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# Taxonomy and conservation status of hawk-eagles (genus *Nisaetus*) in South-East Asia

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# TAXONOMY AND CONSERVATION STATUS OF HAWK-EAGLES (GENUS *NISAETUS*) IN SOUTH-EAST ASIA

by

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PhD Thesis

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*The time will come I believe, though I shall not live to see it, when we shall have fairly true genealogical trees of each kingdom of nature …*

*Charles Darwin, 1857, letter to T. H. Huxley*

The painting of Javan Hawk-eagle on the front cover is by Trond Haugskott.

# PREFACE

This thesis is based on four research projects. In the period 1997-1998 studies were carried out on the Javan Hawk-eagle *Nisaetus bartelsi* on Java as part of an environmental cooperation programme between Indonesia and Norway funded by the Norwegian government. The aim of the project was to study the conservation status of this rain forest eagle and use it as a flagship species in an attempt to protect threatened rain forests in Indonesia (Røv & Gjershaug 2000). Nils Røv, Torgeir Nygård, Dewi M. Prawiradilaga, Yayat Afianto, Hapsoro and Adam Supriatna have been collaborating with me on this project.

The second project was on taxonomy and phylogeny of some booted eagles in Indonesia, based on molecular genetics as part of the project "Species and subspecies as taxonomical categories used in conservation biology" in collaboration with Kaare Aagaard, Kjetil Hindar, Nils Røv og Kirsti Kvaløy. This project was financed by the Norwegian Research Council (NFR) in 1998-2000. The project was expanded to cover most of the booted eagle taxa in the world as a result of collaboration with Anita Gamauf and Elisabeth Haring at the Museum of Natural History in Vienna.

The third project was on the taxonomy of the Flores Hawk-eagle *Nisaetus floris* on the Lesser Sunda Islands in Indonesia. It was partly an extension of the former project, involving field work in Indonesia in 2002, financed by the Norwegian Institute for Nature Research (NINA). Nils Røv, Kirsti Kvaløy, Dewi M. Prawiradilaga, Usep Suparman and Zaini Rahman have been collaborating with me on this project.

The final project was on the taxonomy of hawk-eagles of the genus *Nisaetus* in India. This was also an extension of the second project and included morphological studies of bird skins at The Natural History Museum at Tring in 2004 and two months field work in India in 2005, financed by NINA, in collaboration with Yngve Espmark, Ola Diserud and Pamela Rasmussen.

## ABSTRACT

Morphological, vocal and molecular data have been used to reevaluate the taxonomy of some Asian *Nisaetus* taxa. This name is used instead of *Spizaetus* because the latter genus is polyphyletic with clades in Asia, South America and Africa. The Changeable Hawk-eagle complex (*N. cirrhatus cirrhatus, N. c. limnaeetus, N. c. floris, N. lanceolatus* and *N. philippensis*) has been studied. We propose that *Nisaetus floris* (Flores Hawk-eagle) should be treated as a distinct species, whereas the taxonomic status of *Nisaetus c. cirrhatus* and *N. c. limnaeetus* is still uncertain. We also propose that the Philippine Hawk-eagle should be split into two species *Nisaetus philippensis* and *N. pinskeri*. In the Mountain Hawk-eagle *Nisaetus nipalensis* complex, we propose that *Nisaetus kelaarti* (Legge's Hawk-eagle) should be treated as a distinct species. The conservation status of *Nisaetus floris*, *Nisaetus kelaarti* and *Nisaetus bartelsi* has been evaluated from population density estimates, which are based on territory size. *N. floris* and *N. bartelsi* qualify for the category "Endangered" on the IUCN Red List, whereas *N. kelaarti* qualifies as "Near Threatened". The changes in taxonomy of *Nisaetus floris* and *N. kelaarti* meet the qualification for being included in the Red List.

## SAMMENDRAG PÅ NORSK

Vi har brukt morfologiske, vokale og molekylære data for å revurdere taksonomien til noen taksa i den asiatiske haukørnslekten *Nisaetus*. Dette navnet er brukt i stedet for *Spizaetus* da denne er polyfyletisk med en gruppe i Asia, en i Sør-Amerika og en art i Afrika. *Changeable Hawk-eagle* - komplekset (*N. cirrhatus cirrhatus, N. c. limnaeetus, N. c. floris, N. lanceolatus* og *N. philippensis*) er studert, og vi har foreslått at *Nisaetus floris* (Flores Hawk-eagle) skal regnes som en egen art, mens den taksonomiske status til *Nisaetus c. cirrhatus* og *N. c. limnaeetus* fremdeles er usikker. Vi har også foreslått at Philippine Hawk-eagle skal splittes i to arter, *Nisaetus philippensis* og *N. pinskeri*. I Mountain Hawk-eagle *Nisaetus nipalensis* komplekset foreslår vi at *Nisaetus kelaarti* (Legge's Hawk-eagle) regnes som en egen art. Vi har vurdert bevaringsstatusen til *Nisaetus floris*, *Nisaetus bartelsi* og *Nisaetus kelaarti* ut fra populasjonstetthetsestimat som er basert på territoriestørrelse. De to førstnevnte artene kvalifiserer til "direkte truet" på Rødlista, mens *kelaarti* kvalifiserer til kategorien "nær truet". Endringen av taksonomisk status for *Nisaetus floris* og *Nisaetus kelaarti* har vært en forutsetning for å inkludere disse artene på Rødlista.

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**APPENDICES**

A. List of current species of booted eagles
B. Proposed new taxonomy of booted eagles

# LIST OF PAPERS

I. Gamauf, A., Gjershaug, J.O., Røv, N., Kvaløy, K. & Haring, E. 2005. Species or subspecies ? The dilemma of taxonomic ranking of some South-East Asian hawk-eagles (genus *Spizaetus*). *Bird Conservation International* 15: 99-117.

II. Gjershaug, J.O., Kvaløy, K., Røv, N., Prawiradilaga, D. M., Suparman, U. &  Rahman, Z. 2004. The taxonomic status of Flores Hawk Eagle *Spizaetus floris*. *Forktail* 20: 55-62.

III. Gjershaug, J. O., Diserud, O., Rasmussen, P. C. & Espmark, Y. On the taxonomic status of the Changeable Hawk-eagle *Nisaetus cirrhatus* in India.  (Manuscript)

IV. Gjershaug, J. O. & Espmark, Y. Intra-individual and geographical variation in the calls of the Changeable Hawk-eagle *Nisaetus cirrhatus* in India. (Manuscript)

V. Gjershaug, J. O., Diserud, O. & Rasmussen, P. C. An overlooked threatened eagle species: Legge's Hawk-eagle *Nisaetus kelaarti*.  (Manuscript)

VI. Gjershaug, J.O., Røv, N., Nygård, T., Prawiradilaga, D.M., Afianto, Y., Hapsoro & Supriatna, A. 2004. Home-range size of the Javan Hawk-eagle (*Spizaetus bartelsi)* estimated from direct observations and radiotelemetry. *Journal of Raptor Research* 38: 343-349.

The papers are referred to in the text by their Roman numerals.

# INTRODUCTION

## PROBLEM DESCRIPTION

The accurate determination of species limits is a central concern in the conservation of global biodiversity (e.g. Wilson 1992, Hazevoet 1996, Collar 1997, Frankham *et al.* 2002, Newton 2003, Agapow *et al.* 2004). In cases where the taxonomic status of threatened subspecies has not been sufficiently clarified, there is a risk that potentially valid species could become extinct before conservation action is initiated. Currently, subspecies are not included in IUCN's red lists (e. g. BirdLife International 2000, 2001, IUCN 2004). A change of taxonomic status from subspecies to full species will therefore have great importance for its conservation attention. However, it would not be advisable to propose species status for a taxon just for conservation reasons. All such decisions should be made as far as possible according to the same basic criteria (Collar 1997).

## SPECIES CONCEPTS

There has been a long-standing controversy over species concepts. Mayden (1997) discussed 22 concepts of species that are in use today. The biological species concept (BSC) (Mayr 1942, 1963, 1982) has been the dominating species concept in ornithology for most of the last six decades. It is defined as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". However, there has been much debate concerning the difficulty of applying the BSC to allopatric taxa. In particular proponents of the phylogenetic species concept (PSC) have claimed that their species concept is less arbitrary of its treatment of allopatric taxa. They define the species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983, McKitrick & Zink 1988, Hazevoet 1994, 1996). I agree with much of the critique of the PSC (e. g. Collar 1997, Snow 1997, Lee 2003) that the concept is at least as arbitrary and subjective as BSC and has great weakness both from theoretical and practical standpoints. To use the criteria of PSC on human populations would give the controversial result that various geographical populations of humans are different species (Haffer 1997, Bock 2004). Why should they be more appropriate to use on birds? A variant of PSC is called the monophyletic species concept. It stress that the species should be monophyletic, in other words that different populations of the same species should be more closely related to each other than to populations of other species (Mishler & Donoghue 1982, Lidén 1990, Alström 2002). Paraphyly is, however, quite common (e. g. Talbot & Shields 1996, Haffer 1997, Harrison 1998, Omland *et al.* 2000, Funk & Omland 2003). Under budding speciation, the cause of paraphyly is incomplete lineage sorting (Funk & Omland 2003). Some of the critique of the PSC was because the importance of congruence of independent lines of evidence for species limits was not duly emphasised in the early writings of PSC proponents (Zink 1997).

Recently, modified versions of the evolutionary species concept (Simpson 1951, Wiley 1981, Wiley & Mayden 1997) have incorporated the essences of several of the other species concepts as the General Lineage Concept (de Queiroz 1998, 1999). Helbig *et al.* (2002) defined it as: "population lineages maintaining their integrity with respect to other such lineages through time and space, this means that species are diagnosably different, reproductively isolated (otherwise they would not maintain their integrity upon contact) and

members of each (sexual) species share a common mate recognition and fertilization system (otherwise they would be unable to reproduce)".

The Comprehensive Biologic Species Concept (Johnson *et al.* 1999) is another broad, inclusive species concept with the following definition: " An avian species is a system of populations representing an essentially monophyletic, genetically cohesive, and genealogically concordant lineage of individuals that share a common fertilisation system through time and space, represent an independent evolutionary trajectory, and demonstrate essential but not necessarily complete reproductive isolation from other such systems".

There is, however, still no consensus about how best to define species (Dillon & Fjeldså 2005).


SPECIATION

Speciation theory, as many issues in evolutionary biology, began with Darwin (1859). By formulating a theory on how species change he paved the way for the scientific study of speciation. The next big step was taken with the "Modern Synthesis" (Dobzansky 1937, Huxley 1942, Mayr 1942) when Darwin's evolutionary theory was fitted into Mendelian genetics. The definition of species as reproductively isolated groups of organisms (BSC; Mayr 1942) was paralleled by speciation theories, where isolation was believed to be the causal agent.

Allopatric speciation, where new species arise from geographically isolated populations of the same ancestral species, is the most widely accepted of all current speciation models (Mayr 1942, 1963). It can be divided into vicariance and peripatric (peripheral) speciation, depending on the location of the geographical split and the size of the subpopulations. In vicariance speciation a continuous population is split in the centre of its distribution, giving rise to two or more large, isolated sub-populations. With time the sub-populations are thought to evolve reproductive isolation as a by-product of genetic drift and/ or divergent selection pressures. Since vicariance speciation requires a large amount of genetic differentiation to lead to reproductive isolation in secondary contact. The process is generally believed to be rather slow.

Reproductive isolation could evolve somewhat faster (involve fewer genetic changes) in peripatric speciation (Mayr 1954). Here a small peripheral portion of the population becomes isolated and may undergo one or several bottlenecks (Carson 1975). Genetic drift caused by low population size during the bottlenecks, together with relaxed selection pressure under the following flush phase, when the population increases rapidly in size, allows the formation of new gene combinations that would not have survived in the original population. Reproductive isolation is then believed to evolve either as a by-product of the genetic changes (Mayr 1954, Carson 1975, Templeton 1980) or as a consequence of relaxation of mating preferences in bottlenecks (Kaneshiro 1989).

According to another development of the allopatric speciation theory, the reinforcement theory (Dobzhansky 1937), even small genetic differences acquired in isolation might lead to reproductive isolation in secondary contact if the production of hybrids with low fitness selects for prezygotic isolation.

Recent studies indicate that avian speciation involves little genetic change and occurs rapidly in small populations (e.g. Grant and Grant 1997, Smith et al. 1997, Grant and Grant 1998, Grant et al. 2000). Speciation in birds proceeds via the evolution of behavioural barriers to interbreeding, whereas postmating isolation evolves much more slowly, probably occurring only after gene exchange has effectively ceased. Thus, there is considerable potential for introgressive hybridization to influence the evolution of diverging species. This is supported by the very high incidence of interspecific hybridization found in birds, and the fact that even distantly related taxa can produce fertile hybrids (Panov 1989, Grant & Grant 1992). In fact, hybridization may be an important positive factor in avian speciation (Grant 1986, Grant & Grant 1998, Veen et al. 2001).

A much used example of extremely rapid divergence with very little genetic differentiation, is the cichlids in Lake Victoria (Meyer 1993, Seehausen & van Alphen 1998, Turner 1999, Nagl et al. 2000). Fryer (2001) finds however the evidence unconvincing. Other rapid evolution in fish are described for northern freshwater fish species (Rundle & Schluter 2004, Snorrason & Skulason 2004, Østbye *et al.* in press). Uy & Borgia (2000) demonstrated distinct male preferences for bower decorations and female choise for those preferences in two populations of the Vogelkop bowerbird *Amblyornis inornatus* and claimed that this was the first direct evidence for the speciation by sexual selection (SSS) hypothesis in birds. New theoretical and empirical work has increased the plausibility of speciation without geographical isolation (Sympatric speciation). This has motivated a shift of focus away from isolation and towards the very mechanisms that initiate divergence. The old geographical classification of speciation models is no longer taken for granted (Schluter 2001, Via 2001). The concept of ecological speciation, where isolation is an effect of adaptation to divergent selective regimes, has gained consistent support from empirical evidence (Schluter 1998, 2000, 2001). Adaptive speciation is defined as "speciation processes in which the splitting is an adaptive response to disruptive selection caused by frequency-dependent biological interactions" (Dieckmann *et al.* 2004). Without divergent selection, even weak natural selection on female preference may hinder developing disparate mating traits and reproductive isolation from drift (Turelli et al. 2001).

Sexual selection can lead to rapid divergence between populations since it directly affects the traits involved in reproductive isolation and increases the overall rate of change (Andersson 1994, Panhuis et al. 2001). This has spurred an interest among biologists to examine the possible role of sexual selection in speciation. Sexual dichromatism and plumage ornamentation in birds (Barraclough et al. 1995, Møller & Cuervo 1998) has been shown to correlate with species richness. Furthermore, prezygotic (sexual) isolation seems to evolve faster than postzygotic isolation (Coyne & Orr 2004). However, Morrow *et al.* (2005) did not find any evidence for sexual selection as an engine of speciation in birds.

Nevertheless, in the phylogenies of many animal groups, the traits presumably maintained by sexual selection are more often lost than gained (Wiens 2001). This paradoxical fact seems to argue against speciation by sexual selection. The Kaneshiro model (Kaneshiro 1980) however, relates directly to loss of sexually selected traits. This model is a development of peripatric speciation with a special focus on sexual selection. It proposes that sexual selection might act as a stabilising agent on species-specific mating under normal circumstances and that the speciation would appear as a direct consequence of relaxed sexual selection pressures following bottlenecks. This model was used to explain the extreme plumage variation among subspecies of yellow wagtails *Montacilla flava* (Ödeen & Björklund 2003).

No evidence has yet emerged that sexual selection could be important in causing sympatric speciation for birds, nor that different types differ sufficiently in ecology to co-exist in the long term. If sympatric speciation occurs at all in birds, it is likely to affect relatively few species, because few show discontinuity in niche preference linked with mating behaviour (Newton 2003). Possible cases of sympatric speciation are described by Grant & Grant (1979) and Sorenson *et al.* (2003). The crossbills (*Loxia*) could be another possible example. They occur as different ecotypes, which differ in body size, vocalizations, bill size and food preferences (Groth 1988, Marquiss & Rae 2002, Benkman 2003). Allopatric speciation or a two-step process starting in allopatry and finishing in sympatry is, however, the most likely explanation for evolution of new bird species (Newton 2003).

Despite the popularity of models based on genetic drift (Mayr 1963, Templeton 1980, Provine 1989), there is little evidence that drift plays an important role in speciation. There is, in contrast, a growing body of evidence for the importance of natural and sexual selection. The recent "explosion" of works on speciation, however, concentrates almost entirely on reproductive isolation (Coyne & Orr 2004).


SPECIES DELIMITATION

Birds are delimitated using a far more restrictive set of criteria than for other organisms, with field diagnosability being the ultimate criteria of distinctiveness (Watson 2005). As a proponent of the above modified version of the Biological Species Concept, I believe that there should be indications of reproductive isolation (in the meaning of genetic isolation) between the taxa before regarding them as different species. These reproductive barriers can either be pre-zygotic isolation due to differential species or mate recognition, or post-zygotic isolation, where the phenotypic differentiation is so great that hybrids would be selected against ecologically (Grant & Grant 1997, Schluter 2001). Small diagnostic differences, which do not need to have any implications for reproductive isolation, better indicate subspecies rank. Another post-zygotic isolation mechanism is partly or full hybrid sterility, which do not occur between closely related taxa that have been separated less than one million years (Price & Bouvier 2002).

Under the BSC only the vaguest guidelines have been given as how to treat such allopatric populations (Mayr & Ashlock 1991). They argued that it is impossible in some cases of allopatry to obtain clear-cut proof one way or another, and that it is just as serious an error to call a population a species, when it is really only a subspecies, as to do the opposite. They prefer to treat allopatric populations of doubtful rank as subspecies, because the use of trinominal nomenclature conveys two important pieces of information: closest relationship and allopatry.

Large morphological differences between two taxa can indicate that their intermediate offspring might have lower fitness. Ecological speciation occurs when divergent selection on traits between populations in contrasting environments leads directly or indirectly to the evolution of reproductive isolation (Schluter 2000, 2001).

Recently, Helbig et al. (2002) have worked out more detailed guidelines for assigning species rank. According to their criteria, allopatric taxa are assigned species rank if they are fully diagnosable in each of several discrete or continuously varying characters related to different functional contexts, e.g. structural features, plumage colours, vocalisations or DNA

sequences, and the sum of the character differences corresponds to or exceeds the level of divergence seen in related species that coexist in sympatry. To assess these criteria, a comparative analysis of related species is necessary and evidence pertaining to potential incompatibilities of mate recognition systems (e.g. lack of response to song playback) may be particularly relevant.

Allopatric taxa will be termed allospecies (Amadon 1966, Short 1969) if they do not fulfil the criterion above, but have at least one character which is fully diagnostic and the level of divergence is equivalent to that of the most closely related sympatric species, or they are statistically diagnosable by a combination of two or three characters. The characters may be either discrete or vary continuously, but they must be functionally independent. Characters may also be molecular sequences (e.g. of mtDNA), but a single fixed nucleotide difference would not be sufficient to justify allospecies rank: the degree of divergence must be taken into consideration through a comparative analysis. The molecular divergence between allopatric taxa is proportional to the time that has elapsed since the two taxa diverged from a common ancestor and gives a rough indication of how likely it is that reproductive incompatibilities have evolved between the two taxa (Helbig et al. 2002). But it should not be used alone to decide if they are different species.

Where diagnosable taxa meet without hybridization (parapatry) they are ranked as species (Helbig *et al.* 2002). But when a hybrid zone joins them, they are ranked as semispecies, as such zones indicate a substantial restriction of gene flow. Only in cases where the taxa recently have come into contact and the overall divergence suggests that they will remain distinct, they will be ranked as full species (Helbig *et al.* 2002). In sympatry, taxa will be ranked as species if they hybridize only rarely and there is little or no gene flow between them because of low hybrid fitness (Helbig *et al.* 2002).

There has been a tendency in recent years, following Smith (1965), to make a distinction between allopatry, in which populations or taxa are separated by a distributional gap that prevents contact, and parapatry, in which populations of taxa are in contact. Mayr & Ashlock (1991) propose that populations meeting in a zone of contact without any interbreeding should be treated as species, and as subspecies if occasional hybrids occur. The criteria of Helbig et al. (2002) are less stringent than those traditionally applied by most proponents of the BSC, because they place more weight on reproductive incompatibility than on full reproductive isolation. Taxa meeting at a narrow, stable hybrid zone is regarded as semispecies, because the stability and steepness of a zone like this would indicate a restriction of gene flow (Helbig et al. 2002). They argued that hybrid zones probably always indicate an intrinsic barrier to gene flow. The breadth of a hybrid zone relative to the dispersal distance of the taxa involved is a good indicator of the degree to which gene flow is restricted. Diagnosable taxa that hybridize as a result of secondary contact will be ranked as species if they have only recently come into contact either naturally (through range expansion) or artificially (through human habitat alteration or introduction), and the level of their overall divergence suggests that they will remain distinct (Helbig et al. 2002). Parapatry reflects a situation where two taxa are ecologically identical or so similar that they cannot coexist in the same habitat. The fact that they do not hybridize, despite occurring in very close proximity, indicates that some intrinsic reproductive isolation is very likely to be operating.

Theoretical models suggest that the evolution of reproductive isolation can be rapid (Lande 1981, Barton & Charlesworth 1984) and that morphological character states, and even complex morphological structures, can evolve well within one million years (Nilsson &

Pelger 1994). The view that speciation in birds may occur rapidly is supported by empirical data. For instance, mtDNA sequences of Sandford's Sea Eagle *Haliaeetus sandfordi* and White-bellied Sea Eagle *H. leucogaster* differ by only 0,3%. They differ substantially in morphology and in behaviour, and are considered as different species (Wink et al. 1996). In several genera, species pairs with mtDNA genetic distances of less than 2% have been documented (Seibold & Helbig 1995, Shields & Wilson 1987, Kessler & Avise 1984, Avise & Zink 1988). In each of these pairs, taxa are morphologically distinct, have sympatric breeding ranges and would probably be ranked as species under any species concept. Interspecific and intraspecific genetical distances show substantial overlap (Vogler & DeSalle 1994, Helbig et al. 1995).

To delimitate allopatric taxa, Isler et al. (1998, 1999) used a minimum of three differences in vocal characters and one morphological character which identified individuals of at least one sex unambiguously to a particular taxon. With the diversity of song variation and response, the vocal evidence alone is not a credible test of species distinctiveness (Payne 1986). Collar (1997) claimed that it is time that ornithologists considered in depth the entire question of the scientific measurement of vocal differences in relation to taxonomic valuation.

In spite of these guidelines, there will always be borderline cases with subjective taxonomic judgement. The speciation process yields intermediate stages when species status is more or less irresolvable (Coyne & Orr 2004). The way in which species are defined and delineated can, however, have great impact on their conservation status.


## OBJECTIVES

The main objective of this thesis is to obtain knowledge on taxonomy and population status on some *Nisaetus* hawk-eagles in south-east Asia that can be used for conservation of these species.

The specific aims are to report the:

1. phylogeny of the Changeable Hawk-eagle complex (Paper I).
2. taxonomic status of the Flores Hawk-eagle (if *Nisaetus floris* is a distinct species from *Nisaetus cirrhatus limnaeetus* )(Paper II).
3. taxonomic status of the Changeable Hawk-eagle complex (if *Nisaetus limnaeetus* in North India is a distinct species from *Nisaetus cirrhatus* in South India (Paper III and IV)
4. taxonomy of the Mountain Hawk-eagle complex (if *Nisaetus kelaarti* in South India is a distinct species from *Nisaetus nipalensis* in North India (Paper V).
5. home-range size of the Javan Hawk-eagle to make a rough estimate of the population size (Paper VI).

STUDY OBJECTS

Booted eagles

The booted eagles (eagles with feathered tarsi) (Aves, Falconiformes, Accipitridae) are currently regarded as an assemblages of 39 species in nine genera in the tribe Aquilini (*Aquila*, *Ictinaetus*, *Hieraaetus*, *Lophaetus*, *Polemaetus*, *Stephanoaetus*, *Spizaetus*, *Spizastur* and *Oroaetus*) (del Hoyo et al. 1994, Ferguson-Lees & Christie 2001, 2005). The molecular genetical analyses show that the genus *Spizaetus* is polyphyletic, consisting of an Old World and a New World lineage (Gamauf *et al.* 2005, Helbig *et al.* 2005a, Lerner & Mindell 2005, Haring *et al.* in manuscript). Brown & Amadon (1968) stated that *Spizaetus africanus, S. ornatus* and *S. tyrannus* are not obviously tied with any of the other species of the *Spizaetus* genus, but they did not draw any taxonomical consequences from that. This was also recognized by Jollie (1976-77) based on morphological analysis. Based on the same molecular genetical analyses, the genera *Spizastur* and *Oroaetus* should be included in the genus Spizaetus Viellot 1816, and the ten Asian Nisaetus species are monophyletic. They should be assigned to a different genus, for which the name *Nisaetus* Hodgson 1836 is available. I therefore use this name. The Crowned Hawk Eagle *Stephanoaetus coronatus* was found by Helbig *et al. (*2005a) to be sister species of the *Nisaetus* group, whereas Lerner & Mindell (2005) found it to be the first diverging species after the *Nisaetus* and *Spizaetus* eagles. This difference is likely a result of different taxon set used in the two studies. Our results (Gamauf *et al.* 2005, Haring *et al.* submitted) are in accordance with that of Lerner & Mindell (2005), but I have choosen to follow Helbig *et al.* (2005) as their phylogeny is based on both mitochondrial and nuclear DNA with high bootstrap values.

Cassin's Hawk-eagle *Spizaetus africanus* of West Africa should be placed in the genus *Aquila* based on its phylogenetical position (Lerner & Mindell 2005). All *Hieraaetus* eagles except the *H. kienerii* should be included in the genus *Aquila*. *H. kineerii* is phylogenetically distant from its current congeners in *Hieraaetus* (Lerner & Mindell 2005) and is also morphologically very distinct, and should be placed in its own genus. The reuse of the genus name *Astur* used for the first description of this taxon by Saint-Hilaire in 1835 is not possible because it is preoccupied. Brehm has used it already for the genus *Accipiter* in 1831. Therefore, we have proposed to put the monotypic species *Hieraaetus kienerii* into the new genus *Kienastur* gen. nov. (Haring *et al.* submitted). Helbig *et al.* (2005) proposed that the spotted eagles (*Aquila pomarina, A. clanga* and *A. hastata*) should be included in the genus *Lophaetus*, Kaup 1847. As *Ictinaetus malayensis* is probably close related to these eagles (Lerner & Mindell 2005, Haring *et al.* submitted), we have also placed this species in the genus *Lophaetus* (Haring *et al.* submitted).

In addition to the 39 species covered by Ferguson-Lees & Christie (2005), *Nisaetus pinskeri* has been split from *Nisaetus philippensis* (Paper I), *Nisaetus kelaarti* should be split from *Nisaetus nipalensis* (Paper V), and *Hieraaetus weiskei* is probably also a distinct species based on molecular genetics (Bunce *et al.* 2005, Lerner & Mindell 2005). A list of all current booted eagles with English and scientific names is presented in Appendix A. A proposed new taxonomy of booted eagles is presented in Appendix B.

The phylogeny of booted eagles based on molecular genetics has been partly described by Wink & Sauer-Gürth 2004, Helbig et al. 2005a, Bunce et al. 2005, Lerner & Mindell 2005. Based on these papers and our own data (Gamauf *et al.* 2005, Haring *et al.* submitted and

Paper I), I have constructed manually a consensus tree (phylogenetical hypothesis) for all booted eagles (Fig. 1).
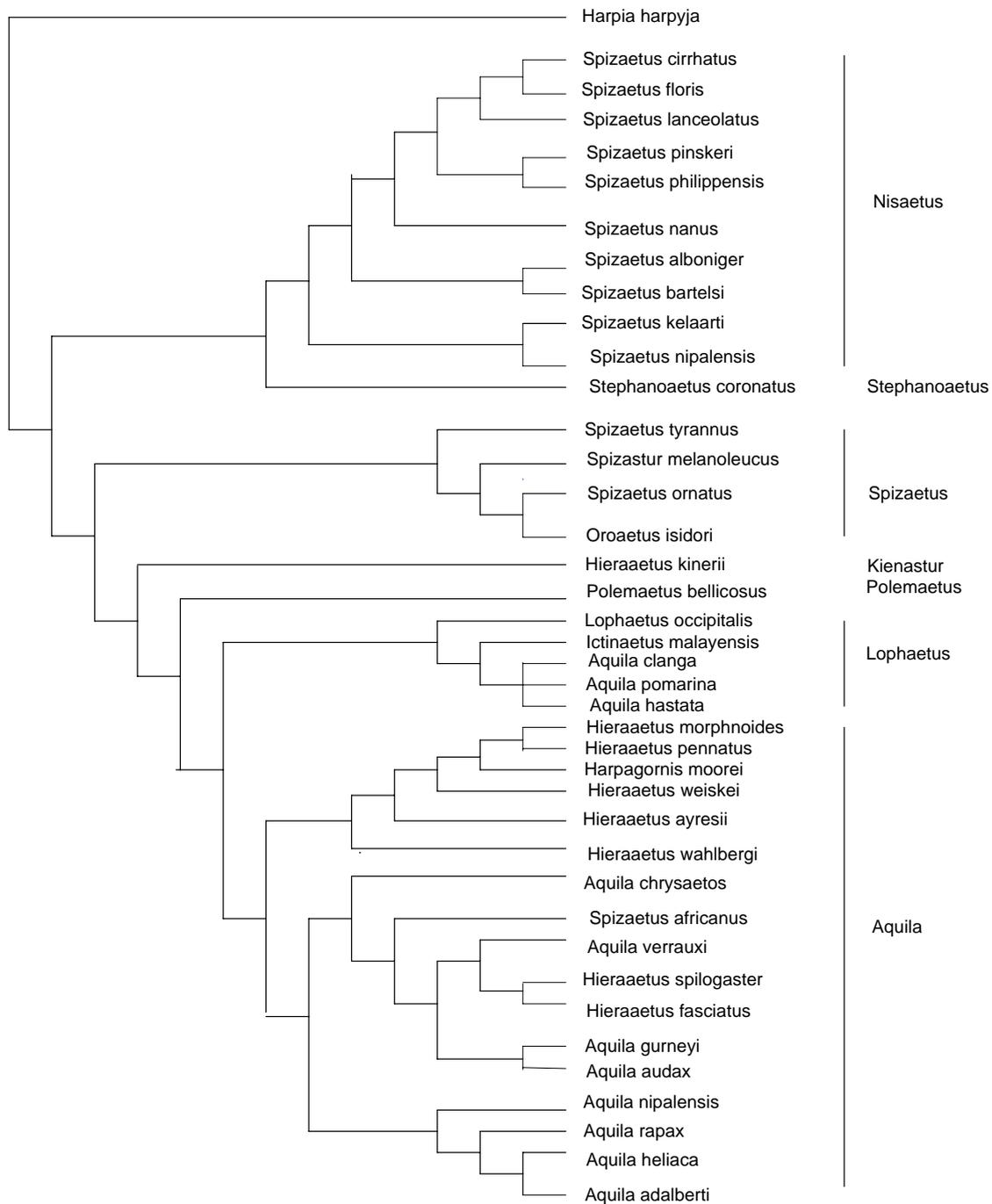


Fig. 1. A phylogenetic hypothesis based on mtDNA for all booted eagles with current nomenclature constructed manually from data in Wink & Sauer-Gürth 2004, Helbig *et al.* 2005a, Bunce *et al.* 2005, Lerner & Mindell 2005, Gamauf *et al.* 2005, Haring *et al.* submitted

and Paper I. *Harpagornis moorei* is an extinct giant eagle from New Zealand. See also Appendices A and B.
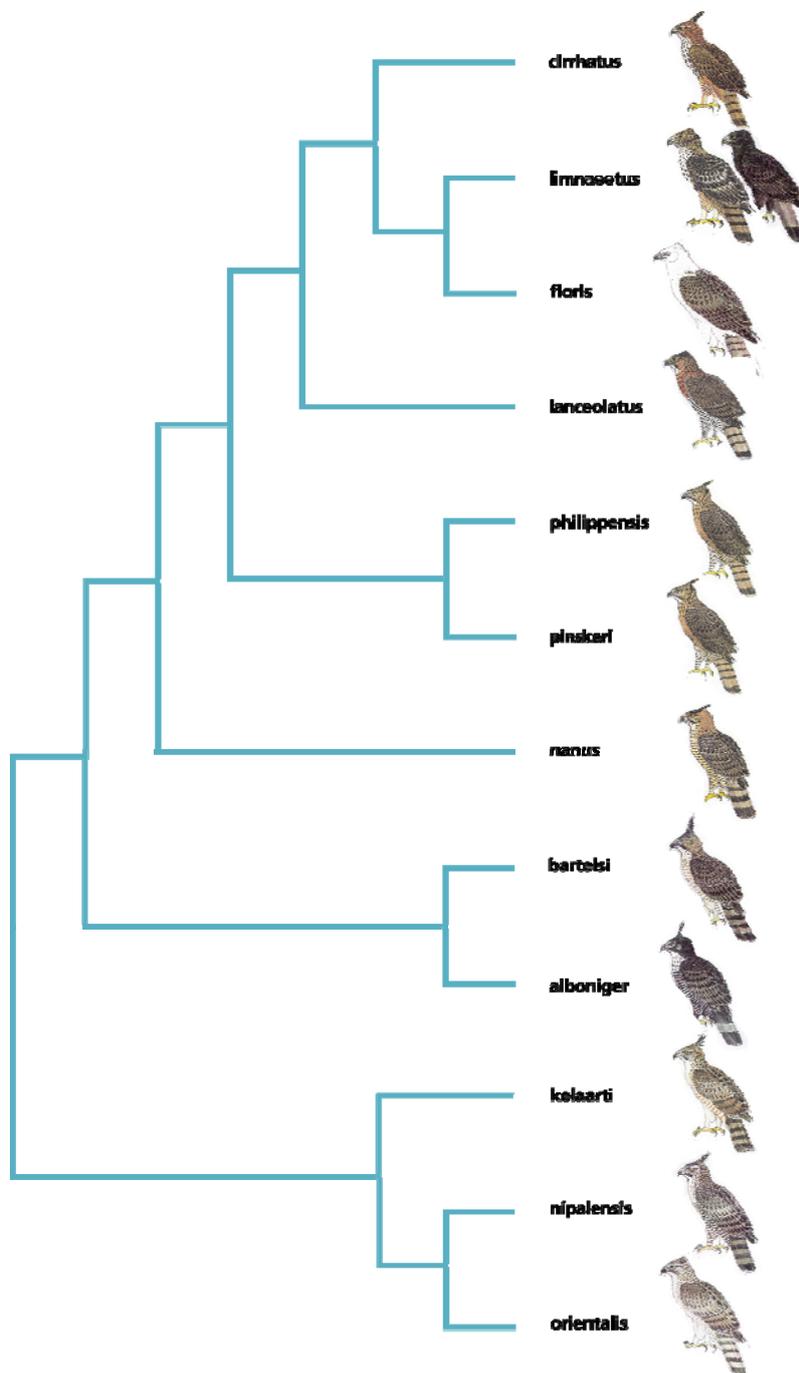


Fig. 2. A proposed phylogenetic hypothesis of Asian *Nisaetus* eagles based on the data in Paper I, Gamauf *et al.* 2005 and Haring *et al.* submitted. The tree is constructed manually. The paintings of eagles are from Weick 1980, with permission from the author.
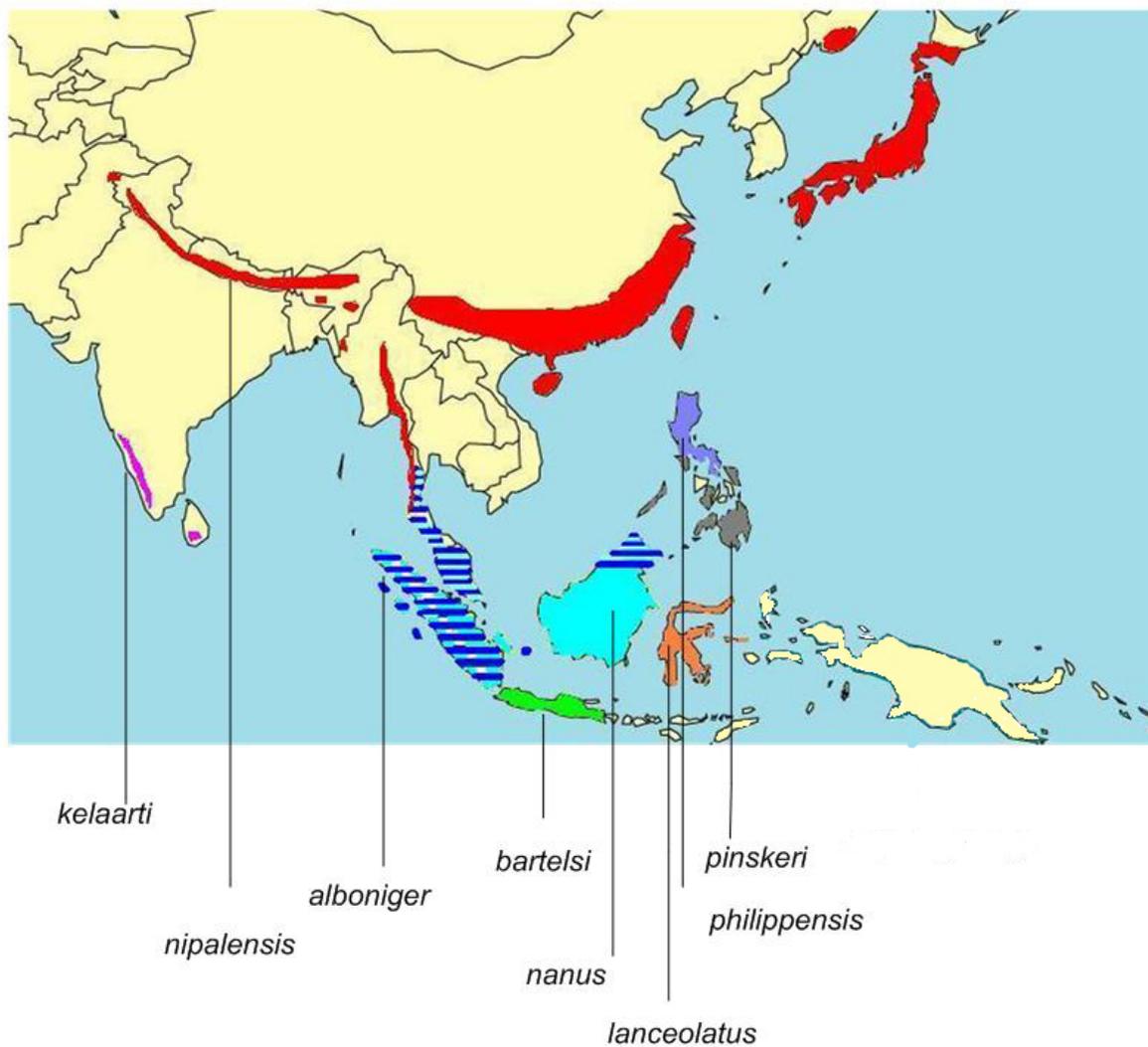
Fig. 3. Distribution of the *Nisaetus* hawk-eagles eagles except the *Nisaetus cirrhatus* complex.

I have studied the following eight species of *Nisaetus* hawk-eagles:

**Changeable Hawk-eagle *Nisaetus cirrhatus***

The Changeable Hawk-eagle is the most widespread of the *Nisaetus* hawk-eagles in South-East Asia, with a geographical distribution from India to the Bali and the Southern Philippine islands. It has five subspecies (Fig. 4): *N. c. cirrhatus* in the Indian subcontinent, *N. c. ceylanensis* in Sri Lanka, *N. c. limnaeetus* from the Himalayan foothills through Indomalaya into the Greater Sundas and the Philippines, *N. c. andamanensis* on the Andaman Islands, *N. c. vanheurni* on Simeulue Island. Ferguson-Lees & Christie (2005) treat *limnaeetus*, *andamanensis* and *vanheurni* as distinct species. It is a small eagle with a weight up to 1.8 kg. It inhabits savannah woodland, cultivation with trees, secondary and open primary forests from sea level up to 2,200 m a.s.l. (del Hoyo *et al.* 1994, Ferguson-Lees & Christie 2001).
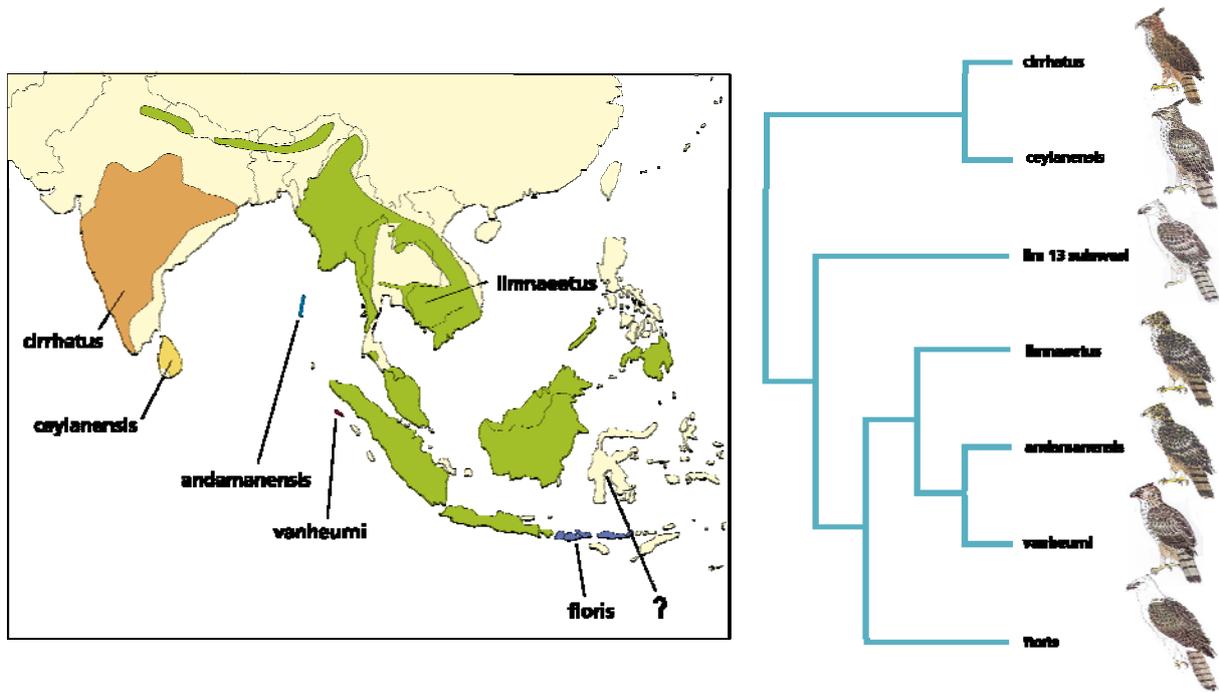
Fig. 4. Distribution of Changeable Hawk-eagle *Nisaetus cirrhatus* complex. The proposed phylogenetic hypothesis is from Paper I, constructed manually. One specimen (lim13) from Sulawesi probably represents an undescribed subspecies (question mark on the map). The Changeable Hawk-eagle is a paraphyletic taxon. The paintings of eagles are from Weick 1980, with permission from the author.

### Flores Hawk-eagle *N. floris*

The Flores Hawk-eagle has been regarded as a subspecies of *N. cirrhatus* until recently. It is found in the Lesser Sundas from Lombok to Flores. This eagle has a juvenile-like adult plumage, and is much larger than *Nisaetus cirrhatus.* It is found in lowland and submontane forests up to 1,600 m, but is found most often in lowland rainforests. Occasionally individuals are seen over cultivated areas, but always close to intact or semi-intact forest.

### Sulawesi Hawk-eagle *N. lanceolatus*

This medium-sized eagle is endemic to Sulawesi. It is found in primary and secondary forests from lowland up to at least 2000 m. (Thiollay & Rahman 2002). Ferguson-Lees & Christie (2001) follows Amadon (1982) and state that it forms a superspecies with *N. nipalensis*, *N. bartelsi, N. alboniger* and *N. philippensis.* Based on our genetical analyses, both *N. lanceolatus* and *N. philippensis* are more related to *N. cirrhatus* than to *N. nipalensis*.

**Northern Philippine Hawk-eagle** *N. philippensis*

This medium sized eagle is distributed in rainforests on the Philippine island of Luzon. The population size is estimated to about 200-220 pairs, which qualifies for the category "endangered" on the Red List (Preleuthner & Gamauf 1998).

**Southern Philippine Hawk-eagle** *N. pinskeri*

Preleuthner & Gamauf (1998) described *pinskeri* as a new subspecies of *N. philippensis*. Based on the morphological and plumage differences found in that study and the differences in mtDNA found later, it is now proposed as a distinct species (Paper I). It has been recorded on eleven of the Phillipine islands, in forested areas with closed canopy. Preleuthner & Gamauf (1998) have estimated the population size to 320-340 pairs, which qualify as "endangered" on the Red List.

**Mountain Hawk-eagle** *N. nipalensis*

This is a large eagle with currently three recognized subspecies: *N. n. nipalensis* from Himalayan foothills to China, Taiwan and western Thailand, *N. n. orientalis* in Japan, and *Nisaetus n. kelaarti* in south west India and Sri Lanka (del Hoyo *et al.* 1994, Ferguson-Lees & Christie 2001). We regard *N. kelaarti* as a distinct species. A recently discovered population in south-east Russia has been identified as *N. n. orientalis* (Nechaev *et al.* 1999), but our genetic studies have shown that it is more related to the birds in China and Taiwan than to the Japanese birds (Haring *et al.* in manus). MacKinnon & Phillips (2000) stated that the race *fokiensis* is a rare resident in Taiwan, and that the race *orientalis* breeds in NE China and winters to Taiwan. This is not in accordance with our genetic studies.

**Legge's Hawk-eagle** *N. kelaarti*

This large eagle has been regarded as a subspecies of *N. nipalensis* until now. It is associated with primary evergreen forests, even though it sometimes uses more degraded forests and cultivated areas for hunting (Thiollay 1993, own observations).

**Javan Hawk-eagle** *N. bartelsi*

The taxonomic status of this eagle has changed several times in the past. Streeseman (1924) first described it as a new subspecies of *N. nipalensis*. Some years later Stresemann (1938) renamed it as *N. nanus bartelsi*. Hoogerwerft (1946) came to the conclusion that it was too large to belong to *N. nanus* and found it premature to make any pertinent statement about its systematic position. Amadon (1953) made a review of the whole group of Asian *Spizaetus* (*Nisaetus*) species and came to the conclusion that, because its range was separated from *N. nipalensis* by *N. alboniger* on Sumatra, he could not recognise *bartelsi* as a subspecies of *N. nipalensis*, and considered it as a full species. Its systematic position has remained unresolved. Our mtDNA analysis has confirmed that it is a distinct species, with *N. alboniger* as its sister species (Haring *et al.* submitted). This medium-sized eagle is endemic to Java. It is

mostly found in the fragmented primary rainforests, but is sometimes even found in secondary forests, and can be observed hunting in cultivated areas.


# METHODS

A broad range of quantitative and qualitative methods have been used in this thesis.

1. Phylogeny based on the mitochondrial DNA cytochrome b and control region genes (Paper I).
2. Biometrical and plumage studies of skins in museums (Paper II, III and V).
3. Studies of plumage in the field (Paper II, III and V).
4. Tape recording, sonagrams and play-back experiments (Paper III and IV).
5. Population density estimation by direct observations of distances between neighbouring territories, distances between nests and by radiotelemetry (Paper VI).


## SEXING OF MUSEUM SPECIMENS

Many studies have demonstrated that a significant percentage of accipitrid specimens are incorrect sexed (Storer 1966, Snyder & Wiley 1976, Bortolotti 1984a, 1984b, Ferrer & de la Court 1992, Knox & Walters 1992, Brooker 1996). We have therefore used Principle Component Analysis of 13 biometrical characters in Paper III to classify unsexed specimens and to identify mis-sexed specimens as proposed by Bortolotti (1984a, 1984b). Because of large sexual dimorphism in *Nisaetus* hawk eagles, mis-sexed specimens could greatly have influenced the biometric comparison between taxa.


## MITOCHONDRIAL DNA SEQUENCES AS A PHYLOGENETIC TOOL

Mitochondrial DNA (mtDNA) sequences have frequently been used in the phylogenetic reconstruction of both deep vertebrate divergences and of relationships with a more recent history. The mtDNA is mainly maternally inherited and thus recombination of mtDNA is rare (Lansman *et al.* 1983). The fixation rate of a gene is directly proportional to the effective population size, given that the population is mating randomly and the gene evolving neutrally. A shorter fixation time is important when investigating rapidly diverging lineages. The risk of reconstructing the gene tree instead of the species tree is reduced considerably when a gene or a set of genes with a short fixation time are used (Moore 1995). Because specific regions of the mitochondrial genome evolve at different rates, it can be used to reconstruct phylogenies at different systematic levels (Mindell 1997, Härlid 1999).

The genetic information is encoded by the sequence of the four DNA bases adenine (A), thymine (T), guanine (G) and cytosine (C). DNA exists as complementary double strands, in which A pairs with T and G with C via hydrogen bonding. Genes are transcribed into messenger RNA (mRNA) which is translated into protein in the ribosomes. Animal genomes contain large regions (up to 98% of total DNA) of non-coding DNA, which are not translated into proteins. Mitochondrial DNA, however, consists mainly of protein encoding and ribosomal RNA (rRNA) genes, which are sequences that code for the RNA components of ribosomes. Uncoding regions are rare except for the control region (Beebee & Rowe 2004).

The mtDNA probably originated from bacterial endosymbionts, which fused with early eukaryotic cells (Margulis 1981).

Most studies on birds have been based on the mtDNA cytochrome b gene, which is thought to diverge in separated bird populations at a rate of about 2% per million years (Lovette 2004). It is most useful for separations that occurred within the past 4-5 million years. The mtDNA control region sequences are the most rapidly evolving region of the mtDNA genome and are useful for dating separations that occurred in the past 10,000 years (Newton 2003). We have therefore used both of these genes in our phylogenetical reconstructions.

DNA was extracted from museum feathers or skin from the foot pads, and polymerase chain reaction (PCR) gave DNA products that were sequenced. The lengths of the sequences were 264 nucleotids for *cyt b* and 237 for the control region. Both distance (neighbour-joining algoritm (Saitou & Nei 1987) and maximum parsimony methods were used to infer the phylogenetic relationships. Figures 5 and 6 provide a schematic overview of the various procedures between the starting point to the final result as a phylogenetical tree.
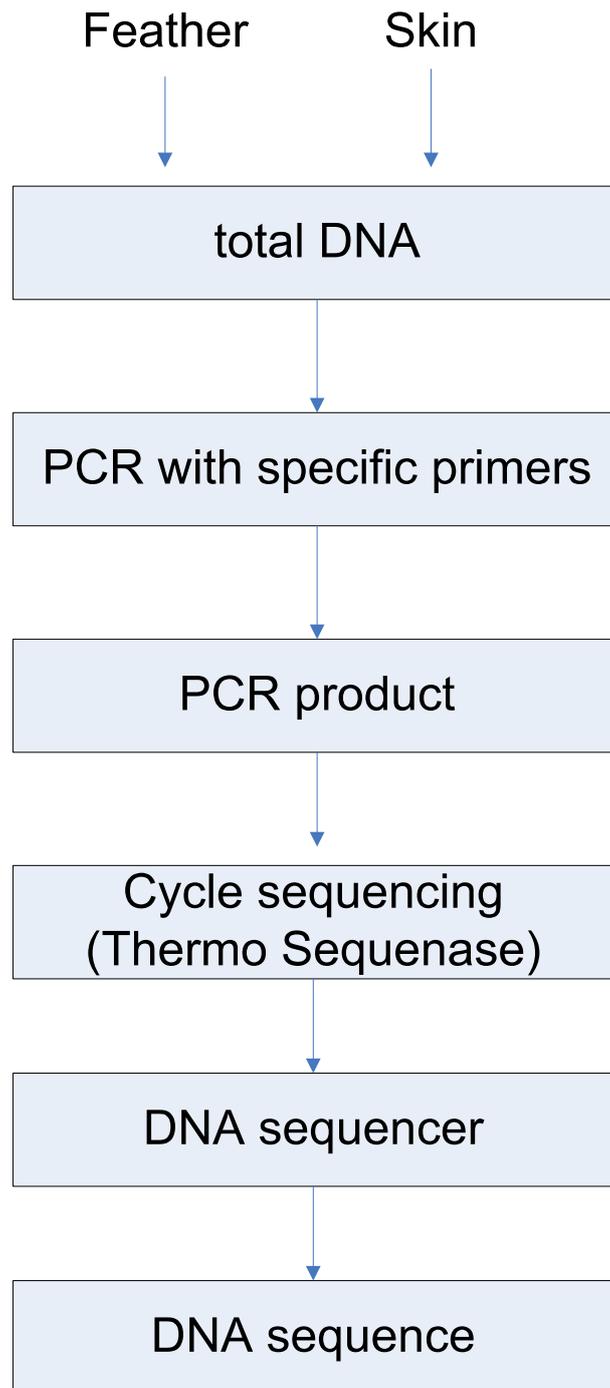
Fig. 5. Schematic illustration of the steps from sample to DNA-sequence (modified after Wink 2000, Fig. 4 on p. 834).
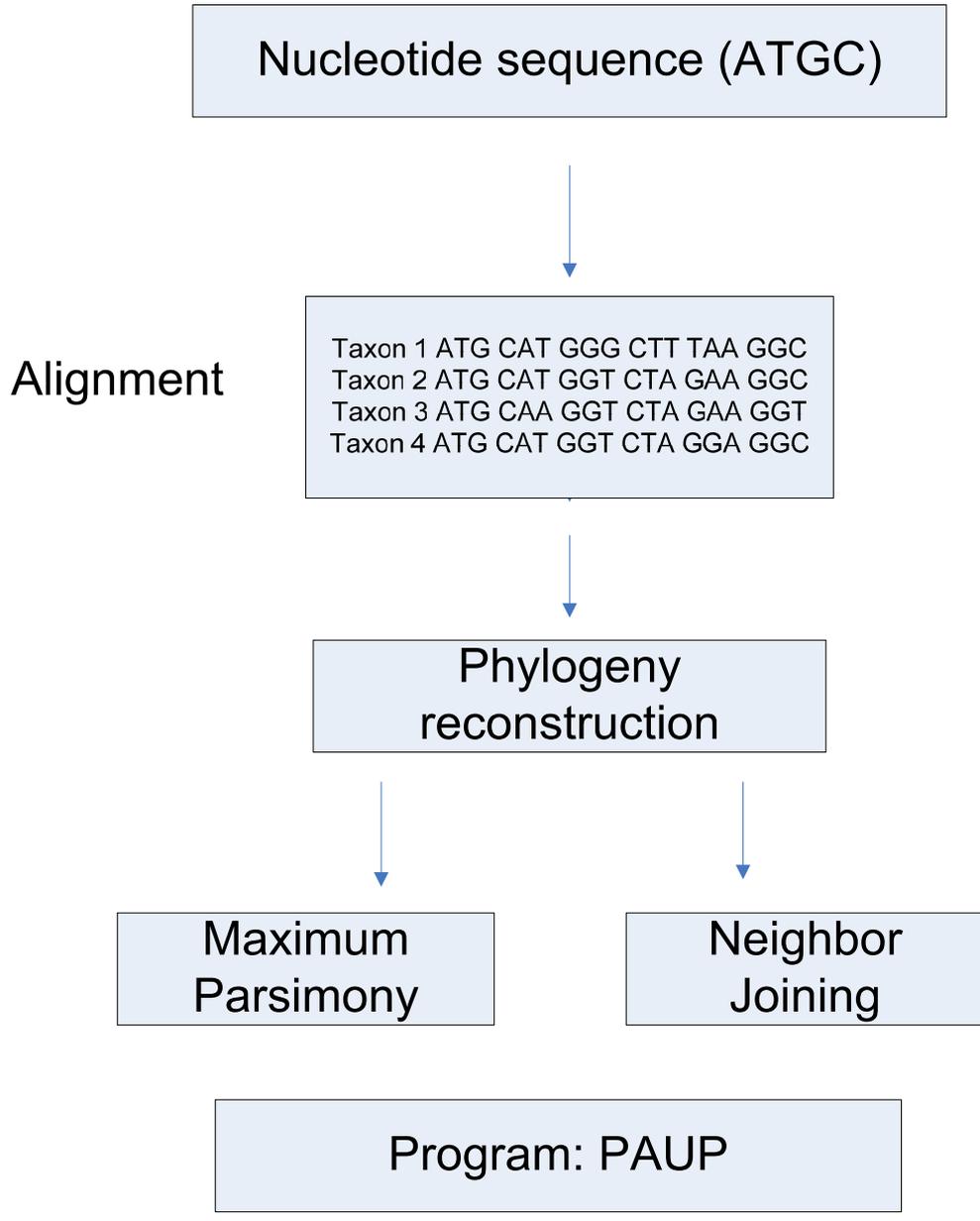
Fig. 6. From DNA-sequence to phylogeny (modified after Wink 2000, Fig. 5 on p. 835).

POPULATION SIZE ESTIMATE

We have used a rough method to obtain a rapid assessment of the population size. The population density has been estimated by the nearest-neighbour distances (NNDs) between pairs as a measure of territorial spacing to estimate population sizes from the available habitat (reviews in Ripley 1985, Krebs 1999). A circular plot (radius = ½ NND) is used as a measure of the density. The nearest-neighbour distances have been estimated either by direct observations of the borders between neighbouring territories or the distances between nests. We have also mapped one territory by radio-telemetry. Similar methods have been used in other studies of tropical rainforest raptors (Thiollay 1989, Whitacre *et al.* 1992, Preleuthner & Gamauf 1998, Lovell *et al.* 2003).

# RESULTS AND DISCUSSION

SPECIES DELIMITATION

**The *Nisaetus cirrhatus* complex (Paper I)**

On bases of the cytochrome *b* gene, the *cirrhatus* complex can be divided into two groups; one comprising *N. c. cirrhatus, N. c. ceylanensis* and *N. c. floris,* the other comprising the other taxa (*N. c. limnaeetus, N. c. vanheurni* and *N. c. andamanensis*). The relationships between these haplogroups are, however, only poorly supported in the bootstrap analyses. The haplotype distribution based on the CR resembles that found for cytochrome *b*, but for this gene, the clade of *N. c. cirrhatus* and *N. c. ceylanensis* no longer cluster with *N. c. floris*, but appear as a sister group of the remaining haplogroups of *N. cirrhatus.* The haplotypes of *N. c. limnaeetus* do not form a monophyletic group nor do they cluster according to geographic affinities in any of the phylogenetical trees. Within *N. cirrhatus* the genetical distances are rather low (0-1.5% in cytochrome *b*). We used *N. lanceolatus* and *N. philippensis* as outgroup taxa in the analyses. This gave the surprising results that *N. p. philippensis* and *N. p. pinskeri* was 3.4% different in cytochrome *b* and they did not form a monophyletic group.

The genetical distances observed within *Nisaetus cirrhatus* are in the range that can be expected at the intraspecific level. There is, however, a wide range of sequence divergences between pairs of presumably closely related bird species (0.1-10.6%) and subspecies (0.1-2.6%) (Seibold & Helbig 1995), which indicates that speciation may occur at different levels of sequence divergence. There is no direct way to deduce species status from observed sequence divergence values. Because additional information to interpret reproductive isolation (e. g. morphology and vocalization) was not available, we did not find good arguments to split this taxon into separate species (as suggested by e. g. Stresemann & Amadon 1979). We advocated the maintenance of the current taxonomy of the *cirrhatus-limnaeetus* complex.

There is a clear genetic distinction between *Nisaetus c. philippensis* and *Nisaetus p. pinskeri*. Based on this, together with their morphological and plumage pattern differences (Preleuthner & Gamauf 1998), we suggest that they should be treated as distinct species.

The use of a molecular clock to date mitochondrial lineages is based on the assumption that mutations in the mitochondrial genome (mtDNA) accumulate over time at rates that can be calibrated against absolute dates derived from fossils or geological evidence. Although the 2% rule for avian mitochondrial evolution is in widespread use, this standard rate is supported by only a small number of calibration studies that show substantial heterogeneity (Lovette 2004).

After having split of *N. floris* as a distinct species, *N. cirrhatus* seems to be a paraphyletic species, due to incomplete lineage sorting.

## *Nis*aetus *floris* (Paper II)

Reproductive isolation between *N. floris* and *N.* (*c.*) *limnaeetus* is suggested based on considerable morphological differences in both adult and juvenile plumages and no mixing of *florid* (n=5) and *limnaeetus* (N=5) mtDNA haplotypes, and no known hybridization despite no effective distribution barriers. We therefore regard *N. floris* as a distinct species according to the Biological Species Concept.

*N. floris* and *N.* (*c.*) *limnaeetus* are commonly regarded as allopatric, being separated only by a narrow strait between Bali and Lombok, perhaps not more than 1 km during the Pleistocene glacial sea-level depression (Van Oosterzee 1997). Changeable Hawk-eagles are able to colonise distant islands (Thiollay 1996, own observations). The distribution boundary between Bali and Lombok could therefore arguably be considered parapatric. The argument that parapatric and ecologically incompatible taxa are best treated as subspecies, because they are necessarily very closely related (Bock 1986, Amadon & Short 1992) is certainly not universally valid (Garcia-Moreno & Fjeldså 1999). Helbig *et al.* (2002) recommended that diagnosable taxa that are strictly parapatric and do not hybridise should be ranked as separate species, because it appears unlikely that such a situation can be maintained without intrinsic reproductive isolation. Natural selection would favour interbreeding between two populations that are in contact at an ecotone or trivial ecological barrier if hybrids have no fitness disadvantage. If such interbreeding does not occur despite the lack of an effective extrinsic barrier, mixing may be being prevented by intrinsic isolation mechanisms.

The genetical distance between *floris* and *limnaeetus* was found to be only 0.8-1.9 % in mtDNA cyt b (Paper I), indicating that they were separated during the Pleistocene. The Flores Hawk-eagle probably evolved in a refuge somewhere in the Lesser Sundas. Theoretical models suggest that the evolution of reproductive isolation can be fast (Lande 1981, Barton & Charlesworth 1984), and that morphological character states can evolve in much less than one million years (Nilsson & Pelger 1994), especially if there is strong selection combined with bottleneck effects. The neotenic (juvenile-like) plumage of adult *floris* may be an effective reproductive barrier for pairing with *limnaeetus*, as selection should work against pairing with juvenile birds. We find no obvious explanation for why *floris* has evolved neoteny, but such a trait might perhaps arise by loss of genetic variation in small populations.

### *Nisaetus cirrhatus* (Paper III and IV)

*Morphology*
Based on biometrics of museum specimens, we found that *N.* (*c.*) *limnaeetus* has a significantly larger bill length and bill depth than *N. c. cirrhatus*, whereas *cirrhatus* has a larger crest length and tail length. Eighteen of 58 museum specimens of *limnaeetus* had more or less intermediate crest length, and of 15 *limnaeetus* observed in the field, four had a crest of intermediate lenght. Using a Principal Component Analysis (PCA) the two taxa were not well separated.

*Vocalization*
Play-back experiments where territorial pairs of *N.* (*c.*) *limnaeetus* were presented vocalizations from both *limnaeetus* and  *cirrhatus* gave no indication of species recognition, as the reaction was very similar for the two type of vocalizations. Sonagraphic analyses of the different types of calls of the two taxa revealed no significant differences between the taxa in the measured parametre.

Rasmussen & Anderton (2005) found that there are some consistent morphological and vocal differences between *cirrhatus* and *limnaeetus*. The difference in crest length has been one of the main reasons for splitting these taxa into two different species. We found that only three of 48 characters were diagnostic different (no overlap) between the two taxa. The most diagnostic character is the longer crest in *cirrhatus.* As we have seen several *limnaeetus* with intermediate crest lengths, we think this perhaps indicates an earlier gene flow between the two taxa.  The differentiation between these taxa in mtDNA cytochrome *b* was 0.4-1.2 % (Paper I). It may be a result of small sample size (only one *limnaeetus* from Nepal).  The crest in hawk-eagles is possibly sympleisomorphic, as this character is found in most species of *Nisaetus* and in many other eagle genera. It has probably little importance in species recognition and mate selection. A similar situation is found in *Nisaetus nipalensis*, where there are both populations with and without a crest, and these are not separated in mtDNA cytochrome *b* (Haring *et al.* submitted). In my opinion the differences between *cirrhatus* and *limnaeetus* are so few and small, that I consider them as conspecific. But as there are different opinions among the authors of Paper III, we recommend more genetical analyses, both mitochondrial and nuclear, to find out if there is any degree of reproductive isolation between the two taxa.

### *Nisaetus nipalensis* and *N. kelaarti* (Paper V)

Statistical analyses of biometrical variables revealed significant differences between *nipalensis* and *kelaarti* in eight variables. A principal component analysis (PCA) gave no overlapping of the two taxa. There were also at least six plumage differences between the two taxa. In addition, the genetic difference between the two taxa is average 4.4 % in mtDNA cytochrome *b.* However, in the control region (CR) the average genetic difference was only 3.2 %, indicating that cyt *b* value may be exaggerated. Founder effects in small relict rainforest habitats during cool and dry periods of the Pleistocene may be an explanation (Haring *et al.* submitted).  From this, we conclude that *N. kelaarti* should be regarded as a distinct species.

The morphological differences between *N. kelaarti* and *N. nipalensis* in bill and feet indicate ecological differences between them. Longer bill and hind claws on *N. kelaarti* suggests that

it may have a higher proportion of mammals in its diet than *N. nipalensis*. The very short primary projection (Kipp's distance) is probably an adaptation either to hunting inside forests or lack of migratory behaviour (Kipp 1959).


CONSERVATION STATUS


### *Nisaetus floris* (Paper II)

On the basis of distances between three neighbouring territories, we estimated that the territory size for Flores Hawk-eagle is ca. 40 km². Given that it is primarily dependent on forest, this implies that the total population size for the species is probably less than 100 pairs (Prawiradilaga *et al.* in prep).

The population density estimate is based only on one territory size. Therefore more studies should be carried out to obtain larger sample size, and thereby more convincing results. But, we are convinced that the population will still qualify at least as Endangered on the Red List under criterion C2a(i) (total population <2,500 individuals and all subpopulations <250 individuals). BirdLife International (2005) has now listed it as Endangered.


### *Nisaetus kelaarti* (Paper V)

The Legge's Hawk-eagle is associated with primary evergreen forests. The current network of forest reserves in the Western Ghats may be inadequate, as it includes a low proportion of the most evergreen forest. Even smaller suitable forest areas remain in Sri Lanka. Based on the population density estimate of one pair per 2,110 ha (Thiollay 1993) and a remaining rainforest area of about 20,000 km² (Collins *et al.* 1991), we obtained a rough population estimate of about 1,000 pairs of *Nisaetus kelaarti* for the Western Ghats. We have used the population density estimate of Thiollay (1993) in lack of own estimates. I am uncertain about the methods used to get this estimate, but the estimate is quite similar to a estimate of one pair per 2,500-2,800 ha for *Nisaetus nipalensis orientalis* in Japan (Yamazaki 2000).

In Sri Lanka, there is very little habitat left for the species. The remaining area of rainforests (lowland and montane) was estimated to be 2135 km² in 1995 (Legg & Jewell 1995), although this has certainly declined since then. The three remaining larger forests (Peak Wilderness, Knuckles Hills and Sinharaja) cover 515 km². Most of the remaining forest patches are less than 10 km². Although the species is known to occur and breed in fragments even this small (D. Warakagoda *in litt.* 2006), they normally prefer larger forest patches. Given these data, Sri Lanka probably supports about one hundred pairs. Thus the total population of the species is likely to less than 2,500 breeding individuals, with about 10% of these on Sri Lanka.

The taxon has not previously been included on the IUCN Red List as this lists species only (e.g. BirdLife International 2001). As a distinct species, we suggest it would qualify as Near Threatened, because although it falls under the threshold of 2,500 individuals for the category Endangered, it does not have more than 95% of the mature individuals in one subpopulation as required under criterion C2a(ii). For the category Vulnerable it is required that all mature individuals are in one subpopulation. Using the C1 criterion it should qualify as Vulnerable if

the population decline has been more than 10% within three generations (since 1981), which is probable based of habitat loss during this period. The dense forest was reduced by 19.5% in southern part of Western Ghats in the period 1973-1995 with an annual rate of 0.8% (Jha *et al.* 2000). If we assume the same rate for the period 1981-2005 (3 generations), it gives 19.2% forest reduction for the period. But the IUCN guidelines (IUCN 2005) requires that the population decline using the C1 criterion has been estimated based on real population data, not "suspected" based on rates of forest loss. I find this unreasonable. If population estimates based on available habitats are acceptable for the C1 criterion, why should not estimates of population decrease by the same method be acceptable? In many cases this is the only possibility to make an estimate. On the national Red List for Sri Lanka it would qualify at the Endangered level under criteria C2a(i), C2a(ii), and D1 (<250 mature individuals).

### *Nisaetus bartelsi* (Paper VI)

The mean home-range size of the Javan Hawk-eagle on Java was estimated to be ca. 400 ha based on three different methods. The distance between nests of neighboring pairs was ca. 3 km in Gede-Pangrango and 2 km in the Salak Mountains. In the Halimun Mountains, the mean distance between territories was 1.8 km. Radiotracking of one adult male indicated a home-range size of 300 ha in the nonbreeding season. This finding suggested that earlier population estimates probably were too low, as they were based on home-range estimates of 2,000-5,000 ha per pair depending on habitat quality.

Our estimates of home-range sizes of 230-710 ha, suggesting a median value of ca. 400 ha are considerably lower than those given by other authors (Meyburg *et al.* 1989, Sözer & Nijman 1995, Thiollay & Meyburg 1988), which ranged from 1,200-12,000 ha. Relatively small home-ranges of ca. 650 ha have been documented in the Crowned Hawk-eagle *Stephanoaetus coronatus* (Shulz 2002). Our results from a single radio-tracked male probably represent the home-range size of a pair. We suggest that the male typically uses the combined home-ranges of the male and the female exploited during the breeding season. We repeatedly saw territorial interactions between neighboring pairs, suggesting that adjacent home-ranges were defended.

Van Balen *et al.* (2000) estimated the size of available Javan Hawk-eagle habitat on all Java at ca. 5,480 km² in 22 forest areas. Based on this finding and a density estimate of one pair per 2,000-5,000 ha, they estimated the total population of Javan Hawk-eagles to be between 137 and 200 pairs (van Balen 1999, Nijman *et al.* 2000). Our data indicated that this estimate probably was too conservative. Extrapolation of our Gede-Pangrango densities to the entire forest habitat would place the population size between 270-600 (median 435) pairs. However, we must admit that the accurancy of our home-range estimates are limited and our island-wide population estimate is based on a number of assumptions. Therefore, we recommend more studies to be carried out in different forest habitats in other parts of Java. Nevertheless, the species should still be regarded as Endangered under criterion C2a(i) (IUCN 2004) or C2a(ii) if we regard Java as one subpopulation; it is threatened by both habitat loss and illegal hunting. Because of this, we urge implementation of the Species Recovery Plan (Sözer *et al.* 1998) proposed by the Javan Hawk-eagle Working Group to ensure the future conservation of this species.

# GENERAL DISCUSSION

## SPECIES DELIMITATION

To delimitate species according to the guidelines of Helbig *et al.* (2002), we have to decide what distributional relationships there are between the taxa.

**Sympatry**. Taxa occurring in the same geographical area remain distinct if there is little or no gene flow between them. The taxa are reproductively isolated, either pre-zygotic (assortative mating) or post-zygotic (low hybrid fitness). *Nisaetus nipalensis* and *N. cirrhatus* can serve as an example of two sympatric eagle species occurring in the same area without hybridization.

**Parapatry**. Taxa that are strictly parapatric are distributed so close to each other that it infers visual and vocal contact, and thus the opportunity for physical contact between individuals of the two taxa (Amadon & Short 1992). Parapatric taxa are probably always in secondary contact after having diverged in allopatry, but have not evolved sufficient ecological differences to be able to co-occur sympatrically (Helbig *et al.* 2002). If they do not hybridze, they should be ranked as species, because it appears unlikely that such a situation can be maintained without reproductive isolation.

The taxa *Nisaetus* (*cirrhatus*) *limnaeetus* and *N. floris* are distributed on each side of the strait between Bali and Lombok. The longest distance of open sea between these islands is 24 km via Nusa Penida, but was even shorter (perhaps not more than 1 km) during the Pleistocene glacial sea-level depressions. Such distribution is normally regarded as allopatric, but we have argued that it better should be regarded as parapatric as this distance of open sea is no effective geographic barrier between these eagles. We regard these two eagles as different species (Paper II).

**Hybrid zones**. A hybrid zone is an area where the local populations contain one or both pure phenotypes plus first-generation and back-cross hybrids. There is a spectrum of natural variation in types of hybrid zones, from complete free interbreeding with no obvious fitness reduction, to occational interbreeding with fitness reduction. Hybrid zones are therefore rather awkward for the taxonomist, because it is largely an arbitrary decision whether to call the hybridizing taxa subspecies or species (Newton 2003). Helbig *et al.* (2002) consider that such cases always indicate a substantial restriction of gene flow. They term diagnosable taxa with such distribution semispecies. This distinguishes it from a clinal transition zone, in which local populations are intermediate between populations on either side of the zone, but are phenotypically uniform. In these situations the taxa are regarded as subspecies. Isler *et al.* (1999) treat taxa meeting at a narrow, stable cline differently. They consider such taxa as conspecific.

Delimitation of the two *Nisaetus* taxa *cirrhatus* and *limnaeetus* in India can serve as an example of how difficult such taxonomical decisions can be (Paper III and Paper IV). Occurrence of birds with intermediate crest lengths together with normal *limnaeetus* without a crest should indicate a hybrid zone. The taxa should then be termed semispecies after the guidelines of Helbig *et al.* (2002), which regard all hybrid zones as indications of restricted gene flow.

An alternative hypothesis is that the restricted gene flow between *limnaeetus* and *cirrhatus* is a result of the geographic separation between them. In that case, we should perhaps regard their distribution as allopatric, and the two taxa should be termed allospecies if they have at least one character fully diagnostic and the level of divergence is equivalent to that of the most closely related sympatric species (Helbig *et al.* 2002). I am not convinced that these two taxa diverge enough to be regarded as different species.

Diagnosability is however, a purely practical undertaking of the taxonomist as it does not matter whether or not characters used in diagnosis are relevant to the birds themselves, for instance in mate recognition. The fact that there are differences between taxa indicates that there has been a period during which genetic differences have accumulated, but not necessarily that they are reproductively isolated. To regard two taxa as different species, I think there should be differences in characters that could be part of reproductive isolation mechanisms. This could be related to mate recognition (plumage, courtship behaviour and vocalization) or selection against hybrids with intermediate structure characters relating to foraging strategy (bills and feets). If there are no such indications, I think the taxa are better regarded as conspecific. Collar (2004) also argued that consistency in discrimination of taxonomic rank requires significance of the diagnostic characters. Hybrid sterility could also be a possible post-zygotic isolation mechanism, but do not occur between closely related taxa that have been separated less than 1 million years (Price & Bouvier 2002). Ecological isolation is not probable either, as the two taxa are very similar in structure.

One should expect to find all kind of gradation between pure parapatric and hybrid zones situations with populations in physical contact to pure allopatric situations with geographical barriers preventing gene flow.

**Allopatry.** To delimitate taxa that are geographically separated must be based on a hypothesis as reproductive isolation cannot be observed. To be regarded as separate species, the guidelines of Helbig *et al.* (2002) require that the taxa should be fully diagnosable in each of several characters related to different functional contexts, and the sum of the character differences should correspond to or exceed the levels of divergence seen in related species that coexist in sympatry. This last requirement is sometime difficult to meet if there are no close related sympatric species. This is the situation for the *Nisaetus* hawk-eagles. All close related taxa are either parapatric or allopatric. One of the few examples from other eagle genera is the partly sympatric distribution of the very similar Lesser Spotted Eagle *Aquila pomarina* and the Greater Spotted Eagle *A. clanga.* They could perhaps illustrate how similar two sympatric eagle species can be. There is at least some reproductive isolation between these two taxa (Helbig *et al.* 2005b).

To require that the differences in characters between allopatric species should be as large or exceed the level of divergence seen in related species that coexist in sympatry is perhaps unrealistic, as the differences normally increase in sympatry due to reinforcement.
*Nisaetus nipalensis* and *N. kelaarti* can serve as an example of two allopatric species which meet the requirements of the guidelines (Paper V). With at least one character diagnostic and the level of divergence equivalent to that of the most closely related sympatric species, the taxa will be termed allospecies (Helbig *et al.* 2002). As discussed above, I do not think this is enough. There should be differences in characters that could be part of reproductive isolation mechanisms. All closely related allopatric species could be termed allospecies and be part of a superspecies regardless of the number of diagnostic characters as long as it is reasonable to believe that they are reproductively isolated. Delimitation of allopatric species will be

subjective regardless of use of guidelines. It will always remain a matter of opinion, much under the influence of recent precedent and current practice (Collar 2004). The most important reason for this is that the evolution and speciation are continuous biological processes, so there will inevitably be some borderline cases.


## USE OF MOLECULAR ANALYSIS IN TAXONOMY

The use of molecular methods has revitalised taxonomic research, although they have not removed subjectivity from decision making, as it is still a matter of judgement how different two populations have to be before they are considered as species rather than as subspecies (Newton 2003). There will never be a fixed degree of genetic divergence which defines a speciation event (Knox 1994). DNA divergence merely provides a crude numerical measure of the length of time since cross-breeding between two separate populations became very uncommon. This may not happen at the same time as the speciation event (Avise & Ball 1991). Speciation in birds can occur in a very short period of time, involving very little genetic divergence (Collinson 2001).

The most important contribution of molecular analyses has been in constructing phylogenies. Earlier attempts based on morphological criteria have had problems with convergence. Although convergence can occur with use of DNA also, as the same mutation may occur independently in distantly related species giving a false impression of a close relationship (Maclean *et al.* 2005), this is probably negligible, as it is improbable that many such mutations should happen by chance.

Phylogenies can contribute to taxonomic decisions when they show that two taxa, thought to be conspecific, are not each other's closest relatives. An example of such situation is the Tawny Eagle *Aquila rapax* and the Steppe Eagle *A. nipalensis*. The phylogenetic analyses of Wink (1998), Helbig *et al.* (2005) and Lerner & Mindell (2005) show that *A. rapax* are more related to the Imperial Eagle *A. heliaca* than to *A. nipalensis.* This confirm the split that was made on the basis of morphological characters (Sibley & Monroe 1990, Clark 1992). Another example is the two subspecies of the Little Eagle *Hieraaetus m. morphnoides* and *H. m. weiskei*. The phylogenies of Bunce *et al.* (2005) and Lerner & Mindell (2005) show that *H. m. weiskei* is more related to *H. pennatus* than to *H. m. morphnoides.* A split between these taxa has earlier been suggested by Parry (2001) based on morphological differences, and is included as a distinct species in Appendix B.

Paraphyly in gene trees do not, however, always indicate that the paraphyletic taxa are different species. DNA should not be used on its own to define a species, since different genes may give different results in a phylogenetic analysis (Avise & Wollenberg 1997, Zink & McKitrick 1995). Our gene tree in Fig. 2 and Fig. 4 (from Paper I), where *Nisaetus cirrhatus* appears to be paraphyletic can serve as an example. It may be a result of incomplete lineage sorting between young taxa, or it may be a result of the shortness of our sequences, as there are discrepancies between the cytochrome *b* and the CR trees. This illustrates that it is important to use as many characters as possible, including morphology and vocalization, when taxonomic status is evaluated. But there are also examples of real paraphyletic taxa, where the most genetically similar taxa are not their closest relatives (Funk & Omland 2003). To be regarded as a paraphyletic taxa, there should be no indication of reproductive isolation between populations.

Sometimes, discovery of considerable genetic distance between supposed conspecific taxa can initiate taxonomic research resulting in splitting of such taxa, as, e.g., our work on *N. nipalensis* and *N. kelaarti* (Paper V, Haring *et al.* submitted).

Another use of molecular analysis in taxonomic research is to compare mitochondrial and nuclear gene flow. Much higher nuclear than mitochondrial gene flow can indicate female hybrid sterility (Helbig *et al.* 2001, 2005).

Avian taxonomists have up to now primarily used a single locus (normally mtDNA cytochrome *b*) in analysis of avian phylogeny and divergence. Nuclear genes should also be used in questions of avian taxonomy, even if the interpretation of nuclear histories and the contrast with mtDNA histories will be challenging (Edwards *et al.* 2005).


## USE OF VOCALIZATIONS IN TAXONOMY

As avian species typically retain hybrid viability and fertility for millions of years after speciation, reflecting a general lack of intrinsic isolation mechanisms among closely related species (Price & Bouvier 2002), reproductive isolation in birds will often depend on prezygotic (premating) mechanisms. Thus, divergence in characters involved in mate choice, such as song, plumage, and behavioural displays, likely play a central role in avian speciation (Edwards *et al.* 2005).

Allopatric divergence of songs among suboscines and other birds in which differences in songs are genetically determined may evolve more slowly than in birds that learn their songs, but should also contribute to reproductive isolation. There is a current trend to recognise allopatric taxa with distinctive songs as species rather than subspecies (Sibley & Monroe 1990, Parker 1991, Price 1996, Peterson 1998, Alström & Ranft 2003, Rasmussen & Anderton 2005).

How different must vocalizations be to represent a barrier to gene flow? Isler *et al.* (1998) investigated this question in syntopic antbirds (Thamnophilidae), and found that different species were diagnosable in at least three characters of their song. They later used this criterion to delimitate allopatric taxa (Isler *et al.* 1999). Although this is a very important work, I am a little sceptical of using their criteria uncritically on other groups of birds with genetically determined and so-called "stereotyped" vocalizations. Diagnostic vocal characters can be used equally together with morphological and plumage characters in the evaluation of taxonomical status. But all subtle vocal differences should not uncritically be regarded as an indication of reproductive isolation. Use of play-back experiments can sometimes give a good indication of reproductive isolation, when birds respond to songs from their own taxon, but not to songs from another taxon. Although the lure of experimental playback trials is strong, assessment and interpretation of responses to playback are often problematic (Payne 1986, Kroodsma 1986, 1990).

It has been supposed that songs and calls in most non-passerines and suboscine passerines are stereotyped and innate, and are expected to show little or no vocal variation across their entire distributions (Rasmussen & Anderton 2005). There are, however, several examples of geographic variation in vocalizations in non-passerines, e.g. in the Pied Goshawk *Accipiter albogularis* and the Collared Kingfisher *Halcyon chloris* on different islands in Melanesia (Diamond 2002). Other examples of both learning of songs and geographic variation are

given by Baptista & Kroodsma (2001). Our study (Paper IV) showed that there is large intra-individual variation in the vocalization of *Nisaetus cirrhatus*, a variation depending on the motivation of the birds. This is far from stereotyped. When comparing the vocalizations from different taxa, it is important to compare homologous sounds which include the same levels of motivations.

There is still a need to refine and standardise the methodology for employing vocalization recordings as a taxonomist's tool. Vocalization data alone should never be used in making taxonomic decisions. But together with morphological, DNA, and behavioural data, they are important in taxonomic work.

## TAXONOMY AND CONSERVATION

A change of taxonomic status from subspecies to species will have great importance for their conservation status, because subspecies are not currently included in IUCN's red lists. It is not advisable to propose species status for a taxon just for conservation reasons. All such decisions should be made as far as possible according to the same basic criteria (Collar 1997). However, there are some cases where taxonomic decisions are very uncertain and arbitrary. Evolution and speciation are continuous processes that give rise to some borderline cases. Mayr & Aslock (1991) recommended that allopatric taxa of doubtful rank should be treated as subspecies. They argued that it is just as serious an error to call a population a species, when it is really only a subspecies, as it is to do the opposite. In my opinion, it is a bigger mistake to call a population a subspecies when it is a species, than to do the opposite. If such taxa, as, e. g., many islands endemics, are threatened with extinction, it would be better to follow the "precautionary principal" and treat them as allospecies. They should be given a lower rank only after convincing argumentation is given. In this way the burden of proof is reversed. It should lay on the shoulders of those who would reject these taxa. An alternative is to include threatened subspecies in the global red lists.

## CONSERVATION STATUS

Our population size estimates are based on some assumptions:

1) That the population density estimate is representative for the whole distribution area. This is probably not reasonable as the quality of habitats may be variable.

2) That the species is evenly spaced over its distribution area. This may not be the situation.

If we use a maximum density estimate and the species is not evenly spaced over its distribution area, it gives a too large population estimate. On the other hand, if we use a minimum density estimate with the same spacing, it gives a too low population estimate. The solution is to get better density estimates from as many different areas as possible, and to get a measure of how evenly distributed the species is. This has not been possible in this study, and our estimates must be regarded as rough. However, our first rough estimates may call attention to possible low and threatened populations, and may initiate more thorough studies.

# CONCLUSION AND FUTURE PERSPECTIVES

This thesis has, it is hoped, contributed to clarifying the taxonomic status of some of the many eagle taxa in South East Asia. The delimitation of *Nisaetus floris, N. pinskeri* and *N. kelaarti* as distinct species have great importance for their conservation attention. As they earlier were regarded as subspecies of rather common species, they were not included in IUCN's Red List. The change in taxonomic status will place *N. floris* and *N. pinskeri* as Endangered in the Red List together with *N. bartelsi* and *N. nanus*. *N. kelaarti* will probably be listed as Near Threatened.

A change in the strategy of conservation management is required. The priority of species as the most important evolutionary significant unit (Ryder 1986, Moritz 1994) should not influence taxonomists with respect to their decisions in classification, except when the decisions are very uncertain and arbitrary. In these cases, I have argued for following the "precautionary principal" and to treat them as allospecies. It should not matter whether a particular bird is a species or a subspecies, all biological diversity merits conservation. (Collar 1997, Collinson 1999, Knox 1994). If some of the various taxa under consideration become extinct, academic discussions about the taxonomic status of its populations will no longer be relevant.

There is still much to be done, both on taxonomy and conservation in South-East Asia. The *Nisaetus nipalensis* complex should be investigated in more detail. The taxonomic status of the populations in Japan, south-eastern Russia and Taiwan are still uncertain. The last two populations may be distinct undescribed subspecies. The *Nisaetus cirrhatus* complex should also be investigated in more detail. Their conservation status is little known. It should be possible to get population estimates for these and other little known taxa by using similar methods as described here.

The next step after identifying threatened taxa, is to develop species action plans. An example of such plans is the species recovery plan for the Javan Hawk-eagle (Sözer *et al.* 1998), which was initiated as part of our work in Indonesia (Røv & Gjershaug 2000). The underlying intention of the project on the Javan Hawk-eagle was to focus on rainforest eagles as flagship species in the conservation of the remaining rainforests and their unique biodiversity in Indonesia. The Javan Hawk-eagle is particularly suitable as a flagship species, as it is the national bird of Indonesia, and is similar to the national symbol, Garuda, and therefore draws the attention of the public. Besides forest conservation, the other main topic was to reduce illegal bird trading. Another important output of the project was a greater awareness regarding conservation issues among local people living close to the forests and among NGOs participating in the project. Similar projects could be initiated in other parts of Asia. Involving local people who use the forest resources is a prerequisite for saving the forests and their biodiversity for the future.

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## Appendix A

List of all current species of booted eagles (tribe Aquilini. Nomenclature follows Ferguson-Lees & Christie (2005)

Genus *Ictinaetus* Blyth, 1843
Indian Black Eagle                      *Ictinaetus malayensis* (Temminck, 1822)


Genus *Aquila* Brisson, 1760 (*Aquila chrysaetos*)
Lesser Spotted Eagle                    *Aquila pomarina* C.L. Brehm, 1831
Indian Spotted Eagle                    *Aquila hastata* (Lesson, 1834)
Greater Spotted Eagle                   *Aquila clanga* Pallas, 1811
Tawny Eagle                             *Aquila rapax* (Temminck, 1828)
Indian Tawny Eagle                      *Aquila vindhiana* Franklin, 1831
Steppe Eagle                            *Aquila nipalensis* Hodgson, 1833
Imperial Eagle                          *Aquila heliaca* Savigny, 1809
Spanish Imperial Eagle                  *Aquila adalberti* C. L. Brehm, 1861
Gurney's Eagle                          *Aquila gurneyi* G.R. Gray, 1860
Golden Eagle                            *Aquila chrysaetos* (Linnaeus, 1758)
Wedge-tailed Eagle                      *Aquila audax* (Latham, 1801)
Verreaux's Eagle                        *Aquila verrauxii* Lesson, 1830


Genus **Hieraaetus** *Kaup*, 1844 (*Hieraaetus pennatus*)
Wahlberg's Eagle                        *Hieraaetus wahlbergi* (Sundevall, 1851)
Bonelli's Eagle                         *Hieraaetus fasciatus* (Vieillot, 1822)
African Hawk Eagle                      *Hieraaetus spilogaster* (Bonaparte, 1850)
Booted Eagle                            *Hieraaetus pennatus* (Gmelin, 1788)
Little Eagle                            *Hieraaetus morphnoides* (Gould, 1841)
Ayres's Hawk Eagle                      *Hieraaetus ayresii* (Gurney, 1862)
Rufous-bellied Hawk Eagle               *Hieraaetus kienerii* (Geoffroy Saint-Hilaire, 1835)


Genus *Polemaetus* Heine, 1890
Martial Eagle                           *Polemaetus bellicosus* (Daudin, 1800)


Genus *Spizastur* G.R. Gray, 1841
Black-and-white Hawk Eagle              *Spizastur melanoleucus* (Vieillot, 1816)


Genus *Lophaetus* Kaup, 1847
Long-crested Eagle                      *Lophaetus occipitalis* (Daudin, 1800)


Genus *Spizaetus* Viellot, 1816 (*Spizaetus ornatus*)
Cassin's Hawk Eagle                     *Spizaetus africanus* (Cassin, 1865)
Indian Crested Hawk Eagle               *Spizaetus cirrhatus* (Gmelin, 1788)
Dimorphic Hawk Eagle                    *Spizaetus limnaeetus* Horsfield, 1821
Andaman Hawk Eagle                      *Spizaetus andamanensis* Tytler, 1865
Simeuluë Hawk Eagle                     *Spizaetus vanheurni* Junge, 1936
Flores Hawk Eagle                       *Spizaetus floris* Hartert, 1898
Mountain Hawk Eagle                     *Spizaetus nipalensis* (Hodgson, 1836)
Blyth's Hawk Eagle                      *Spizaetus alboniger* (Blyth, 1845)
Javan Hawk Eagle                        *Spizaetus bartelsi* Stresemann, 1924

Sulawesi Hawk Eagle              *Spizaetus lanceolatus* Temminck & schlegel, 1844
Philippine Hawk Eagle            *Spizaetus philippensis* Gould, 1863
Wallace's Hawk Eagle             *Spizaetus nanus* Wallace, 1868
Black Hawk Eagle                 *Spizaetus tyrannus* (Wied, 1820)
Ornate Hawk Eagle                *Spizaetus ornatus* (Daudin, 1800)

Genus ***Stephanoaetus*** W.L. Sclater, 1922
Crowned Hawk Eagle               *Stephanoaetus coronatus* (Linnaeus, 1766)

Genus ***Oroaetus*** Ridgeway, 1920
Isidor's Eagle                   *Oroaetus isidori* (Des Murs, 1845)

**Appendix B**

Proposed new taxonomy of booted eagles (tribe Aquilini) based on Gamauf *et al.* 2005, Haring *et al.* submitted, Helbig *et al.* 2005, Bunce *et al.* 2005 and Lerner & Mindell 2005.


Genus *Aquila* Brisson, 1760 (*Aquila chrysaetos*)
*Aquila rapax* (Temminck, 1828)
*Aquila nipalensis* Hodgson, 1833
*Aquila heliaca* Savigny, 1809
*Aquila adalberti* C.L. Brehm, 1861
*Aquila gurneyi* G.R. Gray, 1860
*Aquila audax* (Latham, 1801)
*Aquila chrysaetos* (Linnaeus, 1758)
*Aquila verrauxii* Lesson, 1830
*Aquila fasciata* Vieillot, 1822
*Aquila spilogaster* Bonaparte, 1850
*Aquila pennata* Gmelin, 1788
*Aquila morphnoides* Gould, 1841
*Aquila weiskei* (Reichenow, 1900)
*Aquila wahlbergi* Sundevall, 1851
*Aquila africana* (Cassin, 1865)
*Aquila ayresii* Gurney, 1862

Genus *Lophaetus* Kaup, 1847
*Lophaetus occipitalis* (Daudin, 1800)
*Lophaetus malayensis* (Temminck, 1822)
*Lophaetus pomarinus* (C.L. Brehm, 1831)
*Lophaetus hastatus* (Lesson, 1834)
*Lophaetus clangus* (Pallas, 1811)

Genus *Polemaetus* Heine, 1890
*Polemaetus bellicosus* (Daudin, 1800)

Genus *Kienastur* gen. nov. Haring *et al.* submitted
*Kienastur kienerii* (Geoffroy Saint-Hilaire, 1835)

Genus *Stephanoaetus* W.L. Sclater, 1922
*Stephanoaetus coronatus* (Linnaeus, 1766)

Genus *Spizaetus* Viellot, 1816 (*Spizaetus ornatus*)
*Spizaetus tyrannus* (Wied, 1820)
*Spizaetus ornatus* (Daudin, 1800)
*Spizaetus melanoleucus* (Vieillot, 1816)
*Spizaetus isidori* (Des Murs, 1845)

Genus *Nisaetus* Hodgson, 1836
*Nisaetus cirrhatus* (Gmelin, 1788)
*Nisaetus floris* (Hartert, 1898)
*Nisaetus lanceolatus* (Temminck & Schlegel, 1844)

*Nisaetus philippensis* (Gould, 1863)
*Nisaetus pinskeri* (Preleuthner & Gamauf, 1998)
*Nisaetus nanus* (Wallace, 1868)
*Nisaetus bartelsi* (Stresemann, 1924)
*Nisaetus alboniger* Blyth, 1845
*Nisaetus nipalensis* Hodgson, 1836
*Nisaetus kelaarti* (Legge, 1878)

# Paper I

# Species or subspecies? The dilemma of taxonomic ranking of some South-East Asian hawk-eagles (genus *Spizaetus*)

ANITA GAMAUF, JAN-OVE GJERSHAUG, NILS RØV, KIRSTI KVALØY and ELISABETH HARING

## Summary

A molecular phylogeny of the *Spizaetus cirrhatus* complex is presented in this study, based on two sections of the mitochondrial genome: partial sequences of the *cytochrome b* gene and of the control region (CR). The topologies derived from the two sequences are in agreement. Within *S. cirrhatus* distances are rather low (0–1.5% in *cytochrome b*). Among the *cirrhatus* subspecies the island taxa *floris*, *vanheurni* and *andamanensis* form distinct haplogroups in the CR trees, conforming to the earlier subspecific divisions which were based on morphological characters. On the other hand, the most widespread subspecies, *limnaeetus*, does not represent a monophyletic group in the gene trees and its haplogroups do not cluster according to geographic affinities. An unambiguous resolution of relationships among haplotypes and haplogroups, respectively, was not achieved, suggesting a more recent radiation of this group of hawk-eagles in the course of the last ice ages. Concerning the outgroup taxa *Spizaetus philippensis* and *Spizaetus lanceolatus*, our data indicate a clear genetic distinction between the two subspecies *S. p. philippensis* and *S. p. pinskeri*, suggesting that they should be treated as distinct species. Yet the phylogenetic relationships of the three outgroup taxa with respect to *S. cirrhatus* are ambiguous in our trees. The taxonomic consequences of applying different species concepts (BSC, PSC) are discussed. The species concept chosen would result in different conservation strategies.

## Introduction

With the advent of molecular methods in avian systematics (Sibley and Ahlquist 1990, Sibley and Monroe 1990), new interest in bird taxonomy arose in many regions of the world, and in recent years bird phylogeny has been revolutionized by a plethora of DNA sequence data. Moreover, the phylogenetic species concept (Cracraft 1983, Zink and McKitrick 1995), the general lineage concept (Helbig *et al.* 2002), and current trends in the application of the biological species concept (Haffer 1994), are now beginning to influence ornithologists' attitudes towards taxonomy of birds. Many bird taxa formerly treated as subspecies are now being considered full species by many authorities. The aim of national and international legislation, encouraged by conservation organizations, is to prevent the extinction of bird species as well as to reduce the number of globally threatened species by conserving crucial sites and habitats for birds and other fauna and flora (Stattersfield *et al.* 1998). Nevertheless, there are many cases where the level of conservation concern depends heavily on taxonomic decisions (Collar 1997, Frankham *et al.* 2002, Newton 2003). For example,

subspecies are included only exceptionally in conservation efforts, mostly regional or local in scale. Thus, even if population numbers are small and the areas restricted, there is no legislative basis for the protection of subspecies (even if these are arguably specifically distinct).

To escape from this "self-made dilemma", some ornithologists prefer to consider distinctive taxa as species. In particular, taxa restricted to islands have been raised from subspecies to species level to intensify conservation efforts (e.g. Daugherty *et al.* 1999, Boon *et al.* 2000). Time pressure for conservation measures and limited scientific material have sometimes been responsible for such decisions, which were often made without extensive morphological investigations or DNA-based studies (Stattersfield *et al.* 1998, BirdLife International 2000, Gaston 2001). Recent examples among birds of prey are Cape Verde Kite *Milvus fasciicauda*, Juan Fernandez Hawk *Buteo exsul* and Altai Falcon *Falco altaicus* (Ferguson-Lees and Christie 2001). On the other hand, there is a general problem with species concepts and their applicability to taxa which are in the dynamic process of speciation. The application of the Biological Species Concept (BSC: Mayr 1963) or the Phylogenetic Species Concept (PSC: Cracraft 1983) would result in a considerably different number of species.

In the present work we examine these problems in a genetic investigation of the phylogenetic relationships among South-East Asian hawk-eagles of the Changeable Hawk-eagle *Spizaetus cirrhatus* complex and the closely related taxa *Spizaetus philippensis* (Philippine Hawk-eagle) and *Spizaetus lanceolatus* (Sulawesi Hawk-eagle). This group of taxa are small to medium-sized eagles, largely sedentary, with a weight up to 1.8 kg. Changeable Hawk-eagle is the most widespread of the seven *Spizaetus* hawk-eagle species in South-East Asia, with a geographical distribution from India to the Lesser Sundas, and the Philippines. It inhabits savannah woodland, cultivation with trees, secondary and open primary forests from sea level up to 2,200 m a.s.l. (Thiollay *in* del Hoyo *et al.* 1994, Ferguson-Lees and Christie 2001). Of several described subspecies, six are currently recognized (Figure 1): *S. c. cirrhatus* in the Indian subcontinent, *S. c. ceylanensis* in Sri Lanka, *S. c. limnaeetus* from the Himalayan foothills through Indomalaya into the Greater Sundas and the Philippines, *S. c. andamanensis* on the Andaman Islands, *S. c. vanheurni* on Simeulue Island north-west of Sumatra and *S. c. floris* on Sumbawa and Flores (Brown and Amadon 1968, Thiollay *in* del Hoyo *et al.* 1994, Ferguson-Lees and Christie 2001). Since some of these subspecies are endemic to small oceanic islands it is very likely that they are severely threatened by habitat destruction, especially given the large areas required by large raptors. The other two species (*S. philippensis*, *S. lanceolatus*) are restricted to small islands, the Philippines and Sulawesi, respectively. They prefer primary and secondary forests from sea level to mountainous regions (Dickinson *et al.* 1991, Nurwatha *et al.* 2000, Thiollay and Rahman 2002).

*S. cirrhatus* differs from all the South-East Asian *Spizaetus* species by the feathering of the tarsi which terminates abruptly at the bases of the toes (Amadon 1953). Since its distribution range overlaps with all Asian *Spizaetus* representatives (after Amadon 1982), its classification as an independent species has been generally accepted, whereas all the other South-East Asian taxa (including *S. philippensis* and *S. lanceolatus*) were lumped together in a superspecies (Thiollay *in* del Hoyo *et al.* 1994). The various subspecies of *S. cirrhatus* are well differentiated in size and shape, and to a lesser degree in plumage. However, no published data are available about
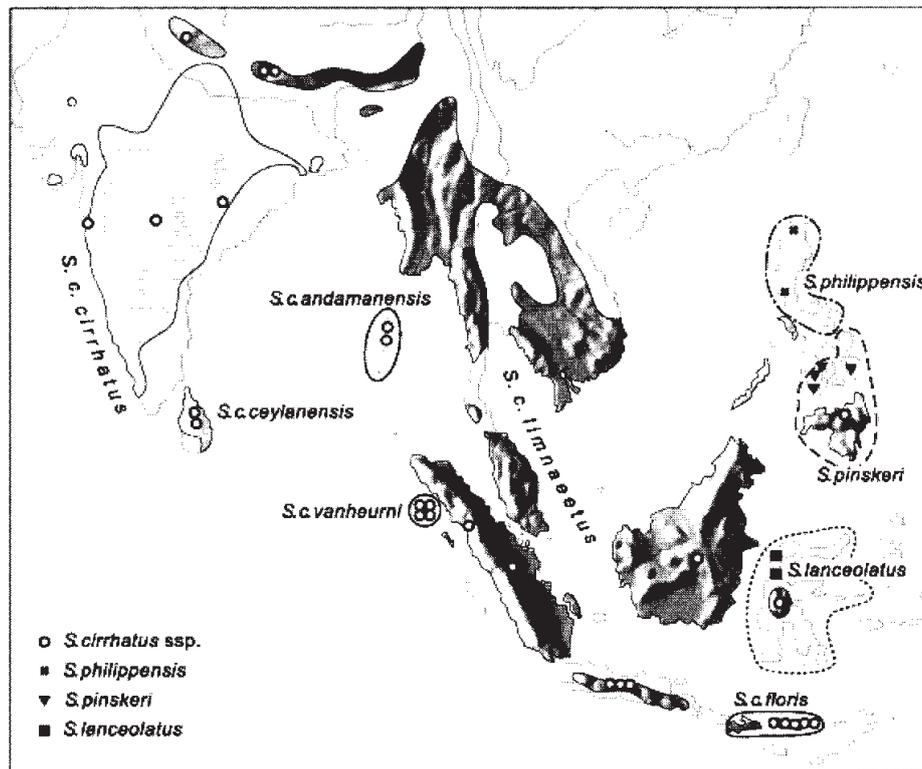
Figure 1. Distribution and localities of samples of *Spizaetus cirrhatus* (various subspecies), *S. philippensis, S. pinskeri* (treated as distinct species as suggested in the present study) and *S. lanceolatus.*

differentiation in vocalizations, behaviour or ecology. The largest and heaviest sub-species occur on the mainland (*cirrhatus, limnaeetus*) and on Sumbawa and Flores (*floris*), whereas populations of the smallest, with approximately less than half the weight (*vanheurni*), are found on the smallest island. The westernmost subspecies *cirrhatus* and *ceylanensis* are long-crested, *andamanensis* (P. Rasmussen pers. comm.) and the other subspecies are more or less un-crested. In most subspecies the ventral plumage is white with longitudinal streaks and more or less intensively barred thighs. Exceptions are the polymorphic *limnaeetus* with colours ranging from pale to mela-nistic, and *floris* which is almost white with a faint pattern. Because of some special features (e.g. lack of a crest, presence of a melanistic morph, vocalization) *limnaeetus* is occasionally considered to be a separate species (Amadon 1953, 1982, Stresemann and Amadon 1979, Rasmussen and Anderton 2004). The differences in plumage pattern and morphological characters are much more pronounced between the sub-species of *S. philippensis* (*philippensis, pinskeri*) than among the subspecies of *S. cirrhatus* (Preleuthner and Gamauf 1998, Gamauf *et al.* 1998a).

In this paper we address the following questions:

(1) Do the morphologically well differentiated *S. cirrhatus* and *S. philippensis* subspecies also differ genetically?

(2) Is *limnaeetus* a distinct species?

(3) How can the taxonomic status of the taxa investigated be interpreted using different species concepts?

(4) What would be the consequences of our data with respect to conservation?

## Material and methods

*Samples*

Twenty-seven samples of *S. cirrhatus* with known geographical origin representing its six subspecies were examined. As outgroup taxa we used *S. philippensis* (six specimens representing two taxa) and *S. lanceolatus* (two specimens). Of the other *Spizaetus* species, these two species seem to be most closely related to *S. cirrhatus*, as will be described elsewhere (Haring *et al.* in prep.). Since it was not possible to obtain fresh tissue from most of the relevant taxa included in this study, we had to rely mainly on museum material (feathers or skin from the foot pads of study skins). Sample codes, source, collecting localities, museum inventory numbers, and GenBank accession numbers are listed in Table 1. In the case of S. c. *vanheurni* all specimens are paratypes. To assess genetic variability within taxa, up to 10 samples per taxon were analysed (e.g. *S. c. limnaeetus*). Two mitochondrial marker sequences were used which were isolated and analysed separately in two laboratories: (1) a section of the cytochrome *b* gene (*cyt b*), which was analysed at the Laboratory of the Institute for Nature Reserve (NINA, Trondheim); (2) a section of the control region (CR), which was analysed at the Laboratory of Molecular Systematics (NHM, Vienna).

*DNA extraction*

DNA extractions were performed following two different protocols. In one of the protocols (NHM, Vienna) a 10% Chelex (Biorad) solution containing proteinase K (0.5 mg/ml) was added. After incubation (4 h, 50°C, with agitation) solutions were heated to 95°C for 5 min and centrifuged for 1 min. For purification and to remove short fragments of degraded DNA the supernatant was purified using the QIA Quick PCR Purification Kit (Qiagen) with a final volume of 30–70 µl elution buffer. Using another extraction method (NINA, Trondheim), DNA from museum feathers was isolated according to Taberlet and Bouvet (1991) except that a Microcon YM-50 filter (Amicon) was used instead of a Centricon 30 (Amicon) to desalt and concentrate the sample. If retentate was not obtained, 10 µl of TEm: buffer (1 mM EDTA, 10 mM Tris-HCl, pH 8.0) was added to the Microcon YM-50 filter (Amicon), and left for 10 min before centrifugation was performed again. Control extractions with pure extraction buffer (without tissue) were prepared for the polymerase chain reaction (PCR) experiments.

*PCR amplification*

At the NHM, PCR was carried out with an Eppendorf Thermocycler, in a volume of 25 µl, containing 1 unit Dynazyme DNA polymerase (Finnzymes OY) 0.5 µM of each primer, and 0.2 mM of each dNTP. Initial denaturation (95°C, 2 min, was followed by 30 reaction cycles: 95°C (10 s), annealing temperature (10 s), 72°C (30 s); final extension at 72°C (5 min). At NINA PCR was performed in a 25 µl reaction mix containing 15 pmol of each primer, 2.0 mM $MgCl_2$, 0.8 mM of each dNTP, 1 µl 10× PCR buffer II and 1–1.25 U AmpliTaq Gold polymerase (Applied Biosystems) or HotStar Taq (Qiagen). After denaturation and activation of AmpliTaq Gold (10 min at 95°C) or HotStar Taq (15 min at 95°C), 40 cycles of 30 s at 94°C, 45 s at 50°C and 90 s at 72°C were performed on a 2600 or 2700 thermocycler (Applied Biosystems).

Table 1. Sample list of *Spizaetus* hawk-eagles. *S. philippensis* and *S. pinskeri* are treated as distinct species as suggested in the present study.

| Taxon | Sample code | Tissue | Locality, Year | Source, Voucher | Marker | GenBank Accession nos. |
|---|---|---|---|---|---|---|
| *Spizaetus c. cirrhatus* | Scircir3 | fe | India, Bombay, 1874 | BMNH 1887.11.1.342 | *cyt b*, CR | AY701097, AY701067 |
| | Scircir4 | pa | India, – | NMW 85.060 | CR | AY701068 |
| | Scircir5 | fe | India, Seoni, 1869 | BMNH 1885.8.19.1424 | *cyt b*, CR | AY701098, AY701069 |
| *S. c. ceylanensis* | Scircey1 | pa | Sri Lanka | AMNH 534.913 | *cyt b* | AY701099 |
| | Scircey5 | fe | Sri Lanka | RMNH 5210 | *cyt b*, CR | AY701100, AY701070 |
| *S. c. andamanensis* | Scirand1 | fe | India, Andaman Is., 1874 | BMNH 1885.8.19.1466 | *cyt b*, CR | AY701113, AY701079 |
| | Scirand4 | fe | India, Andaman Is., 1997 | B. Miller | *cyt b*, CR | AY701112, AY701080 |
| *S. c. limnaeetus* | Scirlim1 | pa | Indonesia, Java, 1931 | NMW 322 | *cyt b*, CR | AY701101, AY701071 |
| | Scirlim2 | pa | Indonesia, Borneo, Bongas/Borabei, 1882 | NMW 46. 498 | *cyt b*, CR | AY701103, AY701072 |
| | Scirlim3 | pa | Indonesia, Sumatra, Deli, 1886 | NMW 71.242 | *cyt b*, CR | AY701102, AY701073 |
| | Scirlim4 | pa | Indonesia, Java, 1884 | NMW 71.241 | *cyt b*, CR | AY701104, AY701074 |
| | Scirlim9 | fe | Nepal (before 1859) | BMNH 1859.3.4.603 | *cyt b* | AY701105 |
| | Scirlim10 | fe | Nepal (before 1859) | BMNH 1859.3.4.602 | *cyt b*, CR | AY701106, AY701075 |
| | Scirlim11 | pa | Indonesia, Java, 1924 | RMNH 14000 | *cyt b*, CR | AY701107, AY701076 |
| | Scirlim12 | pa | Indonesia, Sumatra, 1919 | RMNH 15387 | *cyt b* | AY701108 |
| | Scirlim12a | pa | N India, Uttar Pradesh, Kalnahi, 1947 | AMNH 461.932 | *cyt b*, CR | AY701109, AY701077 |
| | Scirlim13 | fe | Indonesia, Sulawesi, 1935 | RMNH 7208 | *cyt b*, CR | AY701110, AY701078 |
| | Scirlim16a | fe | Philippines, Mindanao, 1993 | P. v. Nievenhuis | *cyt b* | AY701111 |
| *S. c. vanheurni* | Scirvan1 | pa | Indonesia, Simalur Is. (= Simeulue), 1913 | RMNH 87.258, paratype | *cyt b*, CR | AY701114, AY701081 |
| | Scirvan2 | pa | Indonesia, Simalur Is., 1913 | RMNH 87.259, paratype | *cyt b*, CR | AY701115, AY701082 |
| | Scirvan3 | pa | Indonesia, Simalur Is., 1913 | RMNH 87.257, paratype | *cyt b*, CR | AY701116, AY701083 |
| | Scirvan4 | pa | Indonesia, Simalur Is., 1913 | RMNH 87.260, paratype | *cyt b*, CR | AY701117, AY701084 |
| *S. c. floris* | Scirflo1 | pa | Indonesia, S Flores, – | AMNH 534.895 | *cyt b*, CR | AY701118, AY701085 |

Table 1. Continued.

| Taxon | Sample code | Tissue | Locality, Year | Source, Voucher | Marker | GenBank Accession nos. |
|---|---|---|---|---|---|---|
|  | Scirflo2 | fe | Indonesia, Flores, Waeriko, 1976 | RMNH 81.112 | cyt b, CR | AY701119, AY701086 |
|  | Scirflo3 | fe | Indonesia, Flores, – | RMNH 66.257 (4) | cyt b, CR | AY701120, AY701087 |
|  | Scirflo4 | pa | Indonesia, Flores, Sika, 1891 | RMNH 16 XIV 1892 | cyt b, CR | AY701121, AY701088 |
|  | Scirflo6 | fe | Indonesia, Flores, 2002 | J.-O. Gjershaug, N. Røv | cyt b, CR | AY701122, AY701089 |
| S. lanceolatus | Slan1 | pa | Indonesia, Sulawesi, 1931 | ZMB 33.114 | cyt b, CR | AY701129, AY701095 |
|  | Slan3 | fe | Indonesia, Sulawesi, 1887 | BMNH 1887.11.1.337 | cyt b, CR | AY701130, AY701096 |
| S. philippensis | Sphiphi2 | pa | Philippines, N Luzon, 1895 | BMNH 1897.5.13.311 | cyt b, CR | AY701124, AY701090 |
|  | Sphiphi6a | fe | Philippines, Luzon, Manila, 1985 | J. A. James | cyt b, CR | AY701123 |
| S. pinskeri | Sphipin8 | fe | Philippines, Negros, – | NMW, F-399 | cyt b, CR | AY701125, AY701091 |
|  | Sphipin9 | fe | Philippines, S Negros, – | NMW, F-400 | cyt b, CR | AY701126, AY701092 |
|  | Sphipin10 | fe | Philippines, Negros, – | NMW, F-401 | cyt b, CR | AY701127, AY701093 |
|  | Sphipin11 | fe | Philippines, ?Leyte, – | NMW, F-402 | cyt b, CR | AY701128, AY701094 |

Tissue: fe, feathers; pa, skin of foot pad.

Optimal amounts of template DNA extracted from museum material were determined empirically (2–10 µl of the DNA solution) using occasionally dilutions from 1- to 50-fold (from control DNA extracted from blood samples 50 ng DNA template was used). If necessary, re-amplifications were performed with 1–2 µl template. Negative controls for PCR reactions were carried out to screen for contaminated reagents: (1) control extractions (without DNA) instead of template; (2) reaction with A.d. instead of template. Since the major part of the study was based on tissue of museum specimens, the expected maximum length of PCR fragments was < 400 bp.

The two primers that were used both for PCR amplification and direct sequencing of the *cyt b* gene were called mt-A and mt-I. Primer mt-A (L-14970) (5'-CAA CAT CTC AGC ATG ATG AAA CTT CG-3') was modified by Wink (1998) based on the *cyt b* sequence by Kocher *et al.* (1989). Primer mt-I (H-15350) (5'-TGC TGA GAA TAG GTT GGT GAT GAC-3') was isolated and optimized at NINA Trondheim; it was based on *cyt b* sequences of five *Aquila* species (Seibold *et al.* 1996). Of the 381 bp PCR product obtained, 264 bp corresponding to positions 15034 to 15298 of the *Gallus gallus* f. *domesticus* mitochondrial genome (Desjardins and Morais 1990) was used for sequence comparisons. For the control region two primer pairs were used: CR5+: 5'-CCC CCC CTT CCC CCC C-3', CR7–: 5'-GAC CGA CTA AGA GAT AAC CTA-3' (annealing temperature: 50°C), and (for specimens where no PCR product could be obtained with the primer pair CR5+/CR7–) two nested primers CR1+: 5'-ATG TAC TAT TGT ACA TTA AAC-3', CR2–: 5'-CAA GTT ATG ACC TGC TACC-3' (annealing temperature: 50°C).

## Cloning and sequencing

PCR products were extracted from agarose gels using the QIAquick Gel Extraction Kit (Qiagen) and cloned (TOPO TA Cloning Kit, Invitrogen). At the NHM sequencing of cloned PCR products (both directions) was performed by MWG-Biotech (Ebersberg, Germany). At NINA direct sequencing of PCR products was performed (both strands). Successful amplification and approximate quantification of PCR products were checked by running one-fifth of the PCR samples on a 2% agarose gel. PCR products were purified using Qiagen QIAquick-spin PCR purification kits (Qiagen). Approximate yields of PCR products after purification were quantified by agarose gel electrophoresis. Purified PCR products were sequenced on an Applied Biosystems 310 DNA sequencer (Foster City, CA) with *Taq* DNA polymerase and Dye Terminators or Big Dye Terminators as instructed by the manufacturer. PCR conditions for sequencing of PCR products were 30 cycles with 30 s at 96°C, 15 s at 50°C and 4 min at 60°C. The sequence extension products were purified by ethanol precipitation according to the manufacturer's instructions (Applied Biosystems) except that the ethanol was not chilled and the procedure was performed at room temperature. The sequences determined in the course of the present study are registered under the GenBank accession numbers listed in Table 1.

## Sequence analysis

Alignments were produced manually. The alignments have lengths of 264 (*cyt b*) and 237 (CR) sites respectively. The reading frames of all *cyt b* sequences proved to be intact, suggesting that the sequences are derived from functional mitochondrial genes. Both distance (neighbor-joining algorithm, NJ: Saitou and Nei 1987) and maximum

parsimony (MP) methods were used to infer the phylogenetic relationships. All dendrograms were calculated with the software package PAUP (test version 4b6-10; Swofford 2002). For NJ trees uncorrected distances (p-distances) were used. MP trees were generated with heuristic search using the TBR (tree bisection reconnection) algorithm and a random taxon addition sequence (1,000 replicates). All characters were weighted equally.

## Results

Since many samples consisted of only small pieces of tissue from old museum material, it was not possible in some cases to obtain sequences from both markers (Table 1). Thus, both marker sequences were sequenced from 29 samples, from five samples the *cyt b* fragment only was amplified, and from one sample the CR fragment only was obtained. The 29 samples from which both sequences could be analysed were used for the combined trees as well as for comparisons of distances and nucleotide diversity between markers.

As was expected, sequence variability of the protein-coding *cyt b* gene was lower than that of the non-coding CR sequence. For example, within the *S. cirrhatus* complex up to five substitutions (range of p-distances 0.0–1.9%; number of segregating sites: 8) were found among *cyt b* sequences (264 bp), and up to 17 substitutions (range 0.0–7.5%; number of segregating sites: 37) among the CR sections (237 bp). Nucleotide diversity per site was 4 times higher in the CR than in *cyt b* (3.4 vs 0.8). Almost no length variation was observed; only the CR sequence of the specimen Scirlim3 carried a 2 bp deletion. Between ingroup and outgroup taxa (*S. p. philippensis, S. p. pinskeri, S. lanceolatus*) the p-distance range was 2.7–6.3% for *cyt b* and 3.9–10.4% for the CR. Comparing the ranges of p-distances within and between subspecies (Table 2) it becomes apparent that within *S. c. limnaeetus* the variability is in the same range as that found between subspecies.

Among the 34 *cyt b* sequences 11 haplotypes can be distinguished, eight of them within *S. cirrhatus*. As can be seen in the NJ tree calculated from these sequences (Figure 2), two of the island taxa possess their own haplotype (*S. c. floris*), or belong to the same haplogroup (*S. c. vanheurni*). Two of the remaining five haplotypes are shared by two taxa each (*S. c. limnaeetus + S. c. andamanensis, S. c. cirrhatus + S. c. ceylanensis*). The *cirrhatus* complex can be divided into two groups, one comprising *S. c. cirrhatus, S. c. ceylanensis* and *S. c. floris*, the other comprising the other taxa (*S. c. limnaeetus, S. c. vanheurni, S. c. andamanensis*). Nevertheless, relationships between these groups as well as between haplogroups are only poorly supported in the bootstrap analyses (NJ and MP). The two shortest trees found in the MP analysis (TL = 29, CI = 0.828, RI = 0.951, RC = 0.787) have the same topology as the NJ tree (differences between the two MP trees are found only with respect to the outgroup taxa).

Among the 30 CR sequences, 24 haplotypes were found, 21 of which were among the 23 individuals of *S. cirrhatus*. The NJ tree derived from the CR sequences is depicted in Figure 3. The haplotype distribution resembles that found for *cyt b*. Again *S. c. floris* and *S. c. vanheurni* belong to separate haplogroups. In addition, the haplotypes of *S. c. andamanensis* form a distinct branch. As with *cyt b*, *S. c. cirrhatus* and *S. c. ceylanensis* form a clade. But, in contrast to the *cyt b* tree, where these two taxa cluster with *S. c.*

Table 2. Ranges of pairwise p-distances within and between taxa. *S. philippensis* (Sphi) and *S. pinskeri* (Spin) are treated as distinct species as suggested in the present study.

| *cyt b* | Scircir | Scircey | Scirflo | Scirlim | Scirand | Scirvan | Slan | Sphi | Spin |
|---|---|---|---|---|---|---|---|---|---|
| Scircir | 0.0 | 0.0 | 0.4 | 0.4–1.2 | 0.8 | 1.1–1.5 | 4.3 | 3.1 | 4.7 |
| Scircey | | 0.0 | 0.4 | 0.4–1.2 | 0.8 | 1.1–1.5 | 4.3 | 3.1 | 4.7 |
| Scirflo | | | 0.0 | 0.8–1.9 | 1.1 | 1.5–1.9 | 4.7 | 3.5 | 5.1 |
| Scirlim | | | | 0.0–1.1 | 0.0–0.8 | 0.4–1.5 | 3.9–5.1 | 2.7–3.9 | 5.1–6.3 |
| Scirand | | | | | 0.0 | 0.4–0.8 | 4.3 | 3.1 | 5.5 |
| Scirvan | | | | | | 0.0–0.4 | 4.7–5.1 | 2.7–3.1 | 5.9–6.3 |
| Slan | | | | | | | 0.0 | 3.9 | 4.3 |
| Sphi | | | | | | | | 0.0 | 3.5 |
| Spin | | | | | | | | | 0.0 |
| **CR** | | | | | | | | | |
| Scircir | 0.0–0.4 | 2.2–2.6 | 3.9–4.3 | 2.6–5.7 | 3.9–4.3 | 3.9–4.3 | 6.1–6.6 | 4.3–4.8 | 7.1–8.9 |
| Scircey | | 0.0 | 4.4–4.8 | 3.9–7.5 | 5.3–5.7 | 4.4–5.3 | 8.0 | 6.7 | 9.0–10.4 |
| Scirflo | | | 0.0–1.3 | 2.1–5.7 | 2.6–3.9 | 2.1–3.4 | 6.6–8.4 | 4.8–5.2 | 7.5–9.4 |
| Scirlim | | | | 1.3–5.7 | 3.0–5.2 | 2.1–3.0 | 7.1–9.4 | 3.9–7.6 | 6.6–9.4 |
| Scirand | | | | | 1.3 | 2.1–3.9 | 7.5–8.0 | 5.7–6.1 | 7.1–9.4 |
| Scirvan | | | | | | 0.4–0.9 | 7.5–8.4 | 4.8–5.7 | 7.5–8.9 |
| Slan | | | | | | | 0.9 | 8.0 | 7.5–9.8 |
| Sphi | | | | | | | | 0.0 | 4.3–5.7 |
| Spin | | | | | | | | | 0.0–2.1 |

Abbreviations according to Table 1.

*floris*, they appear as sister group of the remaining haplogroups of *S. cirrhatus*. The various *S. c. limnaeetus* haplotypes are scattered among the other haplogroups and do not form a monophyletic group nor do they cluster according to geographic affinities. Bootstrap support is generally low, especially for the relationships among the various haplogroups. The topologies of the NJ and MP trees are in agreement: the 155 shortest trees (TL = 87, CI = 0.655, RI = 0.820, RC = 0.537; bootstrap values are included in Figure 3) differ mainly with respect to the branching pattern of haplogroups within *S. c. cirrhatus*.

The topology of the combined tree (concatenated *cyt b* and CR sequences) is similar to the CR tree with slightly higher bootstrap support, but still the relationships among most haplogroups are poorly supported.

A surprising result of this investigation is the clear genetic distinction between *S. p. philippensis* (from Luzon) and *S. p. pinskeri* (from Negros, Leyte and Mindanao). Distances between these two taxa are within the range (*cyt b*: 3.4%, CR: 4.5–5.8%) observed between each of them and either *S. lanceolatus* or *S. cirrhatus* (*cyt b*: 2.7–5.3%, CR: 4.1–9.5%). The relationships among the three taxa used as outgroups are not unambiguously resolved. In the *cyt b* trees *S. p. philippensis* and *S. p. pinskeri* do not even form a monophyletic group.

## Discussion

The molecular phylogeny of the *S. cirrhatus* complex established in this study is based on two sections of the mitochondrial genome. Despite their different levels of variability the topologies derived from the two sequences are in agreement.
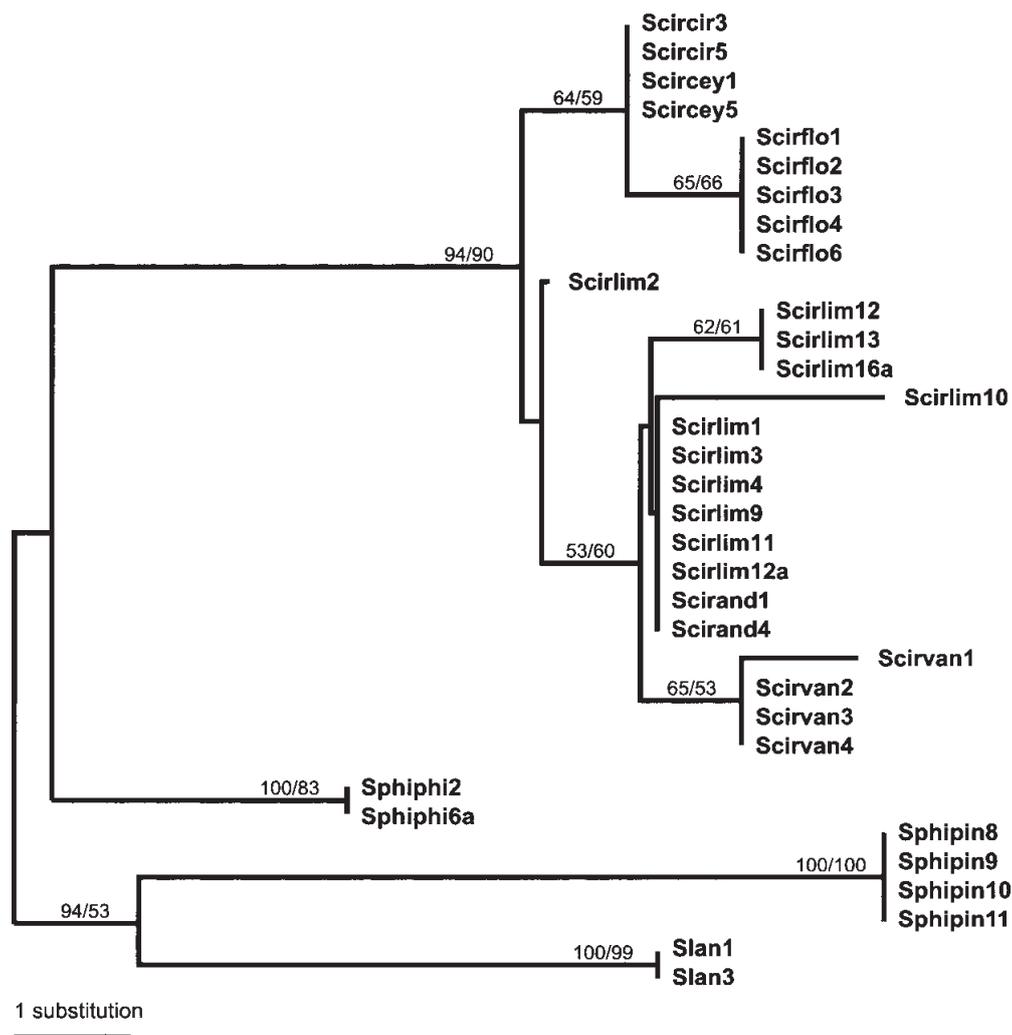
Figure 2. NJ tree based on *cyt b* sequences (midpoint rooting). Bootstrap values (1,000 replicates) >50% are given at the nodes (left: NJ, right: MP). Assignment of sequences is according to specimens in Table 1.

## Genetic differentiation at species level

Although current classification places *S. lanceolatus* and *S. philippensis* either within the *S. nipalensis* "Formenkreis" (Stresemann 1924) or considers them a super-species together with the other South-East Asian species (Amadon 1982, Thiollay *in* del Hoyo *et al.* 1994), preliminary sequence comparisons with other *Spizaetus* species (Haring *et al.* unpublished data) revealed that they are rather closely related to *S. cirrhatus*. This association is also supported by the white juvenile plumage shared by this assemblage, whereas the remaining South-East Asian hawk-eagle taxa (*S. nipalensis, S. alboniger, S. nanus, S. bartelsi*) have buff to orange-brown plumage at this age (Brown and Amadon 1968, Ferguson-Lees and Christie 2001). Consequently, they were taken as outgroup taxa for this study. Moreover, the two taxa can be used for comparisons of intra- and interspecific variability within this genus. As our data show, there is a clear genetic distinction between *S. p. philippensis* and *S. p. pinskeri*. Yet the phylogenetic relationships of the three outgroup taxa with respect to *S. cirrhatus* are not unambiguous in our trees, and *S. philippensis* does not even form a monophyletic group in all trees. Because of the high sequence divergence between the two lineages of *S. philippensis*, together with their clear-cut morphological and plumage pattern

Scircir3
Scircir4  71/67   S. c. cirrhatus   Bombay, India
Scircir5  96/-                       India
88/64                                Seoni, India
Scircey5   S. c. ceylanensis   Sri Lanka
Scirlim13                      Sulawesi, Indonesia
Scirlim2  90/66                Borneo, Indonesia
Scirlim4                       Java, Indonesia
Scirlim11                      Java, Indonesia
Scirlim1   S. c. limnaeetus    Java, Indonesia
Scirlim3                       Sumatra, Indonesia
Scirlim10  75/59  56/-         Nepal
Scirlim12a                     Sumatra, Indonesia
Scirand1  96/84   S. c. andamanensis   Andaman Is., India
Scirand4                              Andaman Is., India
Scirvan1  61/-                 Simeulue Is., Indonesia
Scirvan2   S. c. vanheurni     Simeulue Is., Indonesia
Scirvan4  74/55                Simeulue Is., Indonesia
Scirvan3                       Simeulue Is., Indonesia
Scirflo1                       Flores, Indonesia
Scirflo2  61/63  69/-          Flores, Indonesia
Scirflo3   S. c. floris        Flores, Indonesia
Scirflo4                       Flores, Indonesia
Scirflo6                       S Flores, Indonesia
Slan1  100/100  S. lanceolatus  Sulawesi, Indonesia
Slan3                           Sulawesi, Indonesia
Sphiphi2   S. philippensis   Luzon, Philippines
Sphipin8  98/97              Negros, Philippines
Sphipin10  99/100  S. pinskeri  Negros, Philippines
Sphipin9  96/64              Negros, Philippines
Sphipin11                    Leyte, Philippines
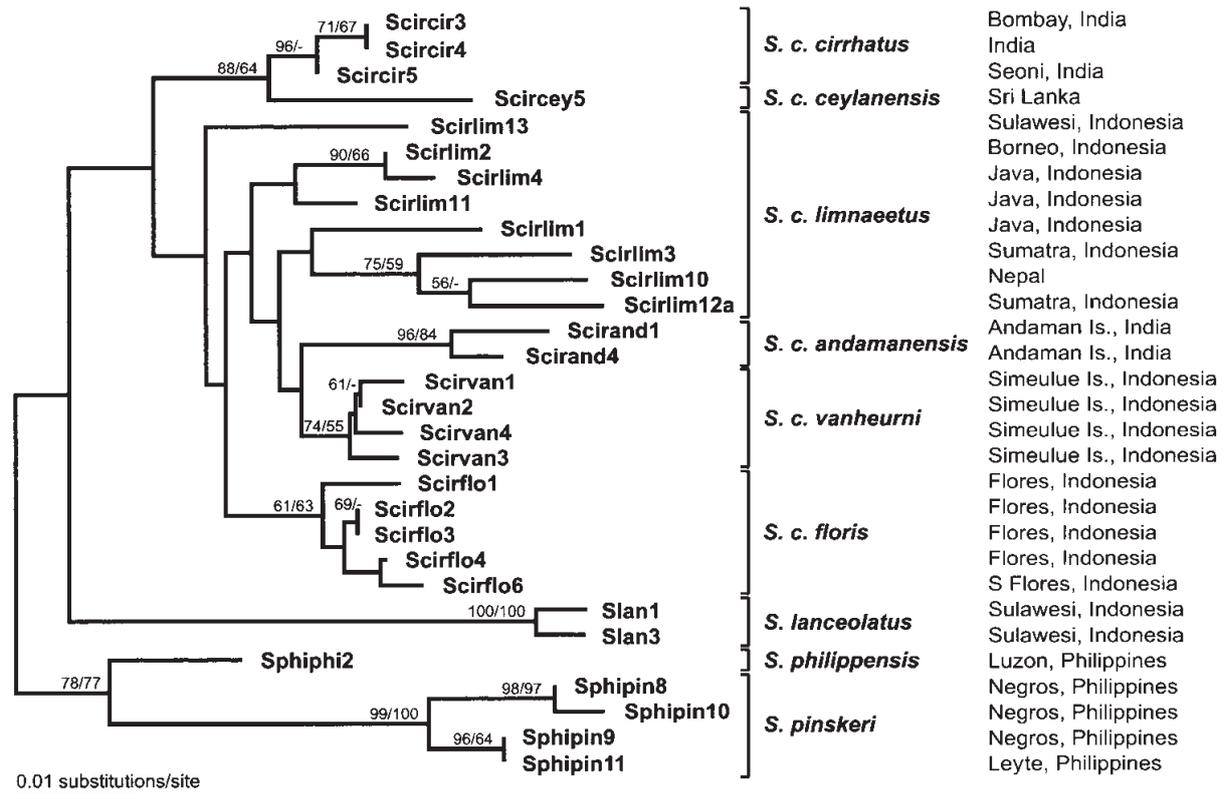78/77

0.01 substitutions/site

Figure 3. NJ tree based on CR sequences (midpoint rooting). Bootstrap values (1,000 replicates) >50% are given at the nodes (left: NJ, right: MP). Assignment of sequences is according to specimens in Table 1. *S. philippensis* and *S. pinskeri* are treated as distinct species as suggested in the present study.

differences (Preleuthner and Gamauf 1998), we suggest that they should be treated as distinct species.

## Genetic differentiation within S. cirrhatus

Within *S. cirrhatus* the distances observed are in a range that can be expected at the intraspecific level. For example, within Eastern Honey-buzzard *Pernis ptilorhyncus* the distances for the same *cyt b* section measured 2.1–3.9% between subspecies groups and 1.5–1.8% between subspecies within groups (Gamauf and Haring 2004). In *S. cirrhatus* variability within subspecies is highest in *S. c. limnaeetus*, which has the widest geographical range including numerous islands and is also the taxon with the highest plumage variability. Lower variability is found within subspecies restricted to islands. In the *cyt b* sequences the number of parsimony-informative sites is rather low (0–5), providing only limited phylogenetic information. The relationships among *cyt b* haplogroups are not clearly resolved and bootstrap support is very low. With the exception of *floris* and *vanheurni* no clear separation of subspecies is obtained with this marker, and even these two subspecies are combined by only one synapomorphic substitution. Whether this substitution can be used as a diagnostic site has to be investigated in a larger sample of specimens. In the CR trees the island taxa *floris* and *vanheurni* (as in *cyt b*), as well as *andamanensis*, form separated haplogroups confirming the subspecific division based on morphological characters. Yet, even with

this highly variable section a clear resolution of relationships among haplotypes and haplogroups, respectively, was not achieved. The island forms appear as haplogroups within the bush-like tree of *limnaeetus* sequences, which does not represent a monophylum. There is no indication of recent gene flow between the island subspecies and *limnaeetus* or *cirrhatus*; however, the sample sizes are comparatively small. In any case, the differentiation of a western group formed by *cirrhatus* and *ceylanensis* becomes apparent, a pattern corresponding partly to that found in the *cyt b* trees. However, with the latter marker this group is associated with *floris*, although this affiliation is based on a single synapomorphic site only.

## Phylogeographic considerations

The *S. c. cirrhatus-limnaeetus* complex may be another example of continuing speciation in birds in South-East Asia, apparently influenced by glacial processes. Similar scenarios have been described for the genus *Pernis* (Gamauf and Haring 2004) and several other bird groups (e.g. Dickinson *et al.* 1991). What kind of conclusions do the sequence data allow with respect to phylogeography? The close association of *S. c. cirrhatus* and *S. c. ceylanensis* (sequence identity within *cyt b*) reflects the geographic proximity of their ranges (India and Sri Lanka), assuming their rather recent separation from each other at the end of the last glaciation when the land connection was severed. The remaining taxa belong to a group that could be designated as "*limnaeetus* radiation", which can also be assumed to have occurred in the more recent past (in the course of one of the last glaciations). The division between the two groups may have occurred during glaciation of the Himalaya massif and its foothills, splitting up the ancestral population into a western (India) and an eastern (South-East Asia) range. In such cold periods with low sea level, the ancestral form of the *limnaeetus* group may have spread throughout the exposed land masses of the Sunda Shelf including the islands of Sumatra, Java and Borneo. These areas were presumably covered mainly by steppe habitats, and dispersed forest "islands" may have been located mainly on the former island areas (van Oosterzee 1997, Wilson *et al.* 2000). Such forest patches were already inhabited by the ancestors of the other South-East Asian *Spizaetus* representatives (e.g. *S. philippensis*, *S. pinskeri*, *S. lanceolatus*, *S. nanus*, *S. bartelsi*, *S. alboniger*). Supposing that the ancestor of the *limnaeetus* group was morphologically adapted to semi-open habitats as it is today (Brown and Amadon 1968, Thiollay 1988, 1996, 1998, Gamauf *et al.* 1998a, b), competition was minimized between the inhabitants of forests and the new invaders. At the end of the last glaciation this continuous geographical range may have split up again due to rising sea levels. Assuming that this species crosses only narrow sea passages, the populations became more or less isolated on their respective islands (e.g. Greater and Lesser Sundas, Andamans, Simeulue), which are at the outermost border of the distribution range. For *S. philippensis* and *S. pinskeri* it could be hypothesized that an ancestral population was subdivided earlier in the Pleistocene into two lineages, one on Greater Mindanao and the other on Greater Luzon. Factors identified as influencing species richness on the Philippines include island area, maximum elevation, and Pleistocene patterns of connection and isolation. In a similar way many other bird groups on the Philippines, especially endemic species, underwent differentiation on these two main island complexes (Peterson *et al.* 2000).

Regarding *limnaeetus,* so far there is no record of this subspecies on Sulawesi (White and Bruce 1986, Coates and Bishop 1997). The specimen Scirlim13 from Sulawesi (RMNH 7208), which had been originally designated as *S. lanceolatus,* turned out to belong to *S. c. limnaeetus* (based on comparisons of plumage characters and measurements carried out by R. Dekker, Naturalis, Leiden). Thus, it seems likely that *limnaeetus* is also distributed on that island. The misidentification had probably happened because of the white head and underparts of the juvenile plumage of this specimen, a character which both taxa share.

## Species concepts and taxonomy of Changeable Hawk-eagle

Genetic diversity is recognized as the fundamental component of biodiversity (Moritz and Faith 1998). How can we use knowledge about genetic diversity and differentiation to draw conclusions concerning taxonomy or to answer the question of what a species is? A wide range of sequence divergences between pairs of presumably closely related bird species (0.1–10.6%, mitochondrial markers) and subspecies (0.1–2.6%) has been reported in Seibold and Helbig (1995). This indicates that, on the one hand, speciation may occur at different levels of sequence divergence. Moreover, species which, according to morphological similarities, appear to us as closely related may in fact have diverged a long time ago. Some examples for sequence divergences (*cyt b*) between birds of prey are 1.8% for Spanish Imperial Eagle *Aquila adalberti* versus Imperial Eagle *A. heliaca,* as well as Greater Spotted Eagle *A. clanga* versus Lesser Spotted Eagle *A. pomarina.* White-tailed Sea-eagle *Haliaeetus albicilla* and Bald Eagle *H. leucocephalus* differ by 2.5% (Seibold and Helbig 1995), and two honey buzzard species *Pernis celebensis* and *P. ptilorhyncus* by 4.0–5.7% (Gamauf and Haring 2004). Nevertheless, there is no direct way to deduce species status from observed sequence divergence values.

Although many definitions exist for the term "species" (Amadon and Short 1992, Haffer 1992, 1994), none of them are universally accepted. The Biological Species Concept (BSC: Mayr 1963) is that predominantly used in evolutionary ornithology. According to the BSC a species represents a group of interbreeding (or potentially interbreeding) natural populations that are reproductively isolated from other such groups. Since speciation can occur gradually over longer periods of time, the BSC also includes a dynamic aspect of gene pool differentiation allowing the designation of subspecies (Futuyma 1998). These are groups of populations that share a unique geographic range and/or habitat and are distinguishable from other subdivisions of the species by multiple, independent, genetically based traits (Avise and Ball 1990, O'Brien and Mayr 1991). The BSC has been increasingly challenged in recent years and a number of alternative species concepts have been proposed, which will not be treated here in detail. Island-rich South-East Asia represents a worst-case situation for the BSC, which meets its most serious challenges in insular situations (Zink and McKitrick 1995, Peterson *et al.* 2000), where reproductive isolation cannot usually be tested. Although a recent interpretation of the BSC (AOU 1998, Helbig *et al.* 2002) allows recognition of allopatric forms as species units (in common with the PSC), classification based on molecular markers without knowledge of reproductive isolation is always arbitrary, especially if no additional data, e.g. concerning karyotypes, behaviour or vocalizations, exist (Frankham *et al.* 2002). Such additional information which could serve as hints for possible reproductive isolation between the allopatric

forms of the Changeable Hawk-eagle are not yet available. At the moment, the only known barrier between the taxa is due to the isolation on islands.

In practice, two morphologically differentiated allopatric populations are often considered as distinct species if their degree of genetic differentiation matches that of two well-recognized species in a related group (e.g. *Cyanopica*: Fok *et al.* 2002). Within the *cirrhatus* complex the differences between subspecies are in the lower range observed so far for other pairs of raptor species. However, low genetic differences do not exclude species status. Between *Haliaeetus leucogaster* and *Haliaeetus sanfordi*, for example, sequence divergence is only 0.3%, although species status of these taxa may be a matter of dispute.

Nevertheless, the low genetic diversity within *S. cirrhatus* could also be interpreted as intraspecific variation for two reasons: (1) the most widespread subspecies *S. c. limnaeetus* does not represent a monophyletic group in the gene trees, and (2) its haplogroups do not cluster according to geographic affinities. Although the subspecies are geographically isolated, there is no evidence for reproductive barriers. Thus, applying the BSC there is no good argument to split this taxon into separate species (as suggested by e.g. Stresemann and Amadon 1979), although morphological differences exist (e.g. between *S. c. cirrhatus* and *S. c. limnaeetus*). At best, the sequence data suggest a separation of the western forms (*S. c. cirrhatus*, *S. c. ceylanensis*) from the rest.

Concerning *S. philippensis*, sequence data as well as clear morphological differentiation would justify the split into two species according to the PSC. As is generally the case with most island taxa, no data about reproductive barriers required by the BSC are available. However, we know from other examples that the separation between the northern and southern Philippine islands (Greater Luzon and Greater Mindanao during periods of low sea level) has led to speciation in many bird taxa (e.g. Dickinson *et al.* 1991, Peterson *et al.* 2000).

In the Phylogenetic Species Concept (PSC: Cracraft 1983) a species is considered as the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent. With this definition the PSC evades the problem of reproductive isolation between diagnosable allopatric forms by treating them all as species. Taking into account the clear morphological differences, the six taxa comprising the *S. c. cirrhatus* group would deserve species status under the PSC. Accordingly, the more or less erratic haplotype distribution would be the consequence of incomplete lineage sorting. Also the split of *S. philippensis* into two species would be in accordance with the PSC.

We have tried to show that two different species concepts (BSC, PSC) allow different conclusions. Since even among the authors there are different points of view concerning interpretation of species concepts, there is a dilemma how to come to a final decision concerning the taxonomy of this group. In this paper we advocate the maintenance of the current taxonomy of the *cirrhatus-limnaeetus* complex, which is more in accordance with the BSC. Nevertheless, in a separate paper three of the authors of the present paper (Gjershaug *et al.* 2004) will give additional information on the morphological differences and reproductive isolation between the subspecies *floris* and *limnaeetus*.

*Conservation*

"Correct" diagnosis of the taxonomic status of populations is critical with respect to conservation, because unrecognized species may – due to a lack of protection – become

extinct. Taking into account that species usually are given more importance in conservation measures as "evolutionary significant units" (ESU: Ryder 1986, Moritz 1994, Frankham *et al.* 2002), conservation would be more affected by further progress of the PSC than any other discipline (Collar 1997). What kind of consequences does the application of different species concepts have with respect to the conservation of the *Spizaetus* hawk-eagles? The status of the monotypic *S. lanceolatus* will not be influenced by our results, since Sulawesi still has a high proportion of rain forest (*c.* 60%; Collins *et al.* 1991), and this species still seems to be rather common (Nurwatha *et al.* 2000, Thiollay and Rahman 2002). The situation is different in the Philippines, where the splitting of Philippine Hawk-eagle into two species, *S. philippensis* and *S. pinskeri,* will lead to lower estimates of population sizes: about 200–220 pairs for *S. philippensis* on Luzon and 320–340 pairs for *S. pinskeri* on Mindanao (Preleuthner and Gamauf 1998). BirdLife International has already classified the "former" Philippine Hawk-eagle (inclusive *S. pinskeri*) as "Vulnerable" (BirdLife International 2000, Collar 2001). Meanwhile, since the mid-1990s, its rainforest habitat has continuously diminished, and it can be assumed that its population status corresponds to this decline. The populations of *S. pinskeri* endemic to Negros and a few other islands (e.g. Mindanao, Leyte, Samar) are probably also very small. In practice, the splitting of *S. philippensis* into two independent species means that, following the definition of BirdLife International (Stattersfield *et al.* 1998), both taxa should be included in the higher category "Endangered".

The most far-reaching consequences of the application of different species concepts would concern the taxa of the *cirrhatus-limnaeetus* complex with its six morphologically distinct forms. Following the current taxonomy (Ferguson-Lees and Christie 2001) based on the BSC (no evidence for reproductive barriers), *S. cirrhatus* is classified as a single species comprising six subspecies, which as a whole would not be considered threatened. Applying the PSC and similar species concepts, which differentiate all diagnosable "lineages", would lead to an upgrading of the six subspecies to species level, of which three or four would then be considered threatened. It is undisputed that they would deserve protection: three of the taxa are distributed over very small restricted ranges (Stattersfield *et al.* 1998). For example, *andamanensis* inhabits less than 6,475 km², *vanheurni* 1,600 km² and *floris* <50,000 km². Taking into account that birds of prey in general need large home-ranges (Newton 1979) they all appear to be scarce. The only exception is *ceylanensis,* which inhabits Sri Lanka with approximately 65,000 km², is still relatively common and presently not threatened (Harrison 1999). Only the nominate form *cirrhatus* and *limnaeetus* are distributed over larger ranges. Common to all taxa is that they are under more or less heavy pressure and declining (Thiollay 1996, van Balen and Nijman 1998) because of habitat loss. The population of *floris,* which is considered as rare (Butchart *et al.* 1996), is estimated to be 100 pairs maximum (Gjershaug *et al.* 2004). Population numbers of the other island-restricted *S. cirrhatus* taxa are unknown, but at least *vanheurni* is probably rare as well. In general, the existing protected areas are too small, often not very well protected and represent only minor parts of the respective distribution areas (Collins *et al.* 1991, Stattersfield *et al.* 1998). Thus, protected areas do not guarantee protection of whole populations/subspecies. Moreover, there are many taxa, currently threatened and unambiguously good species, for which "immediate protection measures" are still wanting.

Nevertheless, it would not be advisable to propose species status for such comparatively young taxa just for conservation reasons. Such a practice, which could be termed the "conservation species concept", would be a bad compromise and would have no scientific basis. High sequence similarity in one gene does not necessarily mean that these populations do not harbour genetic peculiarities which they maintain as an answer to specific environmental challenges. Morphological differences may only be the most obvious external indicators for such adaptive differentiation. Thus, even if these populations (subspecies) belonged to one biological species, they could contribute considerably to the genetic flexibility of the species and therefore should be managed as separate entities regardless of their formal taxonomic status.

The case of the *S. cirrhatus* complex may serve as an example that a change in the strategies of conservation management is required. The priority of "species" as the most important "evolutionarily significant units" should not influence taxonomists with respect to their decisions in classification. On the other hand the treatment of infraspecific taxonomic groups as evolutionarily significant units (Moritz 1994, Collar 1996) would enable the start of immediate protection measures even if taxonomic status is not clarified. When some of the various forms of Changeable Hawk-eagle have become extinct, academic discussions about the taxonomic status of its populations will no longer be relevant.

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# Paper II

# The taxonomic status of Flores Hawk Eagle
# *Spizaetus floris*

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U. SUPARMAN and Z. RAHMAN

The Changeable Hawk Eagle *Spizaetus cirrhatus* complex ranges from India (*cirrhatus*) through South-East Asia (mainly *limnaeetus*) to Flores, Sumbawa and Lombok, Indonesia (*floris*). The latter taxon is morphologically very distinct from the widespread *limnaeetus*. It has diagnostic white patches on the upperside of the inner parts of the primaries, a juvenile-like adult plumage, and it is much larger than *limnaeetus*. It is allopatric with *limnaeetus* without any known geographical overlap. The large morphological differences indicate that the two taxa are reproductively isolated. We suggest that *floris* be treated as a distinct species with the English name of Flores Hawk Eagle.

## INTRODUCTION

Taxonomic studies within conservation biology have become increasingly important. The IUCN Red List of threatened species (IUCN 2001) is commonly used to help focus conservation priorities on the species at greatest risk of extinction. At present, subspecies are not generally listed (e.g. BirdLife International 2000). In cases where the taxonomic status of rare subspecies has not been sufficiently clarified, there is a risk that potentially valid species could become extinct even before conservation action is initiated.

In Indonesia, the conservation of rainforest raptors has attracted increased attention during recent years. In this region, a number of closely related forest-living hawk eagles *Spizaetus* spp. are found. Changeable Hawk Eagle *S. cirrhatus* comprises a complex of subspecies occuring in two major groups, crested and crestless, but the taxonomic status of the different subspecies has been disputed (del Hoyo *et al.* 1994). Six taxa are normally recognised: two crested taxa comprising *cirrhatus* (India south of Rajasthan and Gangetic plain) and *ceylanensis* (Sri Lanka), and four uncrested taxa comprising *andamanensis* (Andaman islands), *limnaeetus* (north India and Nepal through Myanmar, southern Indochina, Malay Peninsula to Greater Sundas and southern Philippines), *vanheurni* (Simeulue island west of Sumatra) and *floris* (Lombok, Sumbawa and Flores; Fig. 1).

Amadon (1953) divided the subspecies into two groups: the *cirrhatus* group (*cirrhatus*, *ceylanensis* and *andamanensis*) and the *limnaeetus* group (*limnaeetus*, *vanheurni* and *floris*). B. King (personal communication 1994 to Inskipp *et al.* 1996) suggested that *floris* was a separate species because its adult and juvenile plumages were identical, unlike other subspecies of *S. cirrhatus* which have distinct juvenile and adult plumages. The morphological differences between *floris* and *limnaeetus* are so striking that it seems surprising that these forms have been lumped together. One reason could be that museum specimens of adult *floris* look quite similar to juvenile *limnaeetus* (Fig. 2a), leading to the assumption that all museum specimens are juveniles, wrongly aged by the collectors. This has resulted in incorrect illustrations of adult *floris* in many current handbooks and fieldguides (e.g. Weick 1980, del Hoyo *et al.* 1994, Coates and Bishop 1997, Ferguson-Lees and Christie 2001). These all illustrate adult *floris* with a brown head. The first widely available illustration of an adult *floris* was made by Weick (1980). In his first draft he painted the eagle with a white head based on studies of museum specimens. However, Weick was advised by Amadon and Brown that adult *floris* should have a brown head as in other *Spizaetus* species, so the illustration was incorrectly changed (F. Weick *in litt.* 1999).

Another source of misunderstanding could be that ornithologists visiting the Lesser Sundas might have been confused by the presence of four other sympatric species of eagles with fairly similar juvenile plumages, including white underparts (Short-toed Snake Eagle *Circaetus gallicus*, Bonelli's Eagle *Hieraaetus fasciatus*, Rufous-bellied Eagle *H. kienerii* and White-bellied Sea Eagle *Haliaeetus leucogaster*).

Here we give a detailed description of *floris* based on museum specimens and field studies, focusing on the morphological differences between *floris* and *limnaeetus*, and we comment on the distribution, conservation and taxonomic status of *floris*. Elsewhere we describe the phylogenetic relationships within the *Spizaetus cirrhatus* complex based on analyses of mtDNA sequences (Gamauf *et al.* in prep) and provide
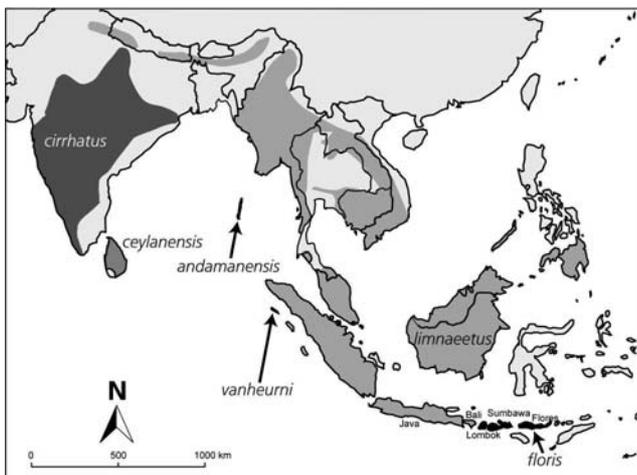


**Figure 1**. Ranges of taxa in the Changeable Hawk Eagle *Spizaetus cirrhatus* complex.

**Plate 1a**. Adult *floris* (right), juvenile *limnaeetus* (left).



**Plate 1d**. Tail of adult *floris* (right) and juvenile *limnaeetus* in moult (left).



**Plate 1b**. Head of *floris*.



**Plate 1e.** Tail of juvenile *floris*.



**Plate 1c**. Wing-patch of adult *floris*.



**Plate 1f**. Tail of adult *floris*.

**Plate 2a.** Ventral side of adult *floris* (right), juvenile *limnaeetus* (middle) and adult *limnaeetus* (left).



**Plate 2d**. Primaries of adult *limnaeetus*.



**Plate 2b**. Dorsal side of the same birds.



**Plate 2e**. Variation in *limnaeetus*, dorsal side. The two birds to left are juveniles.



**Plate 2c**. Primaries of adult *floris*.



**Plate 2f**. Ventral side of the same birds.

a detailed description of the distribution and population status of *floris* (Prawiradilaga *et al.* in prep).

## METHODS

We studied four specimens of *floris* and 155 of *limnaeetus* at the National Museum of Natural History (Naturalis) in Leiden (formerly Rijksmuseum van Natuurlijke Historie, RMNH). One skin of a juvenile *floris* was studied in Bogor Museum (MZB). This individual we confidently identified as being juvenile because of a note on the label recording the lack of ossification of sternal foramina (*Foramina im Brustbein noch nicht verknöchert*: Rensch 1931). In addition we studied photos of two specimens of *floris* from the American Museum of Natural History (AMNH), including the holotype. We suggest that the holotype is a juvenile, because its tail pattern was similar to that of the Bogor specimen. Wing length was measured with the wing flattened and stretched (maximum wing chord). A list of the specimens of *floris* examined is given in Table 1.

A total of 609 hours of field observations were carried out in Lombok, Sumbawa and Flores on 98 days in August–October 2002, December 2002–February 2003 and June–July 2003. Altogether 42 individuals of *floris* were observed, most of which were adult birds of territorial pairs. During studies on Java, a considerable number of *limnaeetus* were observed in the field, as well as in captivity.

## RESULTS

### Morphological differences between *floris* and *limnaeetus*

The head of *floris* is white in both adults and juveniles, sometimes with fine brownish streaks on the crown (Plate 1a,b). The mantle and back are dark brown. The inner vanes of the tertials are pure white. On the inner parts of the outer primaries, the outer vanes are white, forming a large and well-defined white patch on the upperside of the wing (Plate 1c). In some individuals, this patch is less conspicuous and more greyish, but still contrasts with the dark colour of the rest of the upperwing. The tail is brown with six dark bars, the outermost broader than the others (c.44 mm compared to 14 mm). The distance between the two outermost dark bars is slightly larger than between the other bars (23 and 14 mm respectively, Plate 1d). The inner part of the tail and the uppertail-coverts are white, producing a distinctive white patch (Plate 2b). The entire underside, including the thighs and legs, are pure white. One individual (AMNH 534895), described by Hartert (1898) as an adult, has some very faint pale rufous-brown bars on the breast, sides of the breast and thighs (Plate 1f).

In *limnaeetus* two distinct colour morphs are described, one being completely dark (del Hoyo *et al.* 1994). In the Philippines, Gamauf *et al.* (1998) found that 50% of 34 individuals were light morphs, 38% were dark morphs, and 12% were intermediate with a grey-brown breast. Among 155 skins from Indonesia,

**Table 1.** Measurements of *Spizaetus floris*.

| Specimen | Locality | Sex | Age | Wing (mm) | Tail (mm) |
|---|---|---|---|---|---|
| AMNH 534895 | Flores | Male | Adult | 430 | |
| AMNH 534896 | Flores | Male | Juvenile | 450 | 296 |
| RMNH 81112 | Flores | Female | Adult | 456 | 274 |
| RMNH cat. no. 1 | Flores | | Adult | 441 | 255 |
| RMNH cat. no. 2 | Flores | | | 462 | 277 |
| RMNH 66257 | Flores | | Adult | 450 | 272 |
| MZB 11948 | Sumbawa | Male | Juvenile | 438 | 281 |

**Table 2.** Comparison of adult plumage of *Spizaetus floris* and *S. cirrhatus limnaeetus*.

| Characters | *Spizaetus floris* | *S. cirrhatus limnaeetus* |
|---|---|---|
| Morphs | Light | Light, dark and intermediate |
| Head | White, sometimes with fine brownish streaks on crown | Brown |
| Mantle and back | Blackish-brown | Umber-brown with paler edges |
| Primaries | Inner parts of the outer feathers are white, forming a white patch on the upperwing | Brown (no wing patch) |
| Inner webs of tertials | Pure white | Brown |
| Breast and belly | Pure white, sometimes with very faint pale rufous-brown bars | White with bold dark brown streaks |
| Thighs and legs | Pure white, sometimes with very faint pale rufous-brown bars | Buff with fine white bars |
| Tail | Brown with six dark bars. Distance between the outermost dark bars is only a little larger than between the other bars | Brown with 4–5 dark bars. Distance between the outermost dark bars is much larger than between the other bars |

we found that 51% were light morphs, 48% dark and 1% were intermediate. Figs. 3e and 3f show some of the variation in *limnaeetus* from Indonesia.

In light morphs of adult *limnaeetus*, the mantle, back, upperwing-coverts and secondaries are umber-brown with paler edges. The paler-fringed secondary coverts form a narrow band. In contrast to the dark upperparts, the head and neck are pale with numerous fine but distinct streaks, occasionally brownish. The nape feathers are prominent although there is no crest. The chin and throat are white, usually with a black median stripe and lateral stripes. The long tail is concolorous with the upperparts. There is a wide dark subterminal bar, followed by 3–4 narrower dark brown bars towards the base. The distance between the two outer bars is much larger than between the other bars (Plates 1d, 2a,b). The breast and belly are white with bold, dark brown streaks. The long and powerful feathered legs and the undertail-coverts are buff with fine

**Table 3.** Comparison of juvenile plumage of *Spizaetus floris* and *S. cirrhatus limnaeetus*.

| Characters | *Spizaetus floris* | *S. cirrhatus limnaeetus* |
|---|---|---|
| Morphs | Light | Light, dark and intermediate |
| Mantle and back | Blackish-brown | Brown with a saddle-like band formed by lighter-coloured upperwing-coverts |
| Primaries | Distinctive white patch on the upperside of the primaries | No such patch |
| Tail | Terminal bar broader than the other bars | Terminal bar of the same width as the other bars |

**Table 4.** Measurements of mean wing length in mm (range in parentheses) of *Spizaetus floris* and Javan specimens of *S. cirrhatus limnaeetus*.

| *Spizaetus floris* | | | *S. cirrhatus limnaeetus* | |
|---|---|---|---|---|
| Male (n=3) | Female (n=1) | Unknown (n=3) | Male (n=4) | Female (n=4) |
| 439 (430–450) | 456 | 451 (441–462) | 378 (365–387) | 412 (407–426) |

white bars. The primaries have more distinct dark bars than found in *floris* (Plate 2e,d).

In juvenile *floris*, the terminal dark bar of the tail is more diffuse compared with adult birds. This is most easily seen on the ventral side of the tail (Plate 1e,f). The juvenile plumage of *floris* is similar to that of juvenile *limnaeetus*, which also has a pure white head with small dark spots and a white underside. However, the colour of the mantle and back is darker in *floris*, lacking the light saddle-like band on the upperwing-coverts of *limnaeetus*. It also has distinctive white patches on the upperside of the primaries, not found in *limnaeetus*, and the dark terminal tail-bar of *floris* is broader than the other six bars (c.32 mm versus 15 mm), whereas in *limnaeetus* it is of the same width as the other bars (Plates 1d, 2b). The plumage differences between *floris* and *limnaeetus* are summarised in Tables 2–3.

Measurements indicate that *floris* has considerably longer wings than *limnaeetus* from Java (Table 4). However, the number of specimens is small and certainly does not represent the range of variation within each of the two taxa. Brown and Amadon (1968) reported wing lengths of 380–430 mm for male *limnaeetus* and 405–462 mm for females, probably based on measurements of Himalayan specimens. They recorded wing lengths of *floris* to be 485 mm for males and 495 mm for females, but we do not know which birds they measured, as these measurements are larger than on any museum specimens known to us.

**Distribution**

We found that *floris* was distributed in all parts of the islands of Lombok, Sumbawa and Flores, as well as on two satellite islands, Satonda near Sumbawa and Rinca

near Komodo. Six of the seven known specimens of *floris* are from Flores (Table 1). On this island, the species was previously known from about ten sites and it has been assumed to be uncommon (C. Trainor *in litt.* 2000). A specimen at Bogor museum was collected by Rensch (1931) on Sumbawa, and Butchart *et al.* (1996) recorded an individual on Sumbawa in 1993. Verheijen (1961) listed the bird for Paloe, a small island 16 km off the north coast of Flores. Coates and Bishop (1997) also mentioned Komodo in the range for this species, but did not refer to any particular observation. These records do not contain further details that allow verification.

On Lombok, we observed *floris* in Sesaot at the border of Rinjani National Park on 18 September 2002. This is the first record from Lombok. The bird was identified by its white head and underside together with its diagnostic white patch on the upperside of the outer primaries, which distinguish it from immature *limnaeetus*. Later we observed the species at three other locations on the border of Rinjani National Park (Senaru, Pidana and Pusuk: Prawiradilaga *et al*. in prep). These observations are of particular importance since Lombok is just east of Bali, the easternmost extent of the distribution of *limnaeetus*.

**Ecology**

Verhoeye and Holmes (1998) described the habitat of this species as cultivated hills and woodland from sea level to 1,000 m. We observed it in lowland and submontane forest up to 1,600 m, but the majority of individuals were in lowland rainforest. Occasionally individuals were seen over cultivated areas, but always close to intact or semi-intact forest.

In all villages we visited we found that local people were familiar with an eagle with a white head that reportedly hunted chickens and small pigs around villages. However, the possibility of confusion with other raptors cannot be excluded. On one occasion we witnessed a Flores Hawk Eagle hunting in the middle of a village in the early morning, and on several occasion we observed individuals hunting over cultivated landscapes near forest.

In one village in Mbeliling, Flores we were informed about a large tree that was cut down in late August containing a nest with a large nestling hawk eagle. The bird was taken and sold to a bird market. This suggests breeding during the dry season. Verheijen (1964) listed one nest in March, two in April and one in August. However, there is a possibility of misidentification since other sympatric eagles are not mentioned in the paper. Display flight and copulation have also been observed on Flores in June–July 2003 (J.-M. Thiollay *in litt.* 2003).

**DISCUSSION**

**Systematics**

The longest distance of open sea between the islands in the Lombok strait between Bali (where *limnaeetus* occurs) and Lombok (where *floris* occurs) is 24 km (via Nusa Penida). This distance is of the same magnitude as the distances between other islands within the range

of *floris*. During the Pleistocene glacial sea-level depressions this distance was even shorter, perhaps not more than 1 km (Van Oosterzee 1997). A similar situation is found among other *Spizaetus* species within the islands of South-East Asia. For example, Javan Hawk Eagle *S. bartelsi* is separated by the narrow Sunda strait from the closely related Blyth's Hawk Eagle *S. alboniger* and Wallace's Hawk Eagle *S. nanus* on Sumatra.

It is possible that *limnaeetus* and *floris* might have come into secondary contact, after eastward expansion of *limnaeetus*. However, they may not yet have evolved sufficient ecological differences to avoid competition and/or hybridisation. If hybridisation between *floris* and *limnaeetus* commonly occurs, it would be expected that dark morphs (which are common in *limnaeetus* on Java) would have been recorded in the range of *floris*, particularly on Lombok. However, since only four individuals have been identified on Lombok so far, the possibility of a hybrid zone there cannot be rejected. On the other hand, it seems unlikely given the lack of dark morphs (or even dark-headed birds) recorded in a total of 42 field observations and seven specimens of *floris* from Flores and Sumbawa. Thus it is reasonable to conclude that hybridisation is not occurring, at least not frequently.

The distributions of *floris* and *limnaeetus* are commonly regarded as allopatric, being separated only by a narrow strait between Bali and Lombok. However, Changeable Hawk Eagle has a considerable ability to colonise distant islands. For example, Thiollay (1996) found a dark morph *limnaeetus* on Nias 125 km west of Sumatra in 1992 (there had been no previous records), and we observed a light morph *limnaeetus* on Krakatau, 12 km from the Javan mainland, in 1997. The distributional boundary between Bali and Lombok could therefore arguably be considered parapatric.

The argument that parapatric and ecologically incompatible taxa are best treated as subspecies because they are necessarily very closely related (Bock 1986, Amadon and Short 1992) is certainly not universally valid (Garcia-Moreno and Fjeldså 1999). Helbig *et al.* (2002) recommended that diagnosable taxa that are strictly parapatric and do not hybridise should be ranked as separate species, because it appears unlikely that such a situation can be maintained without intrinsic reproductive isolation. Natural selection would favour interbreeding between two populations that are in contact at an ecotone or trivial ecological barrier if hybrids have no fitness disadvantage. If such interbreeding does not occur despite the lack of an effective extrinsic barrier, mixing may be being prevented by intrinsic isolating mechanisms.

No mixing of *floris* (n=5) and *limnaeetus* (n=5) mtDNA haplotypes was observed among birds sampled from Indonesia, suggesting reproductive isolation, albeit based on small sample sizes (Gamauf *et al.* in prep.). The genetic distance between these two taxa was found to be only 1% (Gamauf *et al.* in prep.), indicating that they were separated during the Pleistocene. During that period there were several cool and dry periods (e.g. 80,000 and 190,000 years ago) and biogeographic evidence indicates that Asian rainforests were fragmented (Brandon-Jones 1996). The Flores Hawk Eagle probably evolved in a refuge somewhere in the Lesser Sundas. Theoretical models

suggest that the evolution of reproductive isolation can be fast (Lande 1981, Barton and Charlesworth 1984), and that morphological character states can evolve within well under one million years (Nilsson and Pelger 1994), especially if there is strong selection combined with bottleneck effects and coalescence. This view is supported by empirical data on birds. For instance, mtDNA cyt b sequences differ between Sanford's Sea Eagle *Haliaeetus sanfordi* and White-bellied Sea Eagle *H. leucogaster* by only 0.3% (Wink *et al.* 1996), but they are regarded as separate species. Recent studies indicate that avian speciation can involve little genetic change and occur rapidly in small populations (e.g. Grant *et al.* 2000).

More extensive morphological studies as well as observations on breeding biology, behaviour and vocalisation may lead to the detection of further difference between *floris* and *limnaeetus*. However, using the biological species concept, there exists sufficient evidence to consider *floris* as a full species, principally because of: (1) apparent reproductive isolation based on lack of an effective distribution barrier and apparently no significant hybridisation between *limnaeetus* and *floris*; (2) distinct morphological differences; (3) distinct plumage differences; (4) significant, albeit small, genetic differences between *floris* and *limnaeetus*; and (5) apparently no mixing of mtDNA haplotypes between *floris* and *limnaeetus*.

### Etymology

Hartert (1898) named the species after the island Flores where the holotype was collected. We propose the English name Flores Hawk Eagle and the scientific name *Spizaetus floris* to draw attention to the species's main distribution and restricted range. Sibley and Monroe (1990) used the name Sunda Hawk Eagle, which we find inappropriate, as it is unrecorded from the Greater Sunda islands.

### Neoteny

Extensive field observations and examination of museum specimens confirmed that adult Flores Hawk Eagles have a number of traits (e.g. white head and underparts) that are typical of juveniles in other hawk eagle species e.g. Changeable, Sulawesi *S. lanceolatus*, and Philippine Hawk Eagles *S. philippensis* and the *stresemanni* race of Wallace's Hawk Eagle *S. nanus*. This could be considered a case of neoteny. A similar case is provided by Sanford's Sea Eagle, in which adults have a juvenile-like plumage that is very different from the adult plumage of the closely related White-bellied Sea Eagle (Wink *et al.* 1996).

Neoteny is often associated with increased body size (Gould 1977), and interestingly, Flores Hawk Eagle is much larger than Changeable Hawk Eagle. However, in all birds of prey the skeletal growth is completed before the final development of plumage in the late nestling stage. Thus, the development of the principal determinants of overall size are completed before plumage finishes developing. Neotenous morphology and behaviour is likely to reduce aggression from adults and facilitate sociality (Gould 1977, Lawton and Lawton 1986). This has been proposed as an explanation for neoteny in skuas *Catharacta* spp. (Andersson 1999), but it does not seem relevant to

*Spizaetus* eagles. We find no obvious explanation for why Changeable Hawk Eagle has evolved neoteny, but such a trait might perhaps arise by loss of genetic variation in small populations.

## Conservation

On the basis of distances between three neighbouring territories, we estimate that the territory size for Flores Hawk Eagle is c.40 km$^2$. Given that it is primarily dependent on forest, this implies that the total population size for the species is probably less than 100 pairs (Prawiradilaga *et al.* in prep). The species qualifies at least as Endangered on the IUCN Red List under criterion C2a(i) (total population <2,500 individuals and all subpopulations <250 individuals), and it may even qualify as Critically Endangered under criterion C1 (population <250 individuals and continuing decline >10% per 10 years or three generations) given current rates of habitat destruction in the Lesser Sundas.

Habitat degradation and destruction are the most important threats to Flores Hawk Eagle. Although the species could probably survive in a partly cultivated landscape, protected areas in the species's range are presently too small for its long-term survival. Persecution because of its habit of stealing chickens, and capture for the cagebird trade pose additional threats. We found evidence of a recently robbed nest, and capture for the cagebird trade was also reported by Trainor and Lesmana (2000). We observed a juvenile Short-toed Snake Eagle and an adult White-bellied Sea Eagle that had been similarly captured on Flores.

Flores Hawk Eagle used to be regarded as a totem ('empo') among the Manggarai people in western Flores, who considered it to be an ancestor of humans, and therefore did not hunt it. However, these traditions have now broken down. Fortunately, some work is now underway to inform local people of the importance of this species (C. Trainor *in litt.* 2000).

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# Paper III

# On the taxonomic status of the Changeable Hawk Eagle *Nisaetus cirrhatus* in India

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# Paper IV

# INTRA-INDIVIDUAL AND GEOGRAPHICAL VARIATION IN THE CALLS OF THE CHANGEABLE HAWK-EAGLE *NISAETUS CIRRHATUS* IN INDIA

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# Paper V

# An overlooked threatened eagle species:  Legge's Hawk-eagle *Nisaetus kelaarti*

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# Paper VI

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# Doctoral theses in Biology
## Norwegian University of Science and Technology
## Department of Biology

| Year | Name | Degree | Title |
|---|---|---|---|
| 1974 | Tor-Henning Iversen | Dr. philos Botany | The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism |
| 1978 | Tore Slagsvold | Dr. philos. Zoology | Breeding events of birds in relation to spring temperature and environmental phenology. |
| 1978 | Egil Sakshaug | Dr.philos Botany | "The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton" |
| 1980 | Arnfinn Langeland | Dr. philos. Zoology | Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake. |
| 1980 | Helge Reinertsen | Dr. philos Botany | The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton |
| 1982 | Gunn Mari Olsen | Dr. scient Botany | Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana* |
| 1982 | Dag Dolmen | Dr. philos. Zoology | Life aspects of two sympartic species of newts (*Triturus*, *Amphibia*) in Norway, with special emphasis on their ecological niche segregation. |
| 1984 | Eivin Røskaft | Dr. philos. Zoology | Sociobiological studies of the rook *Corvus frugilegus.* |
| 1984 | Anne Margrethe Cameron | Dr. scient Botany | Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats |
| 1984 | Asbjørn Magne Nilsen | Dr. scient Botany | Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test |
| 1985 | Jarle Mork | Dr. philos. Zoology | Biochemical genetic studies in fish. |
| 1985 | John Solem | Dr. philos. Zoology | Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains. |
| 1985 | Randi E. Reinertsen | Dr. philos. Zoology | Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds. |
| 1986 | Bernt-Erik Sæther | Dr. philos. Zoology | Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach. |
| 1986 | Torleif Holthe | Dr. philos. Zoology | Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna. |
| 1987 | Helene Lampe | Dr. scient. Zoology | The function of bird song in mate attraction and territorial defence, and the importance of song repertoires. |
| 1987 | Olav Hogstad | Dr. philos. Zoology | Winter survival strategies of the Willow tit *Parus montanus*. |
| 1987 | Jarle Inge Holten | Dr. philos Bothany | Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway |
| 1987 | Rita Kumar | Dr. scient Botany | Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium* |

| 1987 Bjørn Åge Tømmerås | Dr. scient. Zoology | Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction. |
|---|---|---|
| 1988 Hans Christian Pedersen | Dr. philos. Zoology | Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care. |
| 1988 Tor G. Heggberget | Dr. philos. Zoology | Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure. |
| 1988 Marianne V. Nielsen | Dr. scient. Zoology | The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*). |
| 1988 Ole Kristian Berg | Dr. scient. Zoology | The formation of landlocked Atlantic salmon (*Salmo salar* L.). |
| 1989 John W. Jensen | Dr. philos. Zoology | Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth. |
| 1989 Helga J. Vivås | Dr. scient. Zoology | Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*. |
| 1989 Reidar Andersen | Dr. scient. Zoology | Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation. |
| 1989 Kurt Ingar Draget | Dr. scient Botany | Alginate gel media for plant tissue culture, |
| 1990 Bengt Finstad | Dr. scient. Zoology | Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season. |
| 1990 Hege Johannesen | Dr. scient. Zoology | Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung. |
| 1990 Åse Krøkje | Dr. scient Botany | The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test |
| 1990 Arne Johan Jensen | Dr. philos. Zoology | Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams. |
| 1990 Tor Jørgen Almaas | Dr. scient. Zoology | Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues. |
| 1990 Magne Husby | Dr. scient. Zoology | Breeding strategies in birds: Experiments with the Magpie *Pica pica*. |
| 1991 Tor Kvam | Dr. scient. Zoology | Population biology of the European lynx (*Lynx lynx*) in Norway. |
| 1991 Jan Henning L'Abêe Lund | Dr. philos. Zoology | Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular. |
| 1991 Asbjørn Moen | Dr. philos Botany | The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands |
| 1991 Else Marie Løbersli | Dr. scient Botany | Soil acidification and metal uptake in plants |
| 1991 Trond Nordtug | Dr. scient. Zoology | Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods. |
| 1991 Thyra Solem | Dr. scient Botany | Age, origin and development of blanket mires in Central Norway |
| 1991 Odd Terje Sandlund | Dr. philos. Zoology | The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism. |
| 1991 Nina Jonsson | Dr. philos. | Aspects of migration and spawning in salmonids. |

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|---|---|---|
| 1991 Atle Bones | Dr. scient Botany | Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase) |
| 1992 Torgrim Breiehagen | Dr. scient. Zoology | Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher. |
| 1992 Anne Kjersti Bakken | Dr. scient Botany | The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.) |
| 1992 Tycho Anker-Nilssen | Dr. scient. Zoology | Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica* |
| 1992 Bjørn Munro Jenssen | Dr. philos. Zoology | Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks. |
| 1992 Arne Vollan Aarset | Dr. philos. Zoology | The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans. |
| 1993 Geir Slupphaug | Dr. scient Botany | Regulation and expression of uracil-DNA glycosylase and $O^6$-methylguanine-DNA methyltransferase in mammalian cells |
| 1993 Tor Fredrik Næsje | Dr. scient. Zoology | Habitat shifts in coregonids. |
| 1993 Yngvar Asbjørn Olsen | Dr. scient. Zoology | Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects. |
| 1993 Bård Pedersen | Dr. scient Botany | Theoretical studies of life history evolution in modular and clonal organisms |
| 1993 Ole Petter Thangstad | Dr. scient Botany | Molecular studies of myrosinase in Brassicaceae |
| 1993 Thrine L. M. Heggberget | Dr. scient. Zoology | Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*. |
| 1993 Kjetil Bevanger | Dr. scient. Zoology | Avian interactions with utility structures, a biological approach. |
| 1993 Kåre Haugan | Dr. scient Bothany | Mutations in the replication control gene trfA of the broad host-range plasmid RK2 |
| 1994 Peder Fiske | Dr. scient. Zoology | Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek. |
| 1994 Kjell Inge Reitan | Dr. scient Botany | Nutritional effects of algae in first-feeding of marine fish larvae |
| 1994 Nils Røv | Dr. scient. Zoology | Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*. |
| 1994 Annette-Susanne Hoepfner | Dr. scient Botany | Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.) |
| 1994 Inga Elise Bruteig | Dr. scient Bothany | Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers |
| 1994 Geir Johnsen | Dr. scient Botany | Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses |
| 1994 Morten Bakken | Dr. scient. Zoology | Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*. |
| 1994 Arne Moksnes | Dr. philos. Zoology | Host adaptations towards brood parasitism by the Cockoo. |
| 1994 Solveig Bakken | Dr. scient Bothany | Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply |
| 1995 Olav Vadstein | Dr. philos Botany | The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions. |

| 1995 Hanne Christensen | Dr. scient. Zoology | Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*. |
|---|---|---|
| 1995 Svein Håkon Lorentsen | Dr. scient. Zoology | Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition. |
| 1995 Chris Jørgen Jensen | Dr. scient. Zoology | The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity |
| 1995 Martha Kold Bakkevig | Dr. scient. Zoology | The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport. |
| 1995 Vidar Moen | Dr. scient. Zoology | Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations. |
| 1995 Hans Haavardsholm Blom | Dr. philos Bothany | A revision of the *Schistidium apocarpum* complex in Norway and Sweden. |
| 1996 Jorun Skjærmo | Dr. scient Botany | Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae. |
| 1996 Ola Ugedal | Dr. scient. Zoology | Radiocesium turnover in freshwater fishes |
| 1996 Ingibjørg Einarsdottir | Dr. scient. Zoology | Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines. |
| 1996 Christina M. S. Pereira | Dr. scient. Zoology | Glucose metabolism in salmonids: Dietary effects and hormonal regulation. |
| 1996 Jan Fredrik Børseth | Dr. scient. Zoology | The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics. |
| 1996 Gunnar Henriksen | Dr. scient. Zoology | Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region. |
| 1997 Gunvor Øie | Dr. scient Bothany | Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae. |
| 1997 Håkon Holien | Dr. scient Botany | Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters. |
| 1997 Ole Reitan | Dr. scient. Zoology | Responses of birds to habitat disturbance due to damming. |
| 1997 Jon Arne Grøttum | Dr. scient. Zoology | Physiological effects of reduced water quality on fish in aquaculture. |
| 1997 Per Gustav Thingstad | Dr. scient. Zoology | Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher. |
| 1997 Torgeir Nygård | Dr. scient. Zoology | Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors. |
| 1997 Signe Nybø | Dr. scient. Zoology | Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway. |
| 1997 Atle Wibe | Dr. scient. Zoology | Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry. |
| 1997 Rolv Lundheim | Dr. scient. Zoology | Adaptive and incidental biological ice nucleators. |
| 1997 Arild Magne Landa | Dr. scient. Zoology | Wolverines in Scandinavia: ecology, sheep depredation and conservation. |

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| 1997 | Kåre Magne Nielsen | Dr. scient Botany | An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*. |
| 1997 | Jarle Tufto | Dr. scient. Zoology | Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models |
| 1997 | Trygve Hesthagen | Dr. philos. Zoology | Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters |
| 1997 | Trygve Sigholt | Dr. philos. Zoology | Control of  Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet |
| 1997 | Jan Østnes | Dr. scient. Zoology | Cold sensation in adult and neonate birds |
| 1998 | Seethaledsumy Visvalingam | Dr. scient Botany | Influence of environmental factors on myrosinases and myrosinase-binding proteins. |
| 1998 | Thor Harald Ringsby | Dr. scient. Zoology | Variation in space and time: The biology of a House sparrow metapopulation |
| 1998 | Erling Johan Solberg | Dr. scient. Zoology | Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment |
| 1998 | Sigurd Mjøen Saastad | Dr. scient Botany | Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity. |
| 1998 | Bjarte Mortensen | Dr. scient Botany | Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial  equilibration system in vitro. |
| 1998 | Gunnar Austrheim | Dr. scient Botany | Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach. |
| 1998 | Bente Gunnveig Berg | Dr. scient. Zoology | Encoding of pheromone information in two related moth species |
| 1999 | Kristian Overskaug | Dr. scient. Zoology | Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach |
| 1999 | Hans Kristen Stenøien | Dr. scient Bothany | Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts) |
| 1999 | Trond Arnesen | Dr. scient Botany | Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway. |
| 1999 | Ingvar Stenberg | Dr. scient. Zoology | Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos* |
| 1999 | Stein Olle Johansen | Dr. scient Botany | A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis. |
| 1999 | Trina Falck Galloway | Dr. scient. Zoology | Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.) |
| 1999 | Torbjørn Forseth | Dr. scient. Zoology | Bioenergetics in ecological and life history studies of fishes. |
| 1999 | Marianne Giæver | Dr. scient. Zoology | Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic |
| 1999 | Hans Martin Hanslin | Dr. scient Botany | The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*. |

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|---|---|---|
| 1999 Ingrid Bysveen Mjølnerød | Dr. scient. Zoology | Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques |
| 1999 Else Berit Skagen | Dr. scient Botany | The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces |
| 1999 Stein-Are Sæther | Dr. philos. Zoology | Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe |
| 1999 Katrine Wangen Rustad | Dr. scient. Zoology | Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease |
| 1999 Per Terje Smiseth | Dr. scient. Zoology | Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*) |
| 1999 Gunnbjørn Bremset | Dr. scient. Zoology | Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions |
| 1999 Frode Ødegaard | Dr. scient. Zoology | Host spesificity as parameter in estimates of arhrophod species richness |
| 1999 Sonja Andersen | Dr. scient Bothany | Expressional and functional analyses of human, secretory phospholipase A2 |
| 2000 Ingrid Salvesen, I | Dr. scient Botany | Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture |
| 2000 Ingar Jostein Øien | Dr. scient. Zoology | The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race |
| 2000 Pavlos Makridis | Dr. scient Botany | Methods for the microbial econtrol of live food used for the rearing of marine fish larvae |
| 2000 Sigbjørn Stokke | Dr. scient. Zoology | Sexual segregation in the African elephant (*Loxodonta africana*) |
| 2000 Odd A. Gulseth | Dr. philos. Zoology | Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard |
| 2000 Pål A. Olsvik | Dr. scient. Zoology | Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway |
| 2000 Sigurd Einum | Dr. scient. Zoology | Maternal effects in fish: Implications for the evolution of breeding time and egg size |
| 2001 Jan Ove Evjemo | Dr. scient. Zoology | Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species |
| 2001 Olga Hilmo | Dr. scient Botany | Lichen response to environmental changes in the managed boreal forset systems |
| 2001 Ingebrigt Uglem | Dr. scient. Zoology | Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.) |
| 2001 Bård Gunnar Stokke | Dr. scient. Zoology | Coevolutionary adaptations in avian brood parasites and their hosts |
| 2002 Ronny Aanes | Dr. scient | Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) |
| 2002 Mariann Sandsund | Dr. scient. Zoology | Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses |
| 2002 Dag-Inge Øien | Dr. scient Botany | Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway |
| 2002 Frank Rosell | Dr. scient. Zoology | The function of scent marking in beaver (*Castor fiber*) |
| 2002 Janne Østvang | Dr. scient Botany | The Role and Regulation of Phospholipase $A_2$ in Monocytes During Atherosclerosis Development |

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|---|---|---|---|
| 2002 | Terje Thun | Dr. philos Biology | Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material |
| 2002 | Birgit Hafjeld Borgen | Dr. scient Biology | Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth |
| 2002 | Bård Øyvind Solberg | Dr. scient Biology | Effects of climatic change on the growth of dominating tree species along major environmental gradients |
| 2002 | Per Winge | Dr. scient Biology | The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and |
| 2002 | Henrik Jensen | Dr. scient Biology | Causes and consequenses of individual variation in fitness-related traits in house sparrows |
| 2003 | Jens Rohloff | Dr. philos Biology | Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control |
| 2003 | Åsa Maria O. Espmark Wibe | Dr. scient Biology | Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L. |
| 2003 | Dagmar Hagen | Dr. scient Biology | Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach |
| 2003 | Bjørn Dahle | Dr. scient Biology | Reproductive strategies in Scandinavian brown bears |
| 2003 | Cyril Lebogang Taolo | Dr. scient Biology | Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana |
| 2003 | Marit Stranden | Dr.scient Biology | Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*) |
| 2003 | Kristian Hassel | Dr.scient Biology | Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum* |
| 2003 | David Alexander Rae | Dr.scient Biology | Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments |
| 2003 | Åsa A Borg | Dr.scient Biology | Sex roles and reproductive behaviour in gobies and guppies: a female perspective |
| 2003 | Eldar Åsgard Bendiksen | Dr.scient Biology | Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt |
| 2004 | Torkild Bakken | Dr.scient Biology | A revision of Nereidinae (Polychaeta, Nereididae) |
| 2004 | Ingar Pareliussen | Dr.scient Biology | Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar |
| 2004 | Tore Brembu | Dr.scient Biology | Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana* |
| 2004 | Liv S. Nilsen | Dr.scient Biology | Coastal heath vegetation on central Norway; recent past, present state and future possibilities |
| 2004 | Hanne T. Skiri | Dr.scient Biology | Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*). |
| 2004 | Lene Østby | Dr.scient Biology | Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment |
| 2004 | Emmanuel J. Gerreta | Dr. philos Biology | The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania |
| 2004 | Linda Dalen | Dr.scient Biology | Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming |

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|---|---|---|---|
| 2004 | Lisbeth Mehli | Dr.scient Biology | Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea* |
| 2004 | Børge Moe | Dr.scient Biology | Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage |
| 2005 | Matilde Skogen Chauton | Dr.scient Biology | Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples |
| 2005 | Sten Karlsson | Dr.scient Biology | Dynamics of Genetic Polymorphisms |
| 2005 | Terje Bongard | Dr.scient Biology | Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period |
| 2005 | Tonette Røstelien | PhD Biology | Functional characterisation of olfactory receptor neurone types in heliothine moths |
| 2005 | Erlend Kristiansen | Dr.scient Biology | Studies on antifreeze proteins |
| 2005 | Eugen G. Sørmo | Dr.scient Biology | Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations. |
| 2005 | Christian Westad | Dr.scient Biology | Motor control of the upper trapezius |
| 2005 | Lasse Mork Olsen | PhD Biology | Interactions between marine osmo- and phagotrophs in different physicochemical environments |
| 2005 | Åslaug Viken | PhD Biology | Implications of mate choice for the management of small populations |
| 2005 | Ariaya Hymete Sahle Dingle | PhD Biology | Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia |
| 2005 | Ander Gravbrøt Finstad | PhD Biology | Salmonid fishes in a changing climate: The winter challenge |
| 2005 | Shimane Washington Makabu | PhD Biology | Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana |
| 2005 | Kjartan Østbye | Dr.scient Biology | The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation |
| 2006 | Kari Mette Murvoll | PhD Biology | Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds? |
| 2006 | Ivar Herfindal | Dr.scient Biology | Life history consequences of environmental variation along ecological gradients in northern ungulates |
| 2006 | Nils Egil Tokle | Phd Biology | Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus* |