertaken, the population must be analyzed to determine whether it is at equilibrium, expanding, or in decline. The construction of a life table is an essential first step before rational utilization of primate resources can be planned.

13. Emphasis is still on data gathering. It is to be hoped that standardization of methodology will make possible field data that are comparable between investigators and study areas and will yield predictive statements concerning the behavior of natural populations.

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APPENDIX A

LANDSAT Data Distribution Centers Operative in 1979

Australia
Australian LANDSAT Station, P.O. Box 13, Woden A.C.T. 2606, Australia

Brazil
INPE, Caixa Postal 01, 12630 Cachoeira, Paulity, SP, Brazil

Canada
CCRS, 3564 Sheffield Road, Ottawa, Ontario, Canada

India
National Remote Sensing Agency, Plot No. 4, Sardar Patel Road, P.O. No. 1519, Secunderabad 500003 (A.P.) India

Iran
Iranian Remote Sensing Center, National Iranian Radio and Television, 80 Sepand Street, Villa Avenue, Tehran, Iran

Italy and Sweden

Earthnet—ESRIN, via Galileo galilei, Casella Postale 04, 00044
Frascati, Italy

Japan

RESTEC, Remote Sensing Technology, Uni-Roppongi Bldg.
7-15-17, Roppongi Minato-ky, Tokyo 106, Japan

United States

EROS Data Center, Geological Survey, U.S. Department of the Interior, Computer Center Division, Sioux Falls Computation
Branch, Sioux Falls, South Dakota 57198

APPENDIX

B

Sources of Interpretive Service for Satellite Imagery in the United States

Bendix Aerospace Systems Division, 3300 Plymouth Road, Ann Arbor, Michigan 48105

Calspan Corporation, P.O. Box 235, Buffalo, New York 14221

COMARC Design Systems, The Agriculture Bldg., Embarcadero at Mission, San Francisco, California 94105

Computer Sciences Corporation, 8728 Colesville Road, Silver Spring, Maryland 20910

Comtal Corporation, 169 North Halstead Street, Pasadena, California 91107

Control Data Corporation, P.O. Box 1249, Minneapolis, Minnesota 55440

Earth Satellite Corporation, 7222 47th Street, Chevy Chase, Maryland 20815

Ecographics, International Environmental Analysis, P.O. Box 706, La Jolla, California 92038

Environmental Research Institute of Michigan, P.O. Box 618, Ann Arbor, Michigan 48107

ESL, Inc., 495 Java Drive, Sunnyvale, California 94086

Ford Aerospace & Communications Corporation, P.O. Box 58487, Houston, Texas 77058

General Electric Company, 5030 Herzel Place, Beltsville, Maryland 20705

Geo Image, Inc., P.O. Box 576, Altadena, California 91001

Geospectra Corporation, 202 East Washington, Suite 504, Ann Arbor, Michigan 48108

HRB—Singer, Inc., Environmental Analysis Group, Science Park—Box 60, State College, Pennsylvania 16801

International Business Machines, 1800 Frederic Pike, Gaithersburg, Maryland 20760

International Imaging Systems, 650 North Mary Avenue, Sunnyvale, California 94086

Interpretive Service for Primate Studies, Image Analysis Center for Ecological Studies, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008

Jet Propulsion Laboratory, 4800 Oak Road, Pasadena, California 91103

Lockhead Electronics Company, 1830 Space Park Drive, Houston, Texas 77058

Mead Technology Laboratory, 3481 Dayton-Xenia Road, Dayon, Ohio 45432

Oregon State University, Environmental Remote Sensing Applications Laboratory, Corvallis, Oregon 97331

Pattern Recognition—Technology and Application, S. S. Viglione and Associates, 551 Peralta Hills Drive, Anaheim, California 92807

Pennsylvania State University, Office of Remote Sensing of Earth Resources, 219 Electrical Eng. West Bldg., University Park, Pennsylvania 16802

Purdue University, Laboratory for the Application of Remote Sensing, West Lafayette, Indiana 47906

Seiscom Delta, Inc., P.O. Box 36789, Houston, Texas 77036

South Dakota State University, Remote Sensing Institute, Brookings, South Dakota 57006

Stanford University, Remote Sensing Laboratory, Stanford, California 94305

Texas A&M University, Remote Sensing Center, College Station, Texas 77843

TRW Systems Group, One Space Park, Redondo Beach, California 90278

University of California, Space Sciences Laboratory, Berkeley, California 94720

University of Kansas, Space Technology Center, Lawrence, Kansas 66045

University of Southern California, Image Processing Institute, Los Angeles, California 90007

APPENDIX C

Sample Data Sheets

This appendix contains examples of data sheets that have been found useful in conducting field surveys of nonhuman primates. Investigators may want to use these as the basis for designing and preparing their own data sheets.

Ground Truth Data Sheet for LANDSAT Coverage

LANDSAT Information

LANDSAT-1: Photo No. ______ Date of Photo ______
LANDSAT-2: Photo No. ______ Date of Photo ______
LANDSAT-3: Photo No. ______ Date of Photo ______

Map Information

Scale ______ Sheet No. ______ Latitude ______ Longitude ______

Field Photography and Data

Attach Photograph Here

Spot-Check No. ______
Location ______
______
______
Date ______
Elevation ______

Location Diagram N ▲

Spot-Check Descriptions

Forest		Nonforest	
Type of forest	1 2 3 4 5 6 7 8 9	Surrounding forest	1 2 3 4 5 6 7 8 9
Forest disturbances	1 2 3 4 5 6	Land use category	1 2 3 4
Crown density	1 2 3	Ownership	1 2 3
Leaf condition	1 2 3	Cover plant	1 2 3
Aspect	1 2 3 4 5 6 7 8	Dominant tree ______	
Slope	1 2 3 4	Height (m) ______ Girth (m) ______	
Macrorelief class	1 2 3 4	Ground moisture condition	1 2 3 4

No.	Prominent species	No. of Trees	Ave. Hi M	No.	Cultivated crop
1				1	
2				2	
3				3	
4				4	
5				5	

Remarks ______
______

Signature ______
Date ______

Codes

Type of Forest and Surrounding Forest	Code
Evergreen forest	1
Mixed deciduous forest	2
Dry dipterocarps forest	3
Pine forest	4
Mangrove forest	5
Bamboo forest	6
Scrub forest	7
Savanna	8
Forest plantation	9

Forest Disturbances	Code
Nondisturbance	1
Cutting—light	2
Cutting—heavy	3
Fire damage	4
Old clearing and shifting cultivation	5
Infestation	6

Crown density	Code
0–25%	1
25–75%	2
75–100%	3

Leaf Condition	Code
Shedding	1
Spring	2
Flowering	3

Ground Moisture Condition	Code
Wet	1
Medium	2
Dry	3
Very Dry	4

Land Use Category	Code
Cultivated	1
Urban	2
Water	3
Others	4

Ownership	Code
Hilltribes	1
Natives	2
Migrants	3

Cover Plant	Code
Weed	1
Shrub	2
Tree	3

Aspect	Code
North	1
Northeast	2
East	3
Southeast	4
South	5
Southwest	6
West	7
Northwest	8

Slope	Code
Very steep (>60°)	1
Steep (46°–60°)	2
Moderately steep (25°–45°)	3
Undulating	4

Macrorelief Class	Code
Mountainous land	1
Hilly land	2
Undulating and rolling land	3
Flat land	4

Census Data Sheet

Location ______________________________

Date ____________ Time ____________ Personnel ____________

Weather ______________________________

Mode of Travel ____________ Speed of Travel ____________

Sightings

Species	Location	Time Sighted	Time Left	Observer-Animal Distance	Animal Path Distance	Initial Height	Initial Activity	Cue to Sighting	No. of Individuals	Sex/Age Composition	Comments

Sighting cue:
AV = Audio visual
AB = Audio branch displacement
VM = Visual moving
VS = Visual stationary

Sex and Age Class:
A♂ = Adult male
A♀ = Adult female
A♀+I = Adult female with infant
SA = Subadult
J = Juvenile
I = Infant

Activity:
T = Traveling
F = Foraging
R = Resting

Monkey Identification Card

Front of card used for written descriptions of key traits.

Troop: ______________ Name: ____________________ Date: ______________

Age and Sex: _________ (Date of birth and mother's name) ________________

Pelage: ____

Head hair: ____

Face color: ____

Ears: ____

Dermal skin: ____

Other: ____

____

____

____

____

____

____

____

____

____

Name: ___________________

Back of card has printed monkey faces used for drawing in the location, size, and configuration of pigment spots, scars, and similar blemishes.

Sample Data Sheet for Collected Animals

Species ______________________ Sex ______________________

Tattoo no. ______________________ Date ______________________

Ear tag no. ______________________ Troop no. ______________________

Freeze brand ______________________ Locality where captured __________

Ear notch position ____

Color code on collar ______________

Time Amount

Scars, injuries, malformations, etc. Anesthetic ____________________

__________________________ __________________________

__________________________ __________________________

__________________________ __________________________

Tooth caste no. ______________ __________________________

Fingerprints no. ______________ __________________________

Measurements

Head and body length ______________ Elbow-digit length ______________

Tail length ______________________ Hand length ______________________

Head length ______________________ Femur length ______________________

Shoulder-elbow length ______________ Tibia length ______________________

Weight ______________________

Mark – Recapture Data Sheet

Date			Observer	Catch Location	Species	New	Animal Number	No. Confused	Sex	Sexual Condition	Age	Animal Condition	Ectopar	Length			Ear (mm)	Hind Foot (mm)	Weight (gm)	Trap	Preparation
Day	Month	Year												Body (mm)	Tail (mm)	Total (mm)					
8-9*	10-11	12-13	14	15-16	17	18	20-23	26	27	28	29	30	31	32-33	34-35	36-37	38	39	40	41	42

*Column heading numbers are for computer use.

APPENDIX D

Checklist of Essential Equipment

Basic Field Work

- Binoculars
- Compass
- Stopwatch
- Watch
- Notebook
- Pen (indelible ink)
- Knife

Mapping

- Tape Measure
- Compass
- Surveyor's tape
- Range finder

Animal Marking

- Traps and bait
- Dartgun and darts
- Blowgun and darts
- Crossbow
- Collars
- Tattoo equipment
- Freeze-branding supplies
- Anesthetic
- Scales
- Calipers
- Measuring tape
- Scissors
- Dye

Field Data Analysis

- Graph paper
- Ruler
- Calculator

Plant Identification

- Plant press
- Corrugated aluminum
- Cardboard sheets
- Newspapers
- Tree tags

Notes