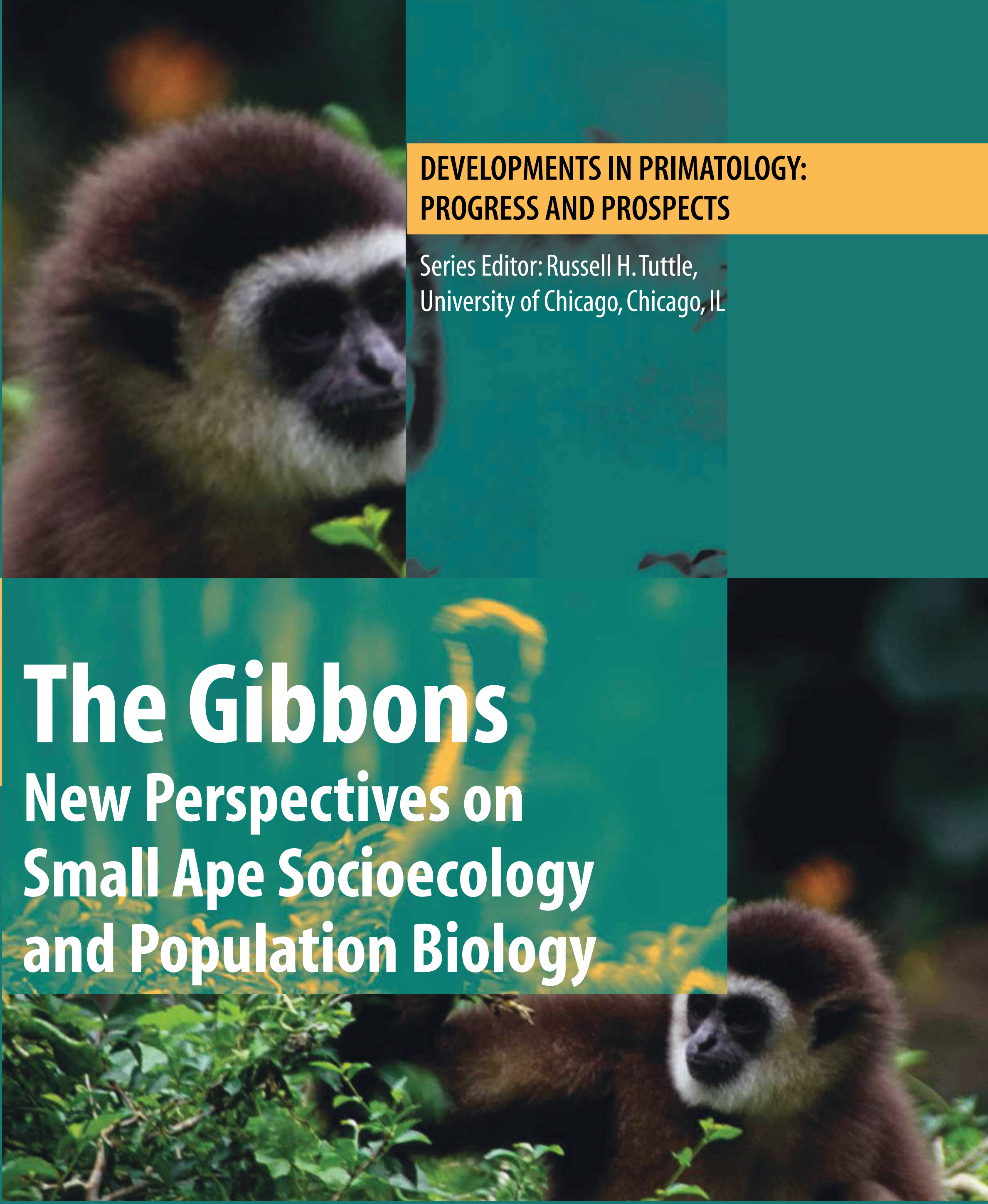

DEVELOPMENTS IN PRIMATOLOGY:
PROGRESS AND PROSPECTS

Series Editor: Russell H. Tuttle,
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The Gibbons

New Perspectives on Small Ape Socioecology and Population Biology

Susan Lappan
Danielle J. Whittaker
Editors

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THE GIBBONS

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THE GIBBONS

New Perspectives on Small Ape Socioecology and Population Biology

Edited by

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Foreword

It is a great honor to be asked to introduce this exciting new volume, having been heavily involved in the first comprehensive synthesis in the early 1980s. Gibbons are the most enthralling of primates. On the one hand, they are the most appealing animals, with their upright posture and body shape, facial markings, dramatic arm-swinging locomotion and suspensory postures, and devastating duets; on the other hand, the small apes are the most diverse, hence biologically valuable and informative, of our closest relatives.

It is hard for me to believe that it is 40 years to the month since I first set foot on the Malay Peninsula to start my doctoral study of the siamang. I am very proud to have followed in the footsteps of the great pioneer of primate field study, Clarence Ray Carpenter (CR or Ray, who I was fortunate to meet twice, in Pennsylvania and in Zurich), first in Central America (in 1967) and then in Southeast Asia. It is 75 years since he studied howler monkeys on Barro Colorado Island in the Panama Canal Zone. It is 70 years since he studied the white-handed gibbon in Thailand.

Ray was a remarkable man for initiating this kind of study and for doing it so well, so perceptively. Perhaps because the howler population had increased markedly over 30 years, I was able to make an original contribution to the understanding of the role of dawn calls in the spacing of groups, showing they avoided their neighbors in any month and lived in overlapping home ranges, that they were not territorial in the classic sense. By contrast, almost every time I thought I had discovered something new about gibbon behavior, I found that if Ray had not seen it, he suggested that it might happen!

The only other student of gibbon behavior was John Ellefson, who studied the white-handed gibbon in coastal forest of east Johore, West Malaysia, in the early 1960s. He produced some excellent results, but few of his data are presented in a manner that allowed full comparison with other studies. I was fortunate to encounter him in the redwoods of California before heading for Malaysia, where I met Naoki Koyama, from the Primate Research Institute, Kyoto, who was tackling the impossible task of studying siamang in the rugged terrain of Fraser's Hill. Thus, I inherited a framework of gibbon socioecology based on monogamy, territoriality, frugivory, suspensory behavior, and duetting (loud melodic group calls/songs), on which we have built over the years.

Susan Lappan and Danielle J. Whittaker are to be congratulated on their very real achievement of bringing together such a breadth and wealth of new information on gibbon biology, spread over two IPS Congresses. There is an impressive blend of biogeography and phylogeny, diets and community ecology, ecology and social organization, mating systems and reproductive biology, and conservation biology. The lack of material on anatomy was a deliberate decision, because it has been dealt with previously, especially in the 1984 synthesis. Readers are reminded of this first conference and book on gibbon biology. Schloss Reisensburg, the castle on the Danube near Ulm, was an amazing and stimulating venue for our very productive conference in 1980, away from the IPS Congress in Florence (which thankfully rejected our symposium proposal, even as a satellite event!). The more formal sessions in the castle lecture room were augmented by genuine round-table discussions, in the turrets close to fridges full of German beer and wine! These sessions, going on late into the night, were very productive in reaching consensus.

The editors' introductory chapter on small ape diversity and the importance of population-level studies sets out clearly the scope and contents of the book. Quantifying the role of gibbons in seed dispersal is a major advance. Gibbons may live in small territories, but they are more effective in dispersal than those traveling greater distances, often depositing seeds onto unsuitable ground. I am reassured that this intensive 'farming' of the forest is most effective, especially in the light of numerous tree-falls and such opportunities for natural forest regeneration.

Perhaps the most exciting new development is the collection of DNA by noninvasive methods to determine genetic relationships within and between gibbon families, particularly to identify paternity. This is an essential aid to understanding the more complex social systems now being described. We will have to await the publication of such results. Systematics and taxonomy is another area with a current flurry of activity, which should soon see the light of day elsewhere.

I am reminded of the conflict generated by the novel use of molecular evidence 30 years ago in defining hominoid relationships and evolution. While paleontologists and anatomists claimed that the ape–human separation was about 14–12 Mya, the molecular biologists suggested 5 Mya, but they had not allowed for increased generation time. The compromise between the two disciplines was resolved at 7–9 Mya, corresponding with the major gap in the fossil record. The DNA story, of closest affinity between African apes and humans, has reawoken the major reservation in those who have shown that ancestral Asian apes share derived morphological features, incompatible with the molecular evidence. I think we may be missing something with the current obsession with the genotype, rather than the phenotype. I live in hope that it will be shown eventually that we are descended from the lovely Asian apes, rather than those unattractive and promiscuous African apes with swollen bottoms!

I also want to caution against ‘swinging’ too far away from the monogamy and territoriality as originally assigned to gibbons. I am very happy to acknowledge the flexibility that it is entirely appropriate to assign to apes and their social systems, and the importance of long-term studies. The fact of the matter is that, in the humid tropics at least (the Sundaic region of the Oriental realm), monogamous families in territories are the norm, at least for the lifetime of the individuals concerned. I have seen this over 20 years in both Peninsular Malaysia and Indonesian Borneo, and heard of it elsewhere. The exceptions now being encountered more frequently and described more forcefully seem to me to be related clearly to isolated, disturbed, or fragmented habitats, and the various problems of overcrowding or imbalanced sex ratios associated with that. Extra-pair copulations, polygyny, and polyandry are fascinating reflections of the abilities and social flexibility of gibbons, and they need to be documented fully and interpreted carefully, without rejecting the key, basic, socioecological adaptations, which separated gibbons from orangutans, langurs, and macaques.

Still more species and subspecies of gibbons are being described, some very endangered, especially in southern China (including Hainan), northern Vietnam, western Java, Bangladesh/Assam, and, probably, Myanmar. All are threatened, some critically. Continuing to publicize and promote action to resolve such crises is urgently needed. The classification of the gibbons of Borneo, in relation to those of Sumatra and Malaya, needs to be resolved. What are the true identities of the species and subspecies? Are agile and Mueller’s gibbons one species or several?

Thus, I commend you to this feast of new information and discussion on so many aspects of gibbon biology, so well assimilated by Susan and Danielle. I hope that it will inspire continued research and the quest for understanding these, the most important of all, primates!

Cambridge, UK David J. Chivers

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Seoul — Susan Lappan
Bloomington, IN — Danielle J. Whittaker

Contents

Part I Introduction

1 **The Diversity of Small Apes and the Importance of Population-Level Studies** 3
Danielle J. Whittaker and Susan Lappan

Part II Biogeography

2 **Evolutionary Relationships Among the Gibbons: A Biogeographic Perspective** 13
Helen J. Chatterjee

3 **Genetic Differentiation of Agile Gibbons Between Sumatra and Kalimantan in Indonesia** 37
Hirohisa Hirai, Azusa Hayano, Hiroyuki Tanaka, Alan R. Mootnick, Hery Wijayanto, and Dyah Perwitasari-Farajallah

4 **Vocal Diversity of Kloss's Gibbons (*Hylobates Klossii*) in the Mentawai Islands, Indonesia** 51
Sally A. Keith, Melissa S. Waller, and Thomas Geissmann

5 **Phylogeography of Kloss's Gibbon (*Hylobates Klossii*) Populations and Implications for Conservation Planning in the Mentawai Islands** 73
Danielle J. Whittaker

6 **Individual and Geographical Variability in the Songs of Wild Silvery Gibbons (*Hylobates Moloch*) on Java, Indonesia** 91
Robert Dallmann and Thomas Geissmann

7 **The Fossil Record of Gibbons** 111
Nina G. Jablonski and George Chaplin

Part III Diet and Community Ecology

8 **Hylobatid Diets Revisited: The Importance of Body Mass, Fruit Availability, and Interspecific Competition** 133
Alice A. Elder

9 **Competition and Niche Overlap Between Gibbons (*Hylobates albibarbis*) and Other Frugivorous Vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia** 161
Andrew J. Marshall, Charles H. Cannon, and Mark Leighton

10 **The Seed Dispersal Niche of Gibbons in Bornean Dipterocarp Forests** 189
Kim R. McConkey

Part IV The Relationship Between Ecology and Social Organization

11 **Ecology and the Social System of Gibbons** 211
Warren Y. Brockelman

12 **The Ecology and Evolution of Hylobatid Communities: Causal and Contextual Factors Underlying Inter- and Intraspecific Variation** 241
Nicholas Malone and Agustin Fuentes

13 **Seasonal Home Range Use and Defendability in White-Handed Gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand** 265
Thad Q. Bartlett

Part V Mating Systems and Reproduction

14 **Monogamy in Mammals: Expanding the Perspective on Hylobatid Mating Systems** 279
Luca Morino

15 **Monitoring Female Reproductive Status in White-Handed Gibbons (*Hylobates lar*) Using Fecal Hormone Analysis and Patterns of Genital Skin Swellings** 313
Claudia Barelli and Michael Heistermann

16 **Patterns of Infant Care in Wild Siamangs (*Symphalangus syndactylus*) in Southern Sumatra** 327
Susan Lappan

17 The Social Organization and Mating System of Khao Yai White-Handed Gibbons: 1992–2006 347
Ulrich H. Reichard

Part VI Conservation Biology

18 Status and Conservation of Yellow-Cheeked Crested Gibbons (*Nomascus gabriellae*) in the Seima Biodiversity Conservation Area, Mondulkiri Province, Cambodia 387
Benjamin Miles Rawson, Tom Clements, and Nut Meng Hor

19 The Distribution and Abundance of Hoolock Gibbons in India 409
Jayanta Das, Jihosuo Biswas, Parimal C. Bhattacherjee, and S.M. Mohnot

20 Census of Eastern Hoolock Gibbons (*Hoolock leuconedys*) in Mahamyaing Wildlife Sanctuary, Sagaing Division, Myanmar 435
Warren Y. Brockelman, Hla Naing, Chit Saw, Aung Moe, Zaw Linn, Thu Kyaw Moe, and Zaw Win

21 The Population Distribution and Abundance of Siamangs (*Symphalangus syndactylus*) and Agile Gibbons (*Hylobates agilis*) in West Central Sumatra, Indonesia 453
Achmad Yanuar

22 Canopy Bridges: An Effective Conservation Tactic for Supporting Gibbon Populations in Forest Fragments 467
Jayanta Das, Jihosuo Biswas, Parimal C. Bhattacherjee, and S.S. Rao

23 The Role of Reintroduction in Gibbon Conservation: Opportunities and Challenges 477
Susan M. Cheyne

24 Saving the Small Apes: Conservation Assessment of Gibbon Species at the 2006 Asian Primate Red List Workshop 497
Danielle J. Whittaker

Index 501

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Part I
Introduction

Chapter 1
The Diversity of Small Apes and the Importance of Population-Level Studies

Danielle J. Whittaker and Susan Lappan

Most primatologists, biologists, and laypeople agree that gibbons, with their incredible acrobatic displays and haunting duets, are absolutely marvelous animals. For all of their beauty and grace, however, they have received relatively little attention from the scientific community and the public alike. This volume is an attempt to begin addressing this problem by summarizing the progress of gibbon studies to date, identifying the key areas for future research, and cautioning against the belief that we already know everything worth knowing about gibbons.

Over two decades have passed since the publication of the seminal volume *The Lesser Apes: Evolutionary and Behavioural Biology* (Preuschoft et al. 1984). That book was based on a conference, the first of its kind focusing on gibbons, held in 1980 in Ulm, Germany. *The Lesser Apes* comprises a thorough summary of progress in gibbon studies up to that time, focusing on conservation, functional morphology, ecology, social behavior, and evolutionary biology. The contributors identified several areas that required additional study, including calls and songs; the basic behavioral biology of little understood species (*Hoolock* spp.*, Nomascus* spp.); molecular phylogenetic studies, particularly of *Hoolock* and *Hylobates klossii*; and the fossil record. In the decades since the publication of *The Lesser Apes*, progress toward many of these goals has been made.

Twenty years later, gibbonologists gathered again, at two International Primatological Society symposia: “Gibbon Diversity and Conservation” in Beijing in 2002 and “Wild Gibbons as Members of Populations” in Torino in 2004. This book is the product of those two symposia and has been assembled in recognition of the fact that a great deal of progress has been made in the field since 1984, allowing new perspectives on gibbon socioecology.

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Gibbon Diversity

A number of changes in gibbon taxonomy have been proposed in recent years. The four subgenera have been raised to genus level (*Hylobates*, *Nomascus*, *Symphalangus*, and *Hoolock* [formerly *Bunopithecus*]). Additional species have been identified within *Nomascus*. Also, within *Hylobates*, some evidence (e.g., Hirai et al. this volume) suggests that the Bornean taxon generally classified as *H. agilis albibarbis* may in fact be sufficiently distinctive from *H. agilis* and *H. muelleri* to be classified as a full species. Though not all researchers agree on this classification, and further study is clearly warranted, we have used the name *H. albibarbis* throughout this volume for the sake of consistency; its use by individual authors is at the editors' request and does not necessarily imply acceptance of this taxonomy. Helen Chatterjee (Chapter 2) reviews the progress to date in understanding gibbon evolution and biogeography, while Nina Jablonski (Chapter 7) discusses the role of environmental change in the evolution of gibbons. Robert Dallmann and Thomas Geissmann (Chapter 6), Hirohisa Hirai et al. (Chapter 3), Sally Keith et al. (Chapter 4), and Danielle Whittaker (Chapter 5) examine genetic and vocal evidence for and against divergence within species.

In the past two decades, our knowledge of the behavior, ecology, and evolution of gibbons has been greatly increased by additional studies on previously un- or under-studied taxa, with an emphasis on field studies. In particular, researchers have given more attention to the crested gibbons (*Nomascus* spp.: e.g., Jiang et al. 1999; Fan et al. 2006; Konrad and Geissmann 2006), hoolock gibbons (*Hoolock* spp.: e.g., Choudhury 1991; Islam and Feeroz 1992; Ahsan 1995), the Kloss's gibbon (*Hylobates klossii*: Whittaker 2005a, b), and the Javan or silvery gibbon (*H. moloch*: Andayani et al. 2001; Geissmann and Nijman 2006). Work has also continued on previously studied species (e.g., *H. lar*, *H. agilis*, *Symphalangus syndactylus*), with particular attention to understanding variation in group compositions and social and mating behavior (e.g., Brockelman et al. 1998; Reichard 2003; Lappan 2007), as well as the ecological role of gibbons in tropical forests (McConkey et al. 2002; McConkey et al. 2003). A number of long-term studies have been conducted at field sites across the gibbon distribution range, including but not limited to Khao Yai National Park in Thailand, 1979–present; Ketambe, Sumatra, Indonesia, 1980–1999; Way Canguk Research Station, Sumatra, Indonesia, 1997–present; Barito Ulu, Kalimantan, Indonesia, 1988–present; Legok Heulang Research Station, Java, Indonesia, 1994–present; and Borajan Reserve, Assam, India 1995–present. This emphasis on long-term study has revealed a great deal of previously unanticipated complexity in the social lives of gibbons. Such perspectives were impossible in shorter projects, which only gave us a "snapshot" of the lifestyles of these long-lived primates.

Gibbon Socioecology: Flexibility

The first generation of intrepid researchers to study gibbons in the field described small, nuclear families, with both adults behaving as “paragons of fidelity” (Fuentes 1999, 2000): the very poster children for monogamy in the primate world. Ongoing field research, however, has on one hand, confirmed that unimale unifemale grouping is the most common pattern in all gibbon species studied to date, yet, on the other hand, it has also made clear that much more lies under the surface of gibbon social and mating systems. Far from the previously imagined enduring and faithful male–female pairs plus offspring in the style of 1950s-era American television shows, gibbon groups can include multiple adult males, multiple adult females, retained adult offspring, swapped mates, and more. Gibbon group compositions over 17 years at Khao Yai are described in Chapter 17 by Ulrich Reichard, clearly demonstrating that gibbon social and mating behavior is far from static. This flexibility in mating behavior is far more typical of other “monogamous” species, and gibbons are placed into the broader context of mammalian monogamy by Luca Morino (Chapter 14). Warren Brockelman (Chapter 11) argues for the importance of considering gibbon ecological adaptations in interpreting gibbon social monogamy. Ecological hypotheses have been suggested previously to be insufficient to explain monogamy in gibbons (van Schaik and Dunbar 1990); Thad Bartlett (Chapter 13) revisits the issue and finds evidence to the contrary. Nicholas Malone and Agustin Fuentes (Chapter 12) warn against the assumptions generated by the use of terms like “monogamous” and call for a more rigorous description of gibbon social and mating behavior. It is perhaps worth noting that primatologists appear to struggle to define monogamy and to understand any exceptions from the one-male, one-female pairing and mating rule in generally monogamous systems, whereas other biologists, who have long known that many monogamous bird species engage in extrapair mating and may change social mates every breeding season, have been much more accepting of a more flexible notion of monogamy. It may be that our closer genetic relationship to gibbons makes us susceptible to burdening the term with cultural assumptions, and we therefore feel forced to confront, uncomfortably, our own “deviations” from our ideal.

We still do not understand the social or genetic relationships among neighboring gibbon groups, but recent research has highlighted the fact that the gibbon group cannot be fully understood without reference to its neighborhood and ecological community. Based on the relatively short dispersal distances that have been observed thus far and relatively low levels of aggression among neighbors reported from several sites, it is likely that in many cases neighbors are relatives and form communities interconnected by rich networks of genetic and social ties.

In recent years, genetic methods have become powerful tools for elucidating relationships among individuals in many species and understanding the effects of behavioral and ecological variables on individual reproductive success. Unfortunately, these methods have yet to be implemented fully in gibbon studies due to the difficulty of obtaining samples yielding reliable nuclear DNA from wild individuals. Capturing wild gibbons to draw blood samples is undesirable due to the extreme difficulty and the high potential of injuring or even killing the individual, but non-invasively collected samples (e.g., feces, urine, hair), though they often yield usable mtDNA, have proven problematic for many researchers attempting to amplify nuclear markers for paternity and relatedness analyses (Chambers et al. 2004). Nevertheless, through long-term behavioral observation and mtDNA analyses, much progress has been made in understanding such relationships. Male parental care in siamangs is examined by Susan Lappan (Chapter 16), with a special focus on polyandrous groups; mtDNA data shed some light on the relationship of extra males to the breeding female in these groups. Claudia Barelli and Michael Heistermann (Chapter 15) describe a method of non-invasively monitoring female reproductive status, which may improve researchers' ability to interpret social interactions. We hope that in the future, additional hormonal studies on wild individuals will elucidate the relationships among social variables, physiological variables, and individual behavioral decisions, and that population genetic analyses using nuclear markers will allow us to better understand genetic relationships within and among gibbon groups, neighborhoods, and populations, and the consequences of individual behavioral strategies.

In addition to the unexpected variation that gibbons display in their social and sexual behavior, Alice Elder (Chapter 8) and Nicholas Malone and Agustin Fuentes (Chapter 12) emphasize the extent to which gibbon flexibility extends into the ecological realm. While previous research suggested a dichotomy between large-bodied, folivorous siamangs and other hylobatids (previously lumped as a group into the category of small-bodied frugivores), Malone and Fuentes describe substantial dietary variation within and between gibbon genera, and Elder's analysis of gibbon diets reveals that the diets of siamangs are not significantly more folivorous than those of other gibbons, that the family as a whole is predominantly frugivorous, and that in fact the most folivorous gibbons studied to date belong to the genus *Nomascus*. While the status of most or all gibbon populations as frugivorous is fairly well established, it is clear that the original view of gibbon diets as relatively invariant across populations should be re-examined.

It is important to take a long-term, population-level perspective. Several of the chapters in this book illustrate clearly that a sample of gibbon behavior or population status from a single point in time should not be mistaken for a representation of an equilibrium condition – group compositions, behavior, and population sizes can change in a relatively short period of time, which should inject a cautionary note into conclusions or management plans based on short-term studies.

The Limits of Flexibility

While gibbons display unexpected flexibility in their social behavior, it is becoming clear that they have some fairly rigid limits ecologically. Gibbons are selective feeders, primarily consuming ripe fruits with a specific set of features. Andrew Marshall et al. (Chapter 9) and Kim McConkey (Chapter 10) describe two of the first studies to date on the roles of gibbons in their ecological communities, highlighting different aspects of gibbon community ecology. Marshall et al. evaluate the fruit component of gibbon diets and those of their primary diurnal vertebrate competitors, and conclude that gibbon diets display pronounced overlap with those of not only other primate species but also of many other frugivorous vertebrates, while McConkey considers plant–animal interactions and the role of gibbons as seed dispersers. Both studies make it clear that gibbons are important components of functioning ecological communities in the forests of South and Southeast Asia.

Gibbons have fairly specific habitat requirements, including continuous canopy cover, and respond poorly to habitat conversion and fragmentation. Accordingly, human disturbance is a major threat to gibbon populations. Gibbons live in three of the four most populous nations on Earth (China, India, and Indonesia), as well as four of the ten nations with the highest population growth rates (India, China, Indonesia, and Bangladesh: US Census Bureau 2002). Rapid population growth and economic development in these and other habitat countries have led to an unprecedented rate of habitat destruction across the gibbon distribution range.

Gibbons reproduce relatively slowly, and it is suggested in studies of Kloss's gibbon diversity by Danielle Whittaker (Chapter 5) and Sally Keith et al. (Chapter 4) that evolutionary change in gibbons may lag behind environmental change: a vicariance event that resulted in evolutionary divergence in sympatric primate species has not yet caused genetic or vocal divergence in the gibbons. Such a long latency to change has negative implications for gibbons' ability to adapt genetically to anthropogenic change. Ben Rawson and colleagues (Chapter 18), Jayanta Das and colleagues (Chapter 19), Warren Brockelman (Chapter 20), and Achmad Yanuar (Chapter 21) review the status and distribution of several threatened gibbon species.

The picture is not all bleak, however. Large populations of gibbons remain in some areas (e.g., O'Brien et al. 2004; Cheyne et al. 2007; Rawson et al. this volume; Brockelman et al. this volume), and Rawson et al. demonstrate that effective conservation management can result in sustainable, and even growing, gibbon populations in protected areas. Even in areas that have already been fragmented or depopulated by hunting, appropriate management strategies may result in the preservation of viable gibbon populations. Das et al. (Chapter 22) describe an innovative method to provide connectivity to the discontinuous canopy in badly fragmented habitat, and Susan Cheyne (Chapter 23) discusses the potential of gibbon reintroduction programs. Such solutions are costly in time, money, or both, however, and can meet with only limited success compared with the protection of natural habitats and populations. We believe that the dire conservation status of many gibbon populations and taxa should not be used as an excuse to justify the further neglect of any population, but rather emphasizes the importance of immediate action to protect those that remain.

The True Neglected Apes?

It is well established that public support is necessary for wildlife conservation to succeed. Unfortunately, despite being extremely charismatic, the small apes have received disproportionately little attention from the press, particularly in relation to their cousins, the great apes. Although the orangutan has been referred to as "The Neglected Ape" (Galdikas et al. 1995), orangutans receive far more attention than gibbons. There are up to 16 recognized species of gibbons, and half of them are critically endangered while all are experiencing some level of threat. Arguably, the most endangered extant primate is the Hainan black-crested gibbon (*Nomascus hainanus*) of which only about 17 remain, followed closely by the eastern black-crested gibbon (*Nomascus nasutus*), with ~50 individuals. While all of the living apes are threatened with extinction, no great ape species approaches such a dire situation.

A search on the Discovery Channel website (http://dsc.discovery.com) in April 2008 revealed only three references to gibbons, while chimpanzees, gorillas, and orangutans had 43, 22, and 7 references, respectively, and baboons (11) and macaques (19) also had more coverage. Similarly, a search for articles on the National Geographic Society Publications Index (NGSPI, http://publicationsindex.nationalgeographic.com) online resulted in 89 articles referring to gorillas, 54 references to chimpanzees, 39 references to orangutans, and only 5 references to gibbons. While gibbons are arguably more difficult to study and film than their more conspicuous and less arboreal cousins, this imbalance is unlikely to result simply from an absence of data or the difficulty involved in creating high-quality film footage. After all, another charismatic and endangered (and difficult to observe) animal, the tiger, was referenced 149 times.

One of the problems may be simply a matter of language. Gibbons have historically been referred to as "the lesser apes", following the traditional English terminology used to distinguish smaller animals from their larger or "greater" relatives. However, this may have had the unfortunate consequence of suggesting to the public that the gibbons are somehow less important, interesting, or valuable than other (arguably overgrown) apes. A solution to this problem was suggested at the 2000 conference "The Apes: Challenges for the 21st Century" in Chicago, when David Chivers (2001) proposed referring to gibbons as the "small apes" rather than the "lesser apes." We have adopted this wording in this volume, and encourage others to do the same.

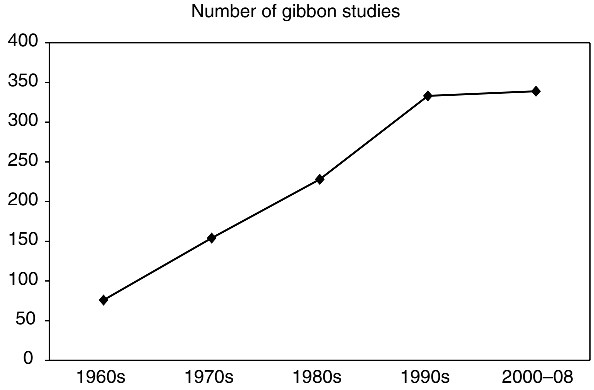

Fig. 1.1 Number of gibbon studies indexed on the search engine Primate Lit (http://primatelit.library.wisc.edu) per decade (accessed on April 10, 2008.)

Despite the lack of attention from the press, the number of scientific studies on gibbons has steadily increased over the years. Figure 1.1 shows the results from Primate Lit searches (http://primatelit.library.wisc.edu/) for each decade, using keywords "gibbon OR Hoolock OR Bunopithecus OR Hylobates OR Nomascus OR Symphalangus." Furthermore, at least 51 honor's, master's, and doctoral theses focusing on gibbons were completed between 1999 and 2006 (http://www.gibbons.de). Our knowledge about gibbons increases steadily, even as their public image stagnates, and their population numbers decline. Researchers themselves may be neglecting opportunities to promote their work (and their study animals) to the general public. Thus, it is incumbent upon gibbon researchers to promote efforts to raise public awareness about the gibbons and their plight whenever and wherever possible. Otherwise, we are risking a future without gibbons, in a world that would be, in the words of H.J. Coolidge in his foreword to *The Lesser Apes*, much impoverished.

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Part II
Biogeography

Chapter 2
Evolutionary Relationships Among the Gibbons: A Biogeographic Perspective

Helen J. Chatterjee

Introduction

The debate regarding gibbon taxonomy and phylogeny has flourished for well over one hundred years. The first gibbon, *Homo lar*, was described by Linnaeus (1771); the siamang as *Simia syndactyla* by Raffles (1821); the first concolor gibbon as *Simia concolor* by Harlan (1826); and the hoolock as *Simia hoolock* by Harlan (1834) (Groves 1972, 2001). Throughout the 19th century, gibbon nomenclature diversified until, by the end of the century, most of the taxonomic names and divisions recognized today had been established. Phylogenetic relationships amongst these taxa have continued to cause discussion and debate, with the advent of molecular methods only serving to accelerate the discourse. In contrast, there has been startlingly little research into the biogeographic history of gibbons, largely due to their incredibly sparse fossil record. This chapter will outline current views regarding gibbon taxonomy, phylogeny, and biogeography, providing an overview of the main areas of consensus and continuing debate.

Taxonomy

The history of gibbon systematics has seen numerous nomenclatural changes. The first gibbon to be published was given the name *Homo lar* in Linneaus' *Systema Naturae* (1771). Over the next two centuries, as new taxa were described, several other names appear in the literature representing different gibbons. The name *Hylobates*, meaning "dweller in the trees," first appeared in the early 19th century (Groves 1972; Nowak 1991). Schultz (1933), Groves (1972, 2001), and Brandon-Jones et al. (2004) provide useful reviews of the classification systems published by other authors.

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No examination of gibbon systematics is complete without reference to some of the landmark texts that have been published. The work of Adolph Schultz in the first part of the last century contributed greatly to the understanding of interspecific variability among gibbons. This was the first large-scale study of internal and external morphological differences among gibbons. Schultz (1933) measured linear variables on the skull, plus postcranial variables including sternal, pelvic, and limb lengths and breadths, counted numbers of vertebrae, and made several observations concerning external morphology, such as hair density and interdigital webbing. On the basis of this study, Schultz postulated that nine taxa should be split into two genera: *Hylobates* and *Symphalangus*. Subsequent classification systems published during the first part of the last century, although differing slightly in their structure and composition, had the same basic form as Schultz's. It was not until the 1970s that major revisions to this taxonomy appeared.

Groves' (1972) monograph remains one of the most comprehensive studies of gibbon systematics, incorporating cranial and postcranial measurements, observations regarding pelage, hair pattern, body proportions, external features, and reproductive anatomy, serology (blood), karyology (chromosomes), distribution patterns, evidence for hybridization and sympatry, behavioral characteristics, plus data from other published sources. On the basis of these data and observations, Groves recognized six species, all confined to the genus *Hylobates*. This was further subdivided into three main subgenera; *Hylobates, Nomascus,* and *Symphalangus*. The subgeneric divisions were based on the diploid number of chromosomes that showed clear-cut differences between different groups of gibbons.

Over the next 20 years or so, several modifications were made to the taxonomy by Groves (1972) as a result of increased understanding of various fields (Creel and Preuschoft 1976; Chivers 1977; Chivers and Gittins 1978; Haimoff et al. 1982; Groves 1984, 1989, 1993). The most significant change to Groves' original classification was the identification of several new species in the subgenus *Hylobates*. These were formed as a result of raising several *lar* subspecies to species level. Marshall and Marshall (1976), Chivers (1977), and Marshall and Sugardjito (1986) agreed on the species status of *agilis*, *moloch,* and *muelleri* on the basis of differences in color patterns of fur on the head and around the face and differences in territorial songs. Marshall and Marshall (1976) and Marshall and Sugardjito (1986) amassed data about pelage and vocalization differences from museum pelts and wild gibbons, respectively. This work remains one of the most comprehensive studies of fur and vocal differences among gibbons. Marshall and Sugardjito (1986) presented a new taxonomy that included Prouty et al.'s (1983a, b) identification of a new subgenus, *Bunopithecus*, for the hoolock gibbon on the basis that the diploid number (*Bunopithecus* = 38) differed from the other three subgenera.

The most significant changes to Marshall and Sugardjito's (1986) classification related to the number of species in the subgenus *Nomascus*. These changes are the result of raising *H.c. leucogenys* and *H.c. gabriellae* to species level, to create *H. leucogenys* (Dao 1983; Ma and Wang 1986; Geissmann 1993) and *H. gabriellae* (Geissmann 1995). These authors provided evidence based on differences in the anatomy of the penis bone, vocalizations, and areas of sympatry in support of species status for these taxa. The resultant taxonomy, incorporating these new species and maintaining Marshall and Sugardjito's (1986) basic structure, was published by Geissmann (1995) and forms the basis for today's widely accepted taxonomic divisions.

In recent years, gibbon taxonomists have begun to reach a general consensus regarding the main gibbon divisions and nomenclature. Groves' *Primate Taxonomy* (2001) and Brandon-Jones et al.'s *Asian Primate Classification* (2004) provide excellent sources of reference and form the basis for the overview provided here. The most recent major advance with respect to gibbon systematics has been the general acceptance that the four gibbon subgenera (*Hylobates*, *Bunopithecus*, *Nomascus,* and *Symphalangus*) should be raised to genus level (Roos and Geissmann 2001; Geissmann 2002; Brandon-Jones et al. 2004). These subgeneric names have been generally accepted as generic names, except for *Bunopithecus*. Mootnick and Groves (2005) propose that the generic nomen *Bunopithecus* is not applicable to hoolock gibbons on the basis of its historical incorporation into gibbon nomenclature. First described by Matthew and Granger (1923), the name *Bunopithecus sericus* was used to document a mandibular fragment from Sichuan, China, apparently similar in size to the hoolock gibbon. Later, *Bunopithecus* was proposed by Prouty et al. (1983b) as the subgeneric division for hoolock gibbons based on its karyological distinction from the other gibbons. The subgeneric name has pervaded the literature for some time; however, Groves (in press) found that the type of *Bunopithecus sericus* is outside the range of modern *Hylobatidae* in its dental characters. With the identity of the type in question it seems sensible to adopt Mootnick and Groves' (2005) recommendation of employing *Hoolock* as the generic description for hoolock gibbons and their scheme will be adopted here.

The family *Hylobatidae* comprises at least 12 distinct species distributed across mainland and archipelagic Southeast Asia. These are subdivided into four morphologically and karyologically distinct genera (see Table 2.1): *Hylobates*, often referred to as the *lar* group (diploid number = 44)*; Hoolock* (diploid number = 38)*; Nomascus*, often referred to as the *concolor* or crested group (diploid number = 52); and *Symphalangus* (diploid number = 50) (Brandon-Jones et al. 2004).

The constituent members of the genus *Hylobates* are: *H. lar, H. muelleri, H. moloch, H. agilis, H. albibarbis, H. pileatus,* and *H. klossii.* There is some debate as to the validity of *H. albibarbis* as a species; Groves (1972) considered *albibarbis* a geographic variant of *H. muelleri*, with no greater difference in pelage than other Bornean gibbons. Marshall and Marshall (1976) found the vocalization range of *albibarbis* to fall within that of *H. agilis.* This has caused somewhat of a puzzle regarding whether pelage or vocalizations have priority in species recognition of gibbons. Hirai et al., in this volume, provide cytogenetic and molecular genetic support for the differentiation of agile gibbon taxa

Table 2.1 Main divisions and geographic distributions of the Family *Hylobatidae* (after Groves 2001; Geissmann 2002; Brandon-Jones et al. 2004)

Genus	Diploid number of chromosomes	Other division names	Species	Common name
Hylobates	44	*lar* group	*H. lar*	White-handed gibbon
			H. agilis	Agile gibbon
			H. albibarbis[a]	White-bearded gibbon
			H. muelleri	Müller's gibbon
			H. moloch	Silvery gibbon
			H. pileatus	Pileated gibbon
			H. klossii	Kloss's gibbon
Hoolock	38		*H. hoolock*	Hoolock
Nomascus	52	*Concolor* group	*N. concolor*	Western black crested gibbon
		Crested gibbons	*N.* sp. cf. *nasutus*[b]	Eastern black crested gibbon
			N. gabriellae	Yellow-cheeked crested gibbon
			N. leucogenys	Northern white-cheeked crested gibbon
			N. siki[c]	Southern white-cheeked crested gibbon
			N. hainanus[d]	Hainan gibbon
Symphalangus	50		*S. syndactylus*	Siamang

[a] As recognized by Groves (2001).

[b] As recognized by Geissmann (2002) and Brandon-Jones et al. (2004).

[c] As recognized by Groves (2001).

[d] As recognized by Groves (2001).

between Sumatra and Kalimantan. Regarding subspecies, Groves (2001) and Brandon-Jones et al. (2004) recognize five *lar* subspecies: *H. lar lar*, *H. lar carpenteri*, *H. lar entelloides*, *H. lar vestitus,* and *H. lar yunannensis*. There are three muelleri subspecies: *H. muelleri muelleri*, *H. muelleri abbotti,* and *H. muelleri funereus*. One or two moloch subspecies are discussed: *H. moloch moloch* and *H. moloch pongoalsoni*; the latter is suggested by Andayani et al. (2001) on the basis of genetic variation of purported distinct geographic lineages, but is yet to be confirmed by other genetic data. Analysis of vocalizations (Dallmann and Geissmann this volume) also reveals two distinct groups, though the proposed dividing line is different from that suggested by Andayani et al. (2001). The subspecies of *H. agilis* are, as discussed above, still a matter of debate. Brandon-Jones et al. (2004) recognize three subspecies: *H. agilis agilis*, *H. agilis albibarbis,* and *H. agilis unko*, while Groves (2001) proposes that *albibarbis* be considered at species level since it differs diagnostically from both *H. agilis* and *H. muelleri*. Genetic data support this distinction of *H. albibarbis* (Hirai et al. this volume). No subspecies variants are proposed for *H. pileatus* or *H. klossii* (Keith et al. this volume; Whittaker this volume).

There is little discussion about the sole species members of *Hoolock* (*H. hoolock hoolock* and *H. hoolock leuconedys*) and *Symphalangus* (*S. syndactylus*), respectively, except that Brandon-Jones et al. (2004) recognize the Malayan siamang as a distinct subspecies: *S. syndactylus continentis*.

Most remaining debates about gibbon taxonomy usually focus around the crested gibbons, genus *Nomascus*. Widely accepted members of the genus include: *N. concolor, N. gabriellae, and N. leucogenys*. Brandon-Jones et al. (2004) offers an attempt to provide a consensus view of the species status of the following populations: *nasutus*, *siki,* and *hainanus*. *N.* sp. cf. *nasutus nasutus* is suggested to be sufficiently distinct from the *concolor* species as to be considered a separate taxon. Likewise, the Hainan Island population may also be distinct from *N. concolor* with respect to vocalizations and is proposed as a subspecies of *nasutus*: *N.* sp. cf. *nasutus hainanus*. The species status of *siki* is also controversial with molecular evidence, leading Zhang (1997) to consider it a distinct species while the consensus view (Brandon-Jones et al. 2004) proposes a more conservative approach, with *siki* included as a subspecies of *N. leucogenys*. Agreed subspecies include four taxa for the concolor group: *N. concolor concolor*, *N. concolor furvogaster*, *N. concolor jingdongensis,* and *N. concolor lu*. Two white-cheeked groups are proposed: *N. leucogenys leucogenys* and *N. leucogenys siki*. Finally, the red-cheeked gibbon (also referred to as yellow-cheeked), *N. gabriellae*, has no proposed subspecies (Brandon-Jones et al. 2004).

Geographic Distributions

The geographic distributions of gibbons are shown in Table 2.2 and Figs. 2.1, 2.2, and 2.3. Excellent detailed distributions of species and subspecies are provided in Geissmann (1995), Groves (2001), and Brandon-Jones et al. (2004) and will not be belabored here, except to provide an overview.

The species of the genus *Hylobates* are broadly distributed in Southeast Asia; *H. lar* over east Burma, Thailand, mainland Malay Peninsula, and southwest Yunnan in China; *agilis* in west and east Sumatra, southwest Borneo (*H. albibarbis*, Groves 2001), and island Malay Peninsula; *H. muelleri* over the rest of Borneo from the northwest to southeast; *H. moloch* on western and central Java; *H. pileatus* in southeast Thailand, west Cambodia, southwest Laos; and *H. klossii* on the Mentawai Islands (Fig. 2.2).

The hoolock gibbon is distributed to the west in India, Burma, and Bangladesh (Fig. 2.1). Gibbons from the genus *Nomascus* have a more easterly distribution over South China, Vietnam, Laos, and Cambodia. The species are distributed in a north-south continuum: *N. concolor* to the north in the Yunnan

Table 2.2 Geographic distributions of the Family *Hylobatidae* (after Groves 2001; Brandon-Jones et al. 2004)

Genus	Species	Distribution (for detail see: Groves 2001; Brandon-Jones et al. 2004)
Hylobates	*H. lar*	Northern Sumatra; Malaysia; Burma; Thailand; China
	H. agilis	Sumatra; Malay Peninsula
	H. albibarbis[a]	Southwestern Borneo
	H. muelleri	Borneo (except southwestern area)
	H. moloch	Java
	H. pileatus	Cambodia; Southwestern Laos; Southeastern Thailand
	H. klossii	Mentawai Islands (Indonesia)
Bunopithecus	*B. hoolock*	India; Northern Burma; China
Nomascus	*N. concolor*	China; Vietnam; Laos
	N. sp. cf. *nasutus*[b]	Northeastern Vietnam
	N. gabriellae	South Laos; South Vietnam; East Cambodia
	N. leucogenys	China; North Laos; Northwestern Vietnam
	N. siki[c]	South Laos; Central Vietnam
	N. hainanus[d]	Hainan Island (China)
Symphalangus	*S. syndactylus*	Sumatra; Malay Peninsula

[a] As recognized by Groves (2001).
[b] As recognized by Geissmann (2002) and Brandon-Jones et al. (2004).
[c] As recognized by Groves (2001).
[d] As recognized by Groves (2001).

province of China, and northerly parts of Vietnam and Laos; *N. leucogenys* in south Yunnan, north and central Vietnam and Laos; *N. gabriellae* in south Laos, south Vietnam, and western Cambodia (Fig. 2.3). The siamang is found on Sumatra and mainland Malay Peninsula (Fig. 2.1).

In most areas, species are separated by rivers or straits (Figs. 2.1, 2.2, and 2.3). These stretches of water could be barriers to gene exchange since it is well documented that gibbons will not cross large bodies of water (Marshall and Sugardjito 1986). There are several areas of contact, however, and these usually occur at the headwaters of the rivers. In such contact areas, there is evidence of hybrid zones forming and these will be discussed shortly. The other main areas of overlap occur where species are sympatric with each other.

The siamang is sympatric with other gibbons across the whole of its range: on southern Sumatra with *H. agilis*, and on northern Sumatra and mainland Malay Peninsula with *H. lar*. These instances of sympatry are presumably made possible by the significant size difference between the siamang and the other gibbons, combined with the fact that the siamang's diet is suggested to be more folivorous and less frugivorous (Chivers 1974; MacKinnon 1977). However, a recent comparison of siamang and other gibbon diets finds no difference in levels of frugivory (Elder this volume).

Geissmann (1995) reports three areas of sympatry among species in the genus *Hylobates* (numbers 1–3 on Fig. 2.2): between *H. lar* and *H. pileatus* at

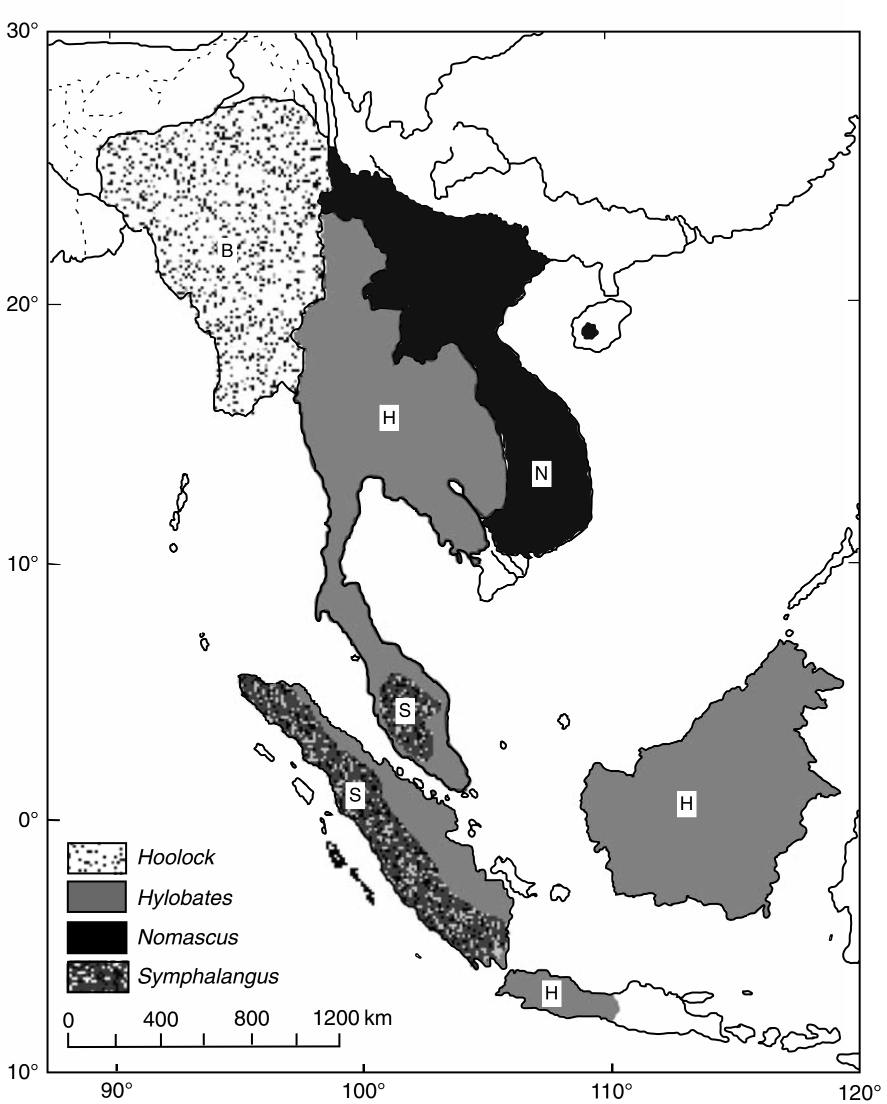


Fig. 2.1 Geographic distributions of gibbons (after Geissmann 1995)

the headwaters of the Takhon River in Khao Yai National Park, about 120 km northeast of Bangkok in Thailand [1]; between *H. lar* and *H. agilis* at the headwaters of the Muda River in the north-western part of mainland Malay Peninsula [2]; and between *H. agilis* and *H. muelleri* at the headwaters of the Barito River in Kalimantan, Borneo [3].

At each of these areas of sympatry, there have been reports of hybrid zones forming. In Khao Yai National Park, the area of overlap between *H. lar* and

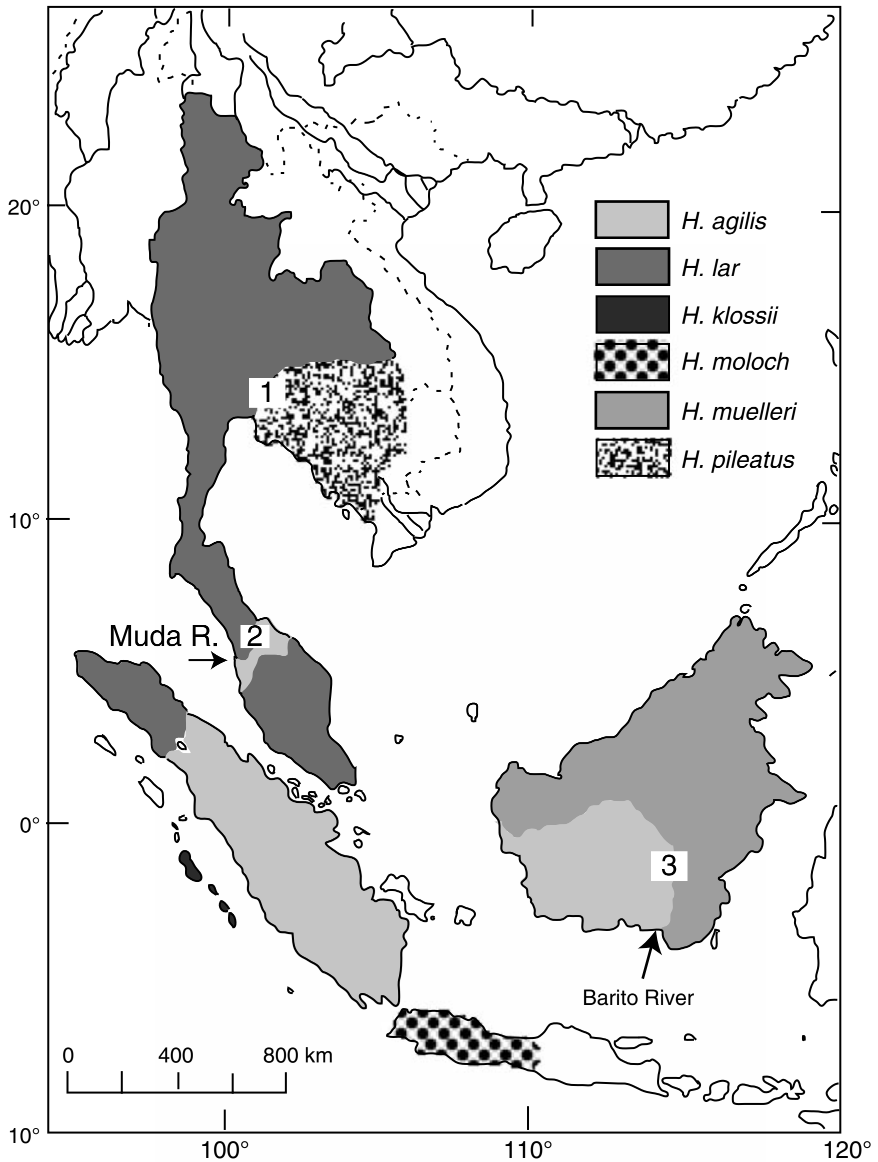


Fig. 2.2 Distribution of species in the genus *Hylobates*, after Geissmann (1995). The numbers represent areas of sympatry: (1) between *H. lar* and *H. pileatus* at the headwaters of the Takhon River in Khao Yai National Park, Thailand; (2) between *H. lar* and *H. agilis* at the headwaters of the Muda River in the north-western part of mainland Malay Peninsula; (3) between *H. agilis* and *H. muelleri* at the headwaters of the Barito River in Kalimantan, Borneo

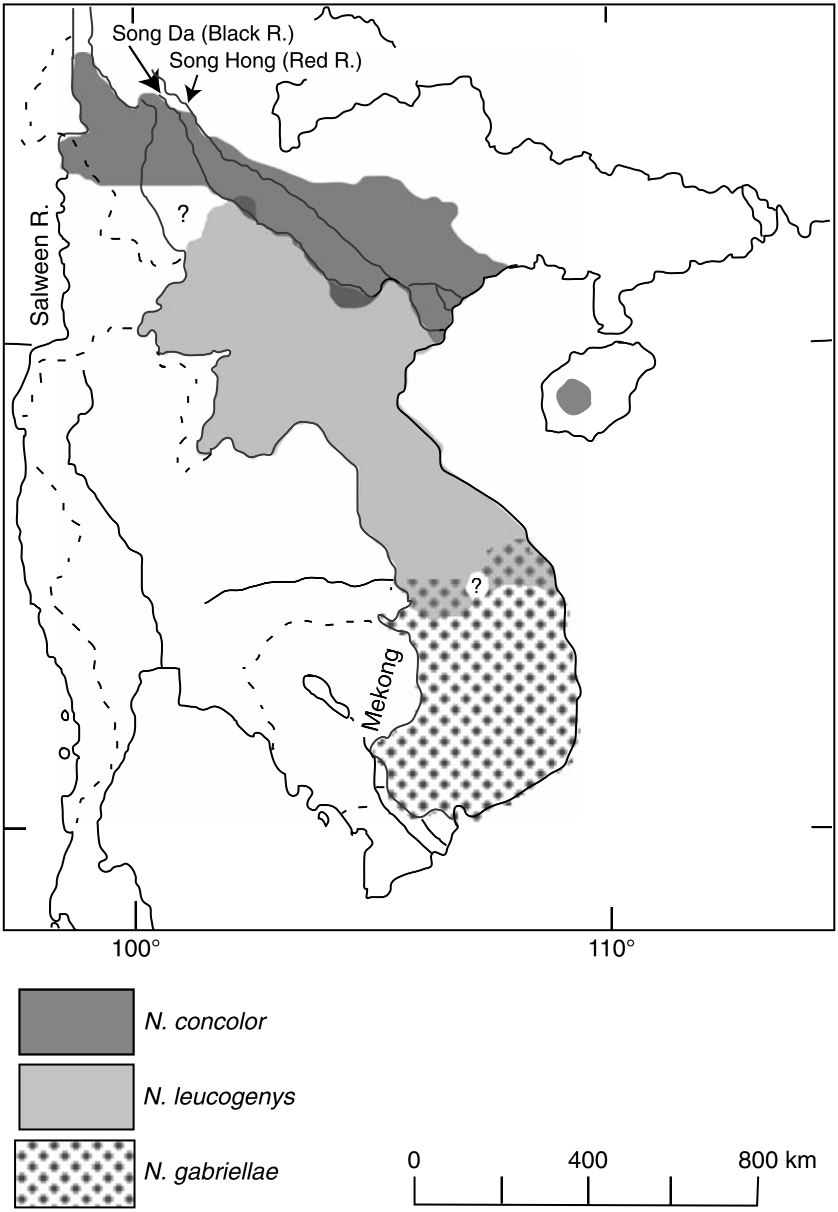


Fig. 2.3 Distribution of species in the genus *Nomascus*, after Geissmann (1995)

H. pileatus is about 100 km^2 with hybrids constituting approximately 5% of the breeding population (Brockelman and Gittins 1984; Marshall and Sugardjito 1986; Marshall and Brockelman 1986). Brockelman and Gittins (1984) and Gittins (1978) report a small number of mixed groups and hybrids of *H. lar* and *H. agilis* on the shores of an artificial lake at the headwaters of the Muda River. Chivers and Burton (1991) report an area of hybridization between *H. agilis* and *H. muelleri* on one part of the Barito River in Borneo (SE Kalimantan), and Mather (1992) reported a zone of at least 3,500 km^2 on Borneo inhabited by an apparently stable hybrid population of *H. agilis* and *H. muelleri.*

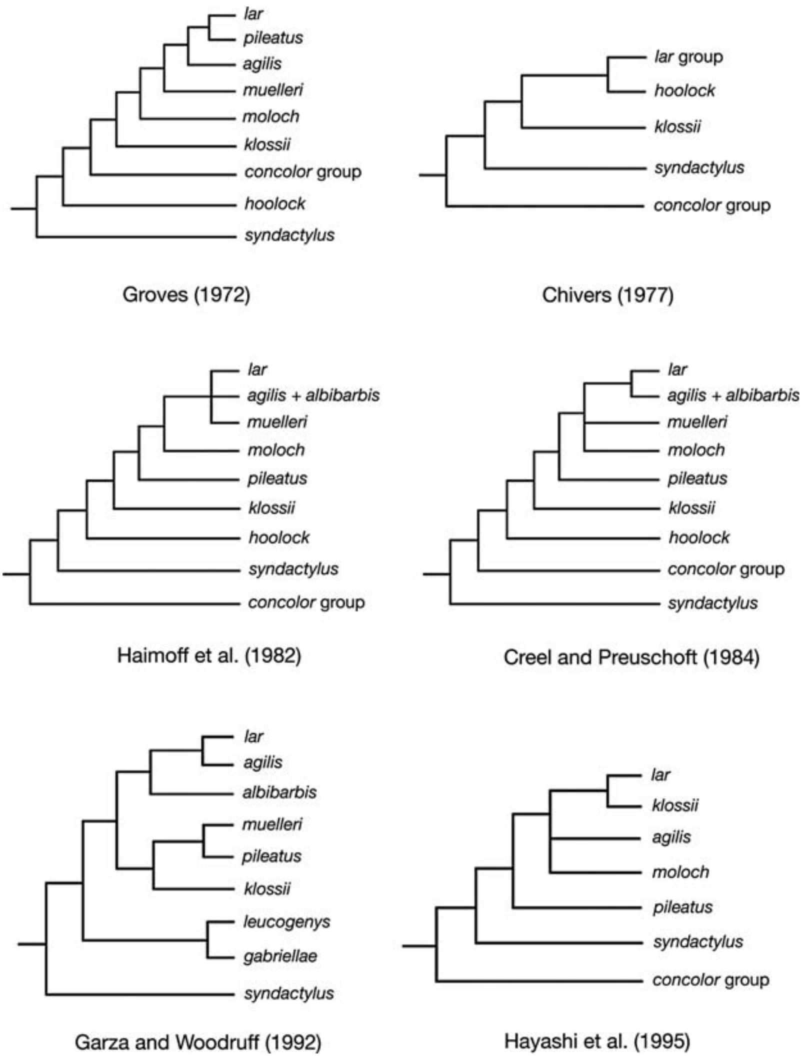
There is also some evidence for the existence of contact zones among species from the genus *Nomascus* (Geissmann 1995). Dao (1983) and Ma and Wang (1986) reported a small area of sympatry between *N. concolor* and *N. leucogenys* in southern Yunnan in China and in northern Vietnam. Furthermore, Geissmann (1995) has described a possible wild-born hybrid between *N. concolor* and *N. leucogenys*. Finally, there is some evidence of hybridization in the areas of contact between *N. gabriellae* and *N. leucogenys siki* in southern Vietnam and Laos (Groves 1972).

The implications for the species status of the breeding pairs in these hybrid zones are potentially profound. The debate regarding gibbon taxonomy largely comes down to which species concept is favored and which phenotypic characters take precedence with respect to species recognition. Most of the above studies regarding gibbon taxonomy are based on the recognition concept, since they rely on auto-recognition factors such as pelage and vocalizations to distinguish species. Regarding the species status of gibbons from hybrid zones, current information relating to the reproductive success of individuals in such hybrid zones is scarce. Until such data become available, the species status of those taxa involved cannot be fully assessed. Continuing molecular studies offer alternative views regarding phylogenetic relationships amongst these taxa and this will be the topic of the proceeding section.

Phylogenetic Inter-relationships

Phylogenetic relationships among gibbon species, and even the four genera, are controversial. Numerous studies based on molecular, morphological, and behavioral data have provided conflicting results (Groves 1972; Chivers 1977; Haimoff et al. 1982; Garza and Woodruff 1992; Hayashi et al. 1995; Purvis 1995; Hall et al. 1996; Zhang 1997; Hall et al. 1998; Zehr 1999; Chatterjee 2001; Roos and Geissmann 2001; Takacs et al. 2005; Chatterjee 2006; Whittaker et al. 2007; Creel and Preucshoft 1984; Fig. 2.4).

There is overwhelming support, from morphological and molecular studies, for the monophyletic grouping of taxa in the genera *Hylobates* and *Nomascus*. There is much less agreement regarding intergeneric relationships, particularly with respect to the earliest gibbon divergence. Many of the morphological approaches to gibbon phylogeny proposed the siamang as the ancestral group, mainly based on its large size. More recent molecular work has been unable to resolve this question, with *Nomascus* (Hayashi et al. 1995; Zhang 1997; Chatterjee 2001; Roos and Geissmann 2001; Chatterjee 2006), *Symphalangus* (Garza and Woodruff 1992; Hall et al. 1998), and *Hoolock* (Zehr 1999; Takacs et al. 2005) being proposed as basal by one or more studies. Others studies have been unable to resolve the basal node showing a polytomy (Purvis 1995; Geissmann 2002).



Groves (1972)

Chivers (1977)

Haimoff et al. (1982)

Creel and Preuschoft (1984)

Garza and Woodruff (1992)

Hayashi et al. (1995)

Fig. 2.4 Gibbon phylogenies based on morphological and molecular characters

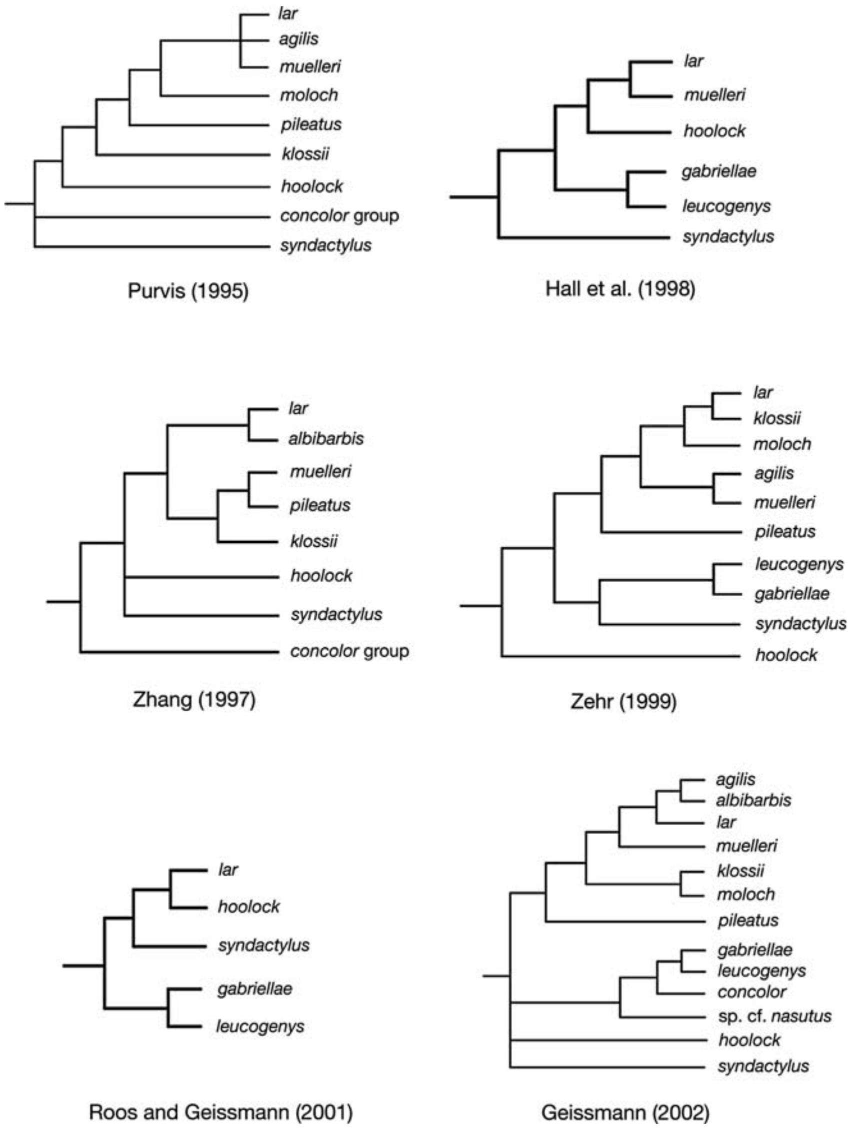
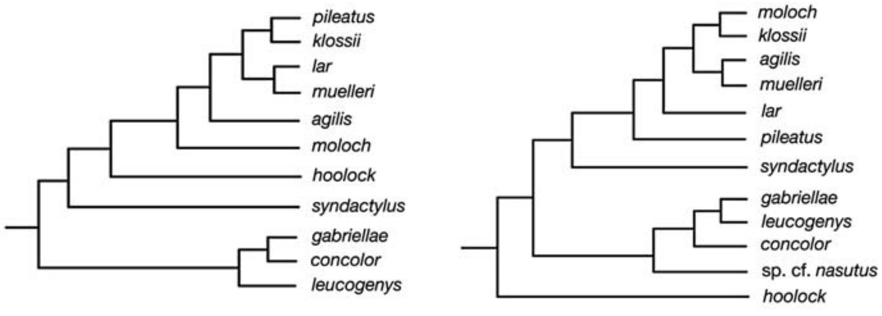


Fig. 2.4 (continued)

There is general agreement that the most recent gibbons to diverge were those in the genus *Hylobates* (the *lar* group); relationships among these taxa are, however, less well understood. Several studies have argued for close affinities between *H. lar* and *H. agilis* (Creel and Preuschoft 1984; Garza and Woodruff 1992; Geissmann 2002), while others have suggested *H. lar* and *H. klossii* are sister taxa (Hayashi et al. 1995; Zehr 1999). It is suggested by Takacs et al. (2005) that while the inclusion of *H. klossii* in the *lar* group is recommended, the



Chatterjee (2006)

Takacs et al. (2005)

Fig. 2.4 (continued)

relationships of *H. klossii* in the context of these studies must be treated with caution since many specimens in both zoos and museums may have been subject to misidentification (Geissmann, unpublished data). Numerous permutations have been suggested regarding inter-relationships amongst *lar*-group taxa. The employment of such diverse forms of data in these analyses, including a variety of genetic loci, pelage, vocalization, and morphological characters, indicate that these taxa likely represent a rapid radiation of closely related taxa and that alternative forms of data may be required to tease out interspecific relationships. Chatterjee's (2001) attempt at using the rapidly evolving control region to address this specific question proved unfruitful. Chatterjee (2001) proposed the use of various genetic loci in a combined analysis, including nuclear genes, Y chromosome markers, and microsatellites. More recently, Whittaker et al. (2007) have shown success with D-loop genetic data, which is in line with morphological and vocal data and provides support for Takacs et al. (2005); their findings suggest *H. klossii* and *H. moloch* are sister taxa (Whittaker et al. 2007).

Relationships among the *concolor* group have been similarly debated, although most molecular studies agree that *N. concolor* forms the basal branch, followed by the sister grouping [*N. gabriellae* and *N. leucogenys*].

Relatively few studies have tackled the issue of divergence dates amongst the various gibbon clades. Numerous estimates have been put forward for the great ape-gibbon split; however, dates for this divergence are controversial, ranging from 12 Ma (million years ago) to 36 Ma, based on a variety of data (e.g. Arnason et al. 1996). Since fossil gibbons are scarce, evidence about their divergence from the other apes has mainly originated from the field of molecular biology. Combined biochemical results, based on analysis of blood groups and histocompatibility antigens, chromosome banding patterns, protein structure and antigenicity, amino acid sequences of proteins, and DNA endonuclease restriction mapping, sequencing and reassociation kinetics, indicate a great ape-gibbon split at no more than 15 Ma (see Tyler 1993 and references therein). More recently, Raaum et al. (2005) estimate a divergence date of 15.0–18.5 Ma based on the entire mitochondrial genome.

Hayashi et al.'s (1995) molecular phylogeny of gibbons inferred from partial sequences of ND4, ND5, and tRNA genes indicated a divergence date of 6 Ma. Zehr et al. (1996) analyzed cytochrome oxidase subunit II sequence data for various species of gibbon and estimated that there was a rapid radiation of gibbons 6–8 Ma. Porter et al. (1997) analyzed sequences of the ε-globin locus from a variety of primate taxa including two species of gibbon and estimated that the gibbon radiation dates to approximately 9.9 Ma. Goodman et al. (1998) estimate a radiation dating to 8 Ma, based on a series of β-type globin genes. Based on a consensus estimate of 15 Ma for the great ape-gibbon split, Chatterjee (2006) undertook molecular clock analyses using cytochrome *b* gene data and suggests the gibbon radiation dates to approximately 10.5 Ma. According to this reconstruction, the clade comprising the genera *Symphalangus, Hoolock,* and *Hylobates* radiated between about 8 and 3 Ma. These estimates also indicate that taxa in the genus *Nomascus* represent a recent radiation between about 1.7 and 0.3 Ma (Chatterjee 2006).

Biogeography

Paleontological Record of Gibbons

The evolutionary history of gibbons has been little understood, largely due to a poor fossil record. Numerous fossil taxa have been nominated as possible gibbon ancestors on the basis of their small body size and simple molar cusp morphology, including *Pliopithecus*, *Laccopithecus*, *Micropithecus*, *Dendropithecus*, *Limnopithecus*, *Dionysopithecus,* and *Platodontopithecus*. Most of these taxa are now generally regarded as early catarrhines (Tyler 1993; Fleagle 1999). For some, however, one of these fossils remains a strong contender for the position of gibbon ancestor: *Laccopithecus robustus* (Wu and Pan 1984, 1985; Jablonski 1993; Tyler 1993). This late Miocene fossil (c. 8 Ma) is known from the Lufeng deposits in Yunnan, China. Evidence for the close phylogenetic relationship between *Laccopithecus* and extant gibbons is largely based on cranial and dental anatomy (Wu and Pan 1984, 1985). Meldrum and Pan (1988) have also presented evidence that the only identified postcranial remains of *Laccopithecus*, a proximal fifth phalanx, is similar to modern siamangs, and hence is typical of a brachiator. However, metric and morphological examination of the upper and lower dentition show a sexual dimorphism that far exceeds extant gibbons (Pan et al. 1989). According to Tyler (1993), if *Laccopithecus* is the ancestor of modern gibbons, it should be an arboreal brachiator, and have minimal sexual dimorphism. Clarification of the placement of *Laccopithecus* within the Hylobatidae warrants further evidence from the skull, auditory region, and postcranium (Tyler 1993; Jablonski this volume).

Wu and Poirier (1995) list mammalian faunas from a site called Hudieliangzi (Butterfly Hill) in Yuanmou, Yunnan, south China, which contains specimens identified as *Hylobates* sp. A more detailed taxonomic description of these specimens in not provided, but Zong et al. (1991) have dated this site to 5–6 Ma.

Undisputed gibbons do not appear in the fossil record until the Pleistocene (Hooijer 1960; Gu 1989; Tyler 1993; Jablonski this volume). Hooijer (1960) presents evidence of fossil gibbons (mainly teeth) from Sumatra (*S. syndactylus, H. agilis*), Java (*S. syndactylus*, *H. moloch*), Borneo (*H. muelleri*), and China (*H. hoolock*). Subsequently, several authors have dated the sites that contain these fossil faunas. De Vos (1983) and Van den Berg et al. (1995) have dated the so-called Punung faunal assemblage on Java and deposits on Sumatra, which contain fossils identified as *S. syndactylus*, to between 60,000 and 80,000 years old. Deposits containing the remains of *H. moloch* on Java have been dated as Recent (Van den Bergh et al. 1995). The evidence for *S. syndactylus* on Java between 60,000 and 80,000 years ago indicates this species was present on the island before *H. moloch*, Java's only present-day gibbon inhabitant.

Long et al. (1996) discuss additional evidence of fossil gibbons from the sites of Lang Trang in Vietnam dated to 80,000 years and Niah in Malaysian Borneo dated to 50,000 years, although details of taxonomic identification are not provided. Gu (1989) presents evidence of fossil gibbons from Chinese Pleistocene deposits. The fossils, mainly teeth, are identified as representing two species: *N. concolor* and *H. hoolock*.

Paleoenvironmental History of Southeast Asia

The paleoenvironmental history of Southeast Asia is complex due to a combination of orogenesis, plate tectonics, and glacial activities. These factors have affected the paleogeography of Southeast Asia, plus its climate, temperature, fauna, and flora. The Indo-Malaysian Islands are part of a complex comprising several structural divisions. At the boundaries of these plates, tectonic activity has created series of volcanoes and areas of submergence, the most dramatic of which can be seen at the margins of the Sunda Shelf (Fig. 2.5). The exposed part of the Sunda Shelf is also known as Sundaland, and comprises the Malay Peninsula, Sumatra, Java, Borneo, and other smaller island groups (Bellwood 1997).

Hall (1996, 1998) has reconstructed the paleoenvironmental history of Cenozoic SE Asia, including the distribution of land and sea. Since the fossil evidence for gibbons and gibbon ancestors dates to no earlier than the middle Miocene (approximately 15 Ma), this date will be used as a benchmark from which to briefly describe the paleoenvironmental history of Southeast Asia.

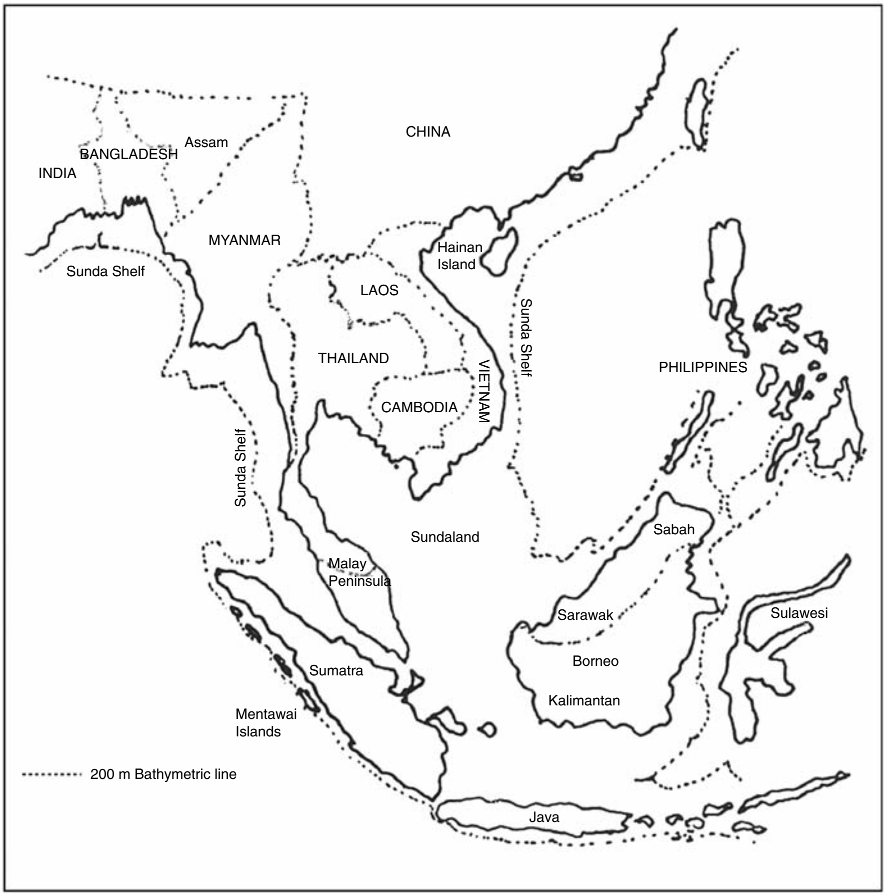


Fig. 2.5 Map of Southeast Asia showing the boundary of the Sunda Shelf, demarked by the 200 m bathymetric line (Chatterjee 2001)

Between 20 and 10 Ma, changes in the orientation of several tectonic plate boundaries throughout Southeast Asia resulted in the tectonic pattern recognizable today (Hall 1998). These changes, described in detail in Hall (1998), had dramatic effects on the paleogeography of the area. Between 15 and 5 Ma, large parts of Sundaland were exposed. According to Hall's reconstruction during the middle Miocene at 15 Ma, emergent land persisted from China, Vietnam, Laos, Cambodia, Thailand, and the Malay Peninsula, connecting these areas with large parts of Borneo. During this time, only the southern parts of Borneo were covered by shallow seas. A ridge of volcanoes running east to west across central Borneo (on the Sarawak-Kalimantan border) created areas of highland. This situation persisted through the late Miocene, approximately 10 Ma. Subduction of the Indian plate under the Sunda Shelf also created a ridge of volcanoes across Sumatra and Java, with patches of emergent land appearing at 15 Ma. By 10 Ma, these isolated patches of land joined to form a long, thin strip of land linking Sumatra, Java, and Sundaland. Between 15 and 10 Ma, Hainan Island was also joined to Mainland China, but by 5 Ma this corridor was covered by shallow seas. At 5 Ma, the area of emergent land was reduced. However, even at this time the Malay Peninsula, Borneo, Sumatra, and Java were linked via emergent land on the Sunda Shelf. Also at this time, patches of emergent land became evident at the position of the present day Mentawai Islands, although these patches were not connected to Sumatra. Throughout this time, deep basins east of Borneo may have represented barriers to dispersal to islands such as the Philippines, Sulawesi, and New Guinea.

Thus, there is evidence indicating that emergent land probably extended from Indochina to Borneo in the Miocene, and according to Morley and Flenley (1987) both seasonal and everwet rain forests were present. Other evidence indicates that tropical rain forest extended as far north as southern China, southern Japan, and westward to northern India during the late Miocene (Heaney 1991; Jablonski 1993). According to Heaney (1991), by approximately 5 Ma the insular and tropical nature of Southeast Asia was well established.

Batchelor (1979) suggests that up until the end of the Pliocene the extent of exposed Sundaland covered some 2,000 km east to west, and incorporated much of the Malay Peninsula, Sumatra, and Borneo. However, at this time major changes in sea level began as a result of glacial activity on a global scale. The major worldwide effects of glaciation were to alter sea levels, temperature, and the extent of vegetation zones. Evidence from deepsea cores and deeply stratified terrestrial gastropod- and pollen-bearing cores indicates that since about 2.5 Ma there have been a number (approximately 20) of glacial and interglacial cycles. During glaciations the vast quantities of water trapped in ice sheets across the globe immobilized large amounts of ^{16}O and the cold seas were as a result relatively rich in ^{18}O. During interglacials the ratio was reversed. Fluctuations in these ratios have been plotted from deepsea cores, and indicate the timing and extent of glacial waxing and waning (Shackleton and Opdyke 1973; Lowe and Walker 1997).

In Southeast Asia, as in many parts of the world, the periodicity of glaciations had the effect of altering sea level and hence the extent of exposed land, as well as affecting climate and vegetation. During periods of low sea level, large parts of Sundaland were exposed to between 120 and 160 m below present sea level (Morley and Flenley 1987; Heaney 1991; Bellwood 1997). This had the effect of linking the islands of Sumatra, Borneo, and Java to the mainland, creating a geography similar to that seen during the Miocene. Several authors present evidence of the environmental effects of Quaternary glaciations in Southeast Asia (e.g. de Vos 1983; Morley and Flenley 1987; Heaney 1991; Jablonski 1993; Van den Bergh et al. 1995; Brandon-Jones 1996). These studies provide evidence of the paleoecological implications of environmental change, plus fossil locality and dating information for numerous sites across Southeast Asia. However, the exact nature and timing of these variations are still actively debated (Jablonski 1993, 1997).

In summary, it is apparent that the prehistory of gibbons remains unclear due to a lack of crucial fossil evidence from the late Miocene and Pliocene. However, according to reconstructions by Hall (1996, 1998) and others (e.g. Heaney 1991; Jablonski 1993), much of the area uniting Sumatra, Borneo, and Java to mainland Malaysia was exposed for long periods during the late Miocene, Pliocene, and periodically throughout the Pleistocene. Furthermore, several studies have shown that tropical rain forests were present in these areas, and that these habitats supported a diverse primate fauna (Morley and Flenley 1987; Heaney 1991; Jablonski 1993). Despite evidence that climatic deterioration from the late Miocene onward affected some primate fauna, this does not appear to be the case with respect to the gibbons (Jablonski 1993). Jablonski (1993, 1998) presents evidence from the paleontological and paleoenvironmental record of China, which indicates that in spite of increased seasonality and habitat fragmentation, gibbons were among the most successful primates. Further, Jablonski (1998) suggests that this success was facilitated by a small body size and efficient life history parameters, such as an advanced age for the onset of reproduction and long inter-birth intervals.

The Radiation of Gibbons in Southeast Asia

Few scenarios have been proposed to describe the pattern of radiation of gibbons in Southeast Asia (Groves 1972; Chivers 1977). Groves (1972) proposed a scenario for the radiation of the *lar* group of gibbons; eustatic lowering of sea level in the Pleistocene was used to explain the dispersal of these gibbons. Chivers (1977) assimilated data on the sequence of geological, climatic, floral, and faunal events during the past few million years. This study provided a chronological history of the paleoenvironment of Southeast Asia, including possible migration routes for different gibbon taxa. Chivers' (1977) and Groves' (1972) schematic illustrations of the radiation of gibbons are useful for visualizing the possible migration routes of different taxa, but they are not congruent with recent advances in molecular estimates of the possible timing of the gibbon radiation.

Chatterjee (2006) employs her estimate of gibbon phylogeny within a cladistic biogeographic framework to provide a new scenario for the radiation of gibbons across Southeast Asia (Fig. 2.6). Published cytochrome *b* gene data were reanalyzed under the assumption of a molecular clock, and the resultant phylogeny employed in a dispersal-vicariance analysis (DIVA) (Ronquist 1996, 1997) to reconstruct the biogeographic history of gibbons. As with other cladistic biogeography methods, DIVA first requires the construction of a taxon-area cladogram showing geographic distributions and relationships. Geissmann's (1995) breakdown of the geographic distribution of gibbon species was used as the basis for determining area characters. Chatterjee's analysis provides a mix of informative and less informative biogeographic data, but in combination with current evidence relating to the environmental evolution of

Fig. 2.6 Pattern and timing of the gibbon radiation (Chatterjee 2006)
(1) The gibbon radiation initiated approximately **10.5 Ma** in Eastern Indochina; (2) Between about **10.5 and 8.6 Ma** gibbons radiated southward to the Malay Peninsula and Sumatra, subsequently, they differentiated into two types of gibbon on Sumatra, representing the two genera *Symphalangus* and *Hylobates*; (3) Approximately **7–8 Ma** *Bunopithecus* spread into Burma, Assam, and Bangladesh; (4) At around **3–5 Ma** there was a second radiation of genus *Hylobates*, involving dispersal into the islands of Borneo, Mentawai and Java; (5) Between **0.3 and 1.8 Ma** taxa in the subgenus *Nomascus* differentiated into Cambodia and Hainan Island.

Southeast Asia and the timing of gibbon radiations derived from molecular clock analyses, a scenario for the pattern of evolution of gibbons is viable at generic level (Fig. 2.6). Results suggest that the gibbon radiation initiated approximately 10.5 Ma in Eastern Indochina. Between about 10.5 and 8.6 Ma gibbons radiated southwards to the Malay Peninsula and Sumatra. Subsequently, they differentiated into two types of gibbon on Sumatra, representing *Symphalangus* and *Hylobates*. Approximately 7–8 Ma *Hoolock* spread into Burma, Assam, and Bangladesh. At around 3–5 Ma, there was a second radiation of taxa in genus *Hylobates*, involving dispersal onto the islands of Borneo, Mentawai, and Java. Between 0.3 and 1.8 Ma taxa in the genus *Nomascus* differentiated into Cambodia and Hainan Island.

Until such time as more gibbon fossils are recovered, our understanding of the pattern and timing of the gibbon radiation will be limited to those reconstructions combining molecular and environmental data. The advancing field of cladistic biogeography offers exciting potential in the developments of such models, but these will only ever be a proxy for the true biogeographic history of gibbons.

Conclusions

The diversity of gibbons with respect to pelage, vocalizations, geographic distributions, and evolutionary and biogeographic history renders these enigmatic apes some of the most intriguing mammals in the world. The past 20 years has seen huge advances with respect to our understanding of gibbon systematics, molecular phylogenetics, and speciation patterns. With continuing methodological developments in these fields, modern techniques offer an exciting opportunity to resolve many aspects of gibbon taxonomy, phylogeny, and biogeography. Our primary concern remains the conservation status of many gibbon taxa. With several species facing extinction, opportunities for studying gibbons are fast running out.

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Chapter 3
Genetic Differentiation of Agile Gibbons Between Sumatra and Kalimantan in Indonesia

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Introduction

The gibbons (Hylobatidae) are a diverse group of small apes that have adapted to the rain forests of South and Southeast Asia and radiated into numerous (12–14) discrete species. Recently, the four subgenera of small apes [*Hoolock*, (previously *Bunopithecus*, Mootnick and Groves 2005), *Hylobates*, *Symphalangus*, and *Nomascus*] were all raised to the level of genera because the genetic distances between them indicated by mitochondrial DNA were larger than those between *Homo* and *Pan* (Hayashi et al. 1995; Roos and Geissmann 2001). Some aspects of gibbon classification are still controversial, in particular the differentiation of subspecies (Groves 2001; Brandon-Jones et al. 2004; Mootnick 2006; Chatterjee this volume). Accurate determination of collection localities is critical for diagnosing subspecies in this group, which is morphologically very diverse in some physical features (e.g., pelage pattern, Marshall and Sugardjito 1986; Mootnick 2006). Thus it is important to use animals of known origin for genetic studies, which are crucial for planning the conservation of evolutionarily significant units (ESUs) (Crandall et al. 2000; Frankham et al. 2002). The taxonomy of agile gibbons is disputed (Chatterjee this volume), with some researchers recognizing a single species (*H. agilis*), and others recognizing one species (*H. agilis*) on the Asian mainland and Sumatra and a second species (*H. albibarbis*, or the white-bearded gibbon) on Borneo. In this chapter, we refer to all gibbons in this group as agile gibbons, but identify the Bornean taxon as *H. albibarbis*. We have aimed to collect samples from gibbons of known origin, and consequently have been able to demonstrate cytogenetic and molecular genetic differentiation of agile gibbon taxa between Sumatra and Kalimantan. These results provide important information on their biogeography and ESUs and a basis for future comprehensive evolutionary genetic investigations of small apes. We summarize the essential points of the data obtained so far, and give our point of view in this chapter.

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The genus *Hylobates*, with 44 chromosomes, is known to include inversion polymorphisms in chromosome 8, which are common to several species (Tantravahi et al. 1975; van Tuinen and Ledbetter 1983; Stanyon et al. 1987), a pattern that is rare in chromosome evolution. Apart from this phenomenon, small apes have undergone drastic chromosome changes that can be detected with human chromosome painting probes: all four genera of small apes show dozens of reciprocal translocations that differentiate them from humans and great apes (Jauch et al. 1992; Koehler et al. 1995; Nie et al. 2001; Müller et al. 2003). Accordingly, chromosomes of small apes likely have some special features, as numerous translocations are typically considered disadvantageous.

Most recently, van Tuinen et al. (1999) identified a new translocation between chromosomes 8 and 9 in three taxa (*H. agilis agilis, H. agilis unko*, and *H. albibarbis*) of agile gibbons. In concurrent investigations using different samples, Hirai et al. (2003) found the same variation, and based on the combined data from the two studies Hirai et al. (2003) postulated that the translocation may be a chromosome variant specific for Sumatran agile gibbons and absent in the Bornean taxon. To further explore the distribution of this translocation and its significance for gibbon evolution, the Primate Research Institute, Kyoto University, Japan, and the Primate Research Center, Bogor Agricultural University, Indonesia, initiated a joint research entitled “Comprehensive study of subspeciation of agile gibbons.” We started by obtaining genetic samples from animals of known origin and analyzing pelage patterns, chromosome structures, and DNA sequences. Surprisingly, combined analyses of such distinct parameters from the same samples have been very few so far. We were particularly conscious of the need to find gibbons of known origin from captivity, private pet owners, and zoological institutions, because analyses of animals of unknown origin have sometimes produced conflicting results regarding the evolution in the family Hylobatidae. It is very difficult to reliably identify species by their morphology, especially in the genus *Hylobates*, without information on their collection locality.

Samples and Identification

Blood sampling was done with permission from the Indonesian Research Authority/*Lembaga Ilmu Pengetahuan Indonesia* (LIPI) and the Indonesian Ministry of Forestry’s Department for the Protection and Conservation of Nature/*Perlindungan Hutan dan Konservasi Alam* (PHKA), and with help from rangers from the local Natural Resources Conservation Offices/*Balai Konservasi Sumber Daya Alam* (BKSDA) in West Sumatra, Central Kalimantan, and South Kalimantan. To obtain samples from as many gibbons of known origin as possible, we conducted interviews with pet owners and zoological institutions about the acquisition process in nearby natural habitats. Chromosome and DNA samples were then imported to Japan following acquisition of the appropriate

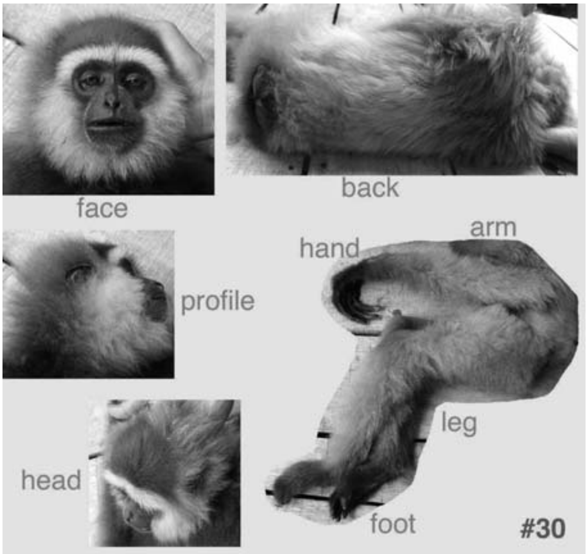

Fig. 3.1 A typical plate of pictures of pelage pattern of *Hylobates agilis albibarbis* from Kalimantan for morphological identification

CITES permits. Species and subspecies identification was conducted with reference to Marshall and Sugardjito (1986), Geissmann (1995), and Mootnick (2006), using information on the locality of collection and pelage photographs of all animals that we collected. We took pictures of the face, profile, back, head, arm, hand, leg, thigh, and foot of each animal while the animal was under ketamine anesthesia (e.g., Fig. 3.1). Pictures of the pelage of all individuals are available in a report edited by Hirai (2004).

We used the following taxonomic criteria for the taxa used in this study:

1. *H. agilis agilis* (Cuvier 1821), the mountain agile gibbon of Sumatra: the pelage of this taxon is buff, reddish-orange, reddish-brown, brown, or black with white cheek patches that connect at the chin and brow. The female's brow is white and not always divided in the middle.
2. *H. agilis unko* (Lesson 1840), the lowland agile gibbon of Sumatra: this taxon possesses few characteristics that reliably distinguish it from *H. a. agilis*. The cheek patches are creamy white to a grizzled white, sparse, and do not connect at the chin or brow. The adult female's brow marking is thin and short and well separated in the middle. Some specimens have a lumbar region that is paler than the rest of the body hair.
3. *H. albibarbis* Lyon 1911, the Bornean white-bearded gibbon: this taxon is light brown, with dark-brown to brown-black underparts, hands, legs, and cap, with a white brow, and a buff lumbar region. This taxon has black fingers and toes. Groves (2001) classified this group as a different species from Sumatran agile gibbons and Mueller's Bornean gibbons.

4. *H. muelleri* (Martin 1841), Mueller's Bornean gibbon: adult male and female are identical in coat color, which varies from gray to gray-brown or blackish. The hair of the adult male's genital tuft is 25 mm long (Marshall and Sugardjito 1986) and is typically darker than the body hair. Infant's coats are lighter than their parents'. This species lacks a uniform appearance in areas of geographic overlap between Mueller's Bornean gibbon subspecies. Marshall and Sugardjito (1986) describe three subspecies: Eastern Mueller's gibbon (*H. m. muelleri*), Abbott's gray gibbon (*H. muelleri abbotti*), and Northern Mueller's gibbon (*H. muelleri funereus*). Samples of this species collected in Kalimantan in this study were all from Eastern Mueller's gibbons. This subspecies is pale gray or gray-brown with a black cap, ventrum, hands, feet, and inner aspects of the limbs, and has a thick white brow.

Taxonomic identification and original locality (wild or captive born) of the 57 gibbons studied are listed in Table 3.1, together with morphs of chromosome 8 and haplotypes of DNA markers. The samples were collected in west Sumatra (Padang, Payakumbuh, Solok Selatan, Kunbang Tungkek, Bukit Tinggi, Panti, and Pasaman Timur), in central Kalimantan (Palangkaraya and Pangkalanbun) and in south Kalimantan (Banjarmasin, Banjar Baru, and Martapura).

Chromosomes

Gibbons of the genus *Hylobates* have 44 chromosomes, and are polymorphic for three pericentric inversions in chromosome 8 (a, b, c), which are shared by several species (Stanyon et al. 1987). Recently, a unique chromosome variation, a translocation between chromosomes 8 and 9 (van Tuinen et al. 1999), was found in the genus *Hylobates*. This variation was confirmed to be a whole-arm translocation between chromosomes 8 and 9 (WAT8/9) by chromosome painting analysis (Hirai et al. 2003). In combined data from previous studies by van Tuinen et al. (1999) and Hirai et al. (2003), the variant seemed to be predominant in Sumatran agile gibbons [*Hylobates agilis agilis* (79%) and *H. agilis unko* (63%)], but occurred in only 15% of Bornean agile gibbons (Hirai et al. 2003). That is, Sumatran agile gibbons (*H. a. agilis* and *H. a. unko*) had WAT8/9 about five times more frequently than Bornean agile gibbons (*H. albibarbis*). We initiated this project to further investigate this apparent pattern, since previous studies included insufficient samples of Sumatran taxa.

As shown in Table 3.1, in this study, only animals that were identified as Sumatran agile gibbons had the WAT8/9 translocation as a polymorphism, while it was not observed in Bornean agile gibbons (*H. albibarbis*) or Eastern Mueller's gibbons (*H. m. muelleri*) (Hirai et al. 2005). A three-color FISH technique using human chromosome paints disclosed that WAT8/9 was present in all 17 Sumatran agile gibbons studied (4 heterozygotes and 13 homozygotes) (Table 3.1), and that it was a translocation between morphs 8c and 9 (Fig. 3.2). WAT8/9 appears to be restricted to the Sumatran taxon.

Table 3.1 Sample and genetic data of *Hylobates agilis* and *H. muelleri* collected from Sumatra and Kalimantan

ID	Sex	Ori	Fac	S/SS	MC8	mt	TSPY	ID	Sex	Ori	Fac.	S/SS	MC8	mt	TSPY
1	M	S. w	pet	AGU	8ab/8c’	*AG* 1	*AG*	26	F	K. w	pet	*AL*	8c/8c	*AL*	–
2	M	S. w	pet	*AGU*	8c’/8c’	*AG* 2	*AG*	27	F	K. w	pet	*AL*	8c/8c	*AL*	–
3	M	S. w	zoo	*AGU/A*	8c’/8c’	*AG* 1	*AG*	28	F	K. w	pet	*AL*	8ab/8c	*AL*	–
4	M	S. w	pet	AGU	8c’/8c’	*AG* 1	*AG*	29	M	–	zoo	*AL*	8ab/8ab	*AL*	*AL*
5	F	S. w	pet	AGU	8c’/8c’	*AG* 1	–	30	M	c	pet	*AL*	8ab/8c	*AL*	*AG*
6	F	S. w	pet	AGU	8ab/8c’	*AG* 2	–	31	M	c	pet	AL	8ab/8c	*AL*	*AL*
7	F	S. w	pet	*AGU/A*	8c’/8c’	*AG* 2	–	32	M	c	pet	*AL*	8c/8c	*AL*	*AL*
8	F	S. w	pet	*AGU/A*	8c’/8c’	*AG* 2	–	33	F	c	pet	*AL*	8c/8c	*AL*	–
9	F	S. w	pet	AG	8c’/8c’	*AG* 1	–	34	F	c	pet	*AL*	8ab/8ab	*AL*	–
10	F	S. w	pet	AGU	8c’/8c’	*AG* 1	–	35	F	c	pet	*AL*	8c/8c	*AL*	–
11	M	c	zoo	AGU	8c’/8c’	*AG* 1	*AG*	36	F	c	pet	*AL*	8ab/8c	*AL*	–
12	M	c	zoo	AGU	8c’/8c’	*AG* 1	*AG*	37	F	c	zoo	*AL*	8ab/8c	*AL*	–
13	M	c	zoo	AGU	8c’/8c’	*AG* 1	*AG*	38	M	K. w	pet	MU	8ab/8c	*MU*	*MU*
14	M	c	zoo	*AGU/A*	8ab/8c’	*AG* 2	*AG*	39	M	K. w	pet	*MU*	8c/8c	*MU*	*MU*
15	M	c	zoo	AGU	8c’/8c’	*AG* 1	*AG*	40	M	K. w	pet	*MU*	8ab/8c	*MU*	*MU*
16	F	c	zoo	AGU	8ab/8c’	*AG* 1	–	41	M	K. w	pet	*MU*	8ab/8ab	*MU*	*MU*
17	F	c	zoo	AGA	8c’/8c’	*AG* 1	–	42	F	K. w	pet	*MU*	8c/8c	*MU*	–
18	M	K. w	pet	AL	8c/8c	*AL*	*AL*	43	F	K. w	pet	*MU*	8ab/8ab	*MU*	–
19	M	K. w	pet	AL	8ab/8ab	*MU*	*MU*	44	F	K. w	pet	*MU*	8ab/8c	*MU*	–
20	M	K. w	pet	AL	8c/8c	*AL*	*AL*	45	F	K. w	pet	*MU*	8ab/8ab	*MU*	–
21	M	K. w	pet	*AL*	8ab/8ab	*AL*	*AL*	46	F	K. w	pet	MU	8ab/8ab	*MU*	–
22	M	K. w	pet	*AL*	8ab/8c	*AL*	*AL*	47	F	K. w	pet	MU	8ab/8c	*MU*	–
23	M	K. w	pet	*AL*	8ab/8c	*AL*	*AL*	48	M?	K. w	pet	*MU*	N	*AL*	N
24	F		pet	*AL*	N	*AL*	–	49	M	c	zoo	*MU*	8ab/8c	*MU*	*MU*
25	F?	K. w	pet	*AL*	8ab/8c	*AL*	–	50	M	c	pet	*MU*	8c/8c	*MU*	*MU*

Table 3.1 (continued)

ID	Sex	Ori	Fac	S/SS	MC8	mt	TSPY	ID	Sex	Ori	Fac.	S/SS	MC8	mt	TSPY
51	F		pet	*MU*	8ab/8c	*MU*	–								
52	M	c	zoo	MU*Hy?*	8c’/8c’	*AG* 1	*AG*								
53	M	c	zoo	MU*Hy?*	8c/8c	*MU*	*MU*								
54	M	K. w	pet	MU*Hy?*	8a.b/8c	*MU*	*MU*								
55	F	c	pet	AL *Hy?*	8a.b/8c	*MU*	–								
56	M?		pet	AL *Hy?*	8ab/8ab	*MU*	N								
57	M	c	pet	MU *Hy?*	8ab/8c	*MU*	*MU*								

ID, individual number. F, female. M, male. Ori., origin of sample. S, Sumatra. K. Kalimantan. w, wild. c, captive. Fac., facility. S/SS, species or subspecies. AGU, *Hylobates agilis unko*. AGA, *H. agilis agilis*. AGU/A, *H. a. unko* or *H. a. agilis*. AL, *H. a. albibarbis*. MU, *H. m. muelleri*. MC8, morph of chromosome 8. 8ab, 8a morph or 8b morph distinguished by a small pericentric inversion. 8c, a morph rearranged by a large pericentric inversion. 8c’, a morph consisting of the short arm of chromosome 8 and the long arm of chromosome 9 formed by a whole-arm translocation between chromosomes 8 and 9 (WAT8/9). mt, mtDNA. Hy?, possible hybrid identified by morphology. N, non-detectable.

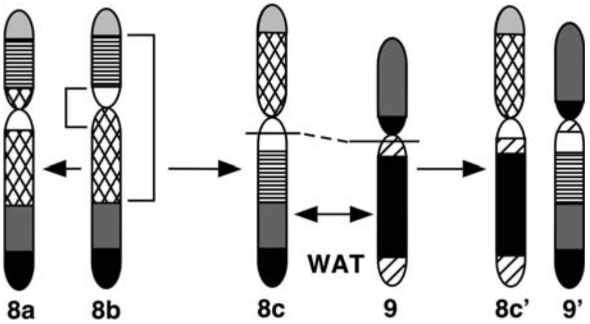

Fig. 3.2 Schematic illustration of the whole-arm translocation (WAT) between chromosomes 8 and 9 found in Sumatran agile gibbons. Each *patch* or *shade* element shows a block stained with the same human chromosome painting probe. The *brackets* indicate the breakpoints of the inversions. The *fine bar* indicates the breakpoints of the translocation. The *numbers* indicate the chromosome, and the *letters* refer to the morph of the chromosome. The *arrows* indicate the directions of chromosome changes. The *double arrowheads* show the exchange of chromosome arms

8a and 8b are other morphs that acquired different inversions, respectively, from 8c (see Fig. 3.2). These two morphs could not always be discriminated in all samples in the painting analysis of this time because of their similarity, though they were easily distinguishable from 8c, so for the purposes of this study we combined them and refer to either 8a or 8b as 8ab. Heterozygotes for WAT8/9 may include these other morphs of chromosome 8, that is, 8ab8c'99' and 8c8c'99'. Both of the heterozygous pairs could form quadrivalents in meiosis-I as shown by van Tuinen et al. (1999). Chromosome composition data deduced from painting (Fig. 3.2) suggest that the former heterozygote is more complicated than the latter. In general, the more complicated chromosome pairing would induce more meiotic non-disjunction, resulting in lower fecundity. However, gibbons investigated in three previous studies showed only the former pairing (8ab8c'99') (van Tuinen et al. 1999; Hirai et al. 2003; Hirai et al. 2005). Researchers have identified 13 individuals with 8ab8c'99' (not including offspring of captive parents with the same chromosome pairing), but none with 8c8c'99'. This suggests that morphs 8c and 8c', which ought to be most similar, may contain elements that make them incompatible with each other. However, the data are not yet sufficient to confirm this, and if such incompatibility exists, the mechanism is unknown.

DNA Analyses

To clarify molecular phylogenetic relationships between Sumatran and Bornean agile gibbons and Eastern Mueller's gibbons, we sequenced the ND4-ND5 region of mitochondrial (mt) DNA and the testis-specific protein Y-encoded

(TSPY) gene from blood. ND4-ND5 sequences (1039 bp) were amplified using two primers (L12686 and H12752R) described in a previous study (Hayashi et al. 1995), and sequenced with BigDye (R) Terminator Ver. 3.0 cycle sequencing kit (Applied Biosystems) (Tanaka et al. 2004). We amplified and sequenced the TSPY gene (739 bp) in nine Sumatran agile gibbons, eight Bornean agile gibbons, and six Eastern Mueller's gibbons using the primers described previously (Kim et al. 1996). We aligned the sequences with CLUSTAL X 1.81 (Thompson et al. 1997) and conducted phylogenetic analyses with PAUP* (Swofford 2003). We drew a network of TSPY haplotypes with TCS (Clement et al. 2000). We also conducted population genetic analyses of the relationship between the three taxa using 14 microsatellite loci (D02S1777, D05S0807, D09S0302, D10S1432, D14S0255, D17S0804, D20S0206, D07S1826, D01S0533, D03S1768, D07S0821, D13S0765, D13S0788, D14S0306) (Hayano et al. unpublished). Analysis of molecular variance (AMOVA, Excoffier et al. 1992) was conducted with ARLEQUIN (Schneider et al. 2000). We calculated F_{ST} distances to measure the extent of genetic distance between groups using the variance of genotypic frequencies in 195 independent alleles. As these data will be described in detail elsewhere, we will only briefly summarize them here.

Clustering analyses of the 40 mtDNA haplotypes found in 52 individuals suggest that Sumatran agile gibbons consist of two distinct groups (*agilis* 1 and *agilis* 2), and that *agilis* 1, *agilis* 2, *albibarbis*, and *muelleri* form a separated lump cluster. *H. albibarbis* and *H. m. muelleri* fall phylogenetically between the *agilis* 1 and *agilis* 2 clusters. However, the two *agilis* clusters do not seem to be in accordance with the subspecies of Sumatran agile gibbons (*agilis* and *unko*) (Tanaka et al. 2004 and unpubl.). On the other hand, 8 TSPY haplotypes were found and network analyses show clear separation of Sumatran agile gibbons (including *agilis* 1 and *agilis* 2) from Bornean agile gibbons (*H. albibarbis*) and Eastern Mueller's gibbons (*H. m. muelleri*) with 2–7 and 6–10 base pair differences, respectively (Fig. 3.3) (see also Tanaka et al. 2004; Hirai et al. 2005).

Six individuals (19, 30, 48, 52, 55, 56) showed mismatches between identifications by pelage pattern and by mtDNA or TSPY or both (Table 3.1). Mismatches detected included *albibarbis* (pelage) – *muelleri* (mtDNA) – *muelleri* (TSPY); *albibarbis* – *albibarbis* – *agilis*; *muelleri* – *albibarbis* – undetected; *muelleri* – *agilis* – *agilis*; *albibarbis* – *muelleri* – none; and *albibarbis* – *muelleri* – undetected. These discrepancies may result from interspecific or intersubspecific hybridization that is likely to cause misidentification, because mtDNA (inherited maternally) and TSPY (inherited paternally) originating from different species are observed in some of these individuals. These cases emphasize the point that morphological and genetic analyses of the same animal are usually required in phylogenetic or conservation studies of gibbons.

The mtDNA and TSPY divergences were confirmed by a genetic distance analysis with microsatellite DNA genotypes. Using 12 microsatellite loci with a total of 195 alleles, we calculated the F_{ST} value and tested for significance using 5000 permutations by AMOVA (Excoffier et al. 1992; Schneider et al. 2000). The AMOVA result indicated significant genetic differences among the three

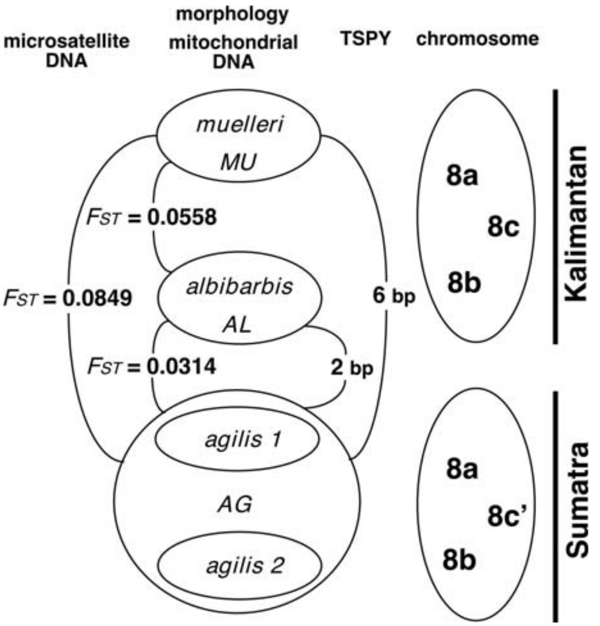

Fig. 3.3 Relationships among four genetic parameters-chromosome, mitochondrial DNA, TSPY, and microsatellite DNA in populations of three species, *H. muelleri muelleri* (*muelleri*), *H. agilis albibarbis* (*albibarbis*), and *H. agilis* (*agilis*) identified with pelage patterns. Network of TSPY differentiation was drawn fine *black lines* and *circles*. An *interval bar* between *circles* indicates one base pair substitution. *Solid circles* show haplotypes of TSPY found in the present study, and blank ones indicate intermediate haplotypes undiscovered so far. For the details see text

groups ($F_{ST} = 0.053, p < 0.001$). Further, significant pairwise F_{ST} values ($p < 0.001$) were found in all three pairwise comparisons: between Sumatran and Bornean agile gibbons (0.0314), Bornean agile gibbons and Eastern Mueller's gibbons (0.0558), and Sumatran agile gibbons and Eastern Mueller's gibbons (0.0849). These results suggest that the three populations are genetically distinct from each other (Fig. 3.3, see also Hirai et al. 2005).

Discussion

We have examined the genetic and morphological features of more than 100 animals of the genus *Hylobates* so far. One point highlighted by our investigations is that knowing the original collection locality for specimens used in genetic monitoring research in gibbons is extremely important, since morphological identification is difficult (van Tuinen et al. 1999). While we were careful in verifying the collection localities for our samples, we found discrepancies between morphological and molecular identifications in six individuals. Most of these are probably caused by interspecific or intersubspecific hybridization, which is comparatively difficult to identify morphologically. However, in our experience, careful photography can sometimes aid in the identification of gibbons in zoological institutions. Therefore, interdisciplinary investigations of morphology and genetics are required to monitor and reduce misidentification of captive animals. Results from such studies should help to overcome deficiencies in the classification of gibbons. The mtDNA ND4-ND5 as well as D-loop regions are probably the best molecular methods for identifying captive gibbons at present, though development of appropriate nuclear DNA markers to detect introgression will be required for more intensive genetic studies. The inclusion of vocalization studies may be helpful for species and subspecies identification and for exploration of phylogenetic relationships among gibbon taxa. Using this more holistic approach may allow researches to obtain more solid data on the evolution of small apes, although data based on DNA and chromosomes have not always yielded consistent results (Fig. 3.3).

Hitherto, genetic studies of gibbons have generally relied on samples from captive-born animals or animals of unknown origin, because of the ease of obtaining blood samples from zoological institutions rather than from pets of known origin or from wild animals. Captive gibbon management is difficult, due to identification problems resulting from the complexities of their morphology, and to inadvertent or unwitting hybridization (van Tuinen et al. 1999). Investigations using zoo samples can thus produce conflicting conclusions, because of the possibility that individuals appearing to belong to the same species actually have distinct genetic structures from different species due to hybridization or misidentification. In our previous investigation, we showed that some individuals of the genus *Hylobates* that have been reared in zoological institutions were misidentified. For example, one of us (ARM) correctly reassigned captive individuals, from *H. klossii* to *H. agilis unko*; from *H. moloch* to *H. muelleri* and *H. agilis unko*; and from *H. muelleri* to *H. albibarbis,* etc. (Hirai et al. 2003). Another study reported a similar experience (van Tuinen et al. 1999). Such re-identifications, and the accumulation of data from numerous individuals, allowed us to estimate the geographical distribution of the WAT8/9 translocation (Hirai et al. 2003), and a project using gibbons of known origin revealed a new variant marker chromosome that identified Sumatran agile gibbons as an ESU (Hirai et al. 2005). To date, our samples have been limited to central and western Sumatra, and have confirmed that the presence of WAT8/9 distinguishes Sumatran agile gibbons in this area from other gibbon taxa. Complete sampling from across their range on Sumatra will be necessary to determine the geographic extent of occurrence of this genetic variant.

Do chromosomal variations drive speciation events? A theoretical analysis of chromosome change and species differentiation suggested that speciation without karyotype alteration predominates in mammals (Imai 1983). Imai (1983) concluded that parapatric distributions of karyotypically distinct populations are a transitional step in karyotype substitution. On the other hand, the stasipatric speciation model states that chromosome changes can be strongly implicated in driving a speciation event by creating a barrier to gene flow, rather than being only a remnant of adaptation by directional selection (White 1978). The WAT8/9 translocation polymorphism, found only in Sumatran agile gibbons, is interpreted as a transitional step toward its fixation by genetic drift. Microsatellite DNA analysis suggested, based on a significant heterozygote deficit, that the sample population of Sumatran agile gibbons has experienced a population bottleneck (A. Hayano, unpubl. data). During the bottleneck, the chromosome alteration may have occurred in a small population, and afterwards may have spread rapidly by genetic drift during an abrupt increase in population size. WAT8/9 apparently occurred on Sumatra after the geographical isolation of Sumatra and Borneo, and thus could be rapidly fixed on Sumatra. However, the chromosome change does not distinguish the subspecies *H. agilis agilis* and *H. agilis unko*, as both subspecies have the same alteration (van Tuinen et al. 1999; Hirai et al. 2005). Data from chromosome and DNA analyses reveal that the two Sumatran subspecies of agile gibbons appear to belong to a single species, *H. agilis*, though they display distinct pelage patterns. Thus, genetic analyses are pivotal tools to define population structure, especially of gibbons with similar pelage patterns.

Will or did the WAT8/9 translocation drive the evolution of Sumatran agile gibbons? The 8c’ element of the translocation appears to have some incompatibility with 8c, which is a direct ancestor of the alteration. The incompatibility might have resulted in selection against chromosome 8c in Sumatran populations of agile gibbons, because other populations of *H. albibarbis* and *H. m. muelleri* without 8c’ still include 8c (Fig. 3.3). If this is indeed the case, then 8c will be eliminated on Sumatra in the future or may already have been eradicated, because it was not observed in the present study. Chromosomal changes such as the translocations described here could result in lowered fitness when in the heterozygous condition because of problems in meiosis. However, Cronin et al. (1984) point out that chromosome variants in gibbons that are generally socially monogamous could become homozygous more rapidly than in animals with a different social structure and mating system. If variants such as 8c’ become homozygous in a population, they recover the same fitness as the ancestral wild-type homozygote. Accordingly, it seems that the Sumatran population of agile gibbons is evolving rapidly toward an 8c’ population as a result of the unique social structure of gibbons. The mechanism of fixation of WAT8/9 is probably a good example of chromosome evolution in gibbons by numerous translocations. Chromosome evolution by translocation may occur more readily in primates with a monogamous mating system than with the polygamous and promiscuous mating systems found in other primate groups. That is, the mating system of gibbons may be tightly linked with chromosome evolution, though there is increasing evidence that the social structure in gibbons is not necessarily as rigid as has been presumed (Hirai et al. 2005).

We have postulated that migration of *muelleri* and *agilis* (or *albibarbis*) gibbons from Sumatra to Borneo may have occurred twice, based on our genetic data and geographic changes in the glacial period (Fig. 3.3). However, Groves (1972) suggested an alternative route from Indochina to Borneo and then from Borneo to Sumatra during the Pleistocene to explain the distribution pattern of gibbons in relation to the geographic data. As our hypothesis was proposed based on data on chromosome change and genetic distance between the three taxa (*H. agilis*, *H. albibarbis*, and *H. m. muelleri*) of Sumatra and Borneo, cladistic calibration with molecular data for ancestral taxa is required to determine the direction of migration of gibbons in Sundaland.

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Chapter 4
Vocal Diversity of Kloss's Gibbons (*Hylobates Klossii*) in the Mentawai Islands, Indonesia

Sally A. Keith, Melissa S. Waller, and Thomas Geissmann

Introduction

Gibbons (family Hylobatidae) are generally described as monogamous, frugivorous, arboreal, and territorial apes and inhabit tropical and subtropical forests of South and Southeast Asia (Marshall and Sugardjito 1986; Leighton 1987; Chivers 2001; Geissmann 2003). All gibbon species are known to produce elaborate, loud, long, and stereotyped patterns of vocalization often referred to as "songs" (Marshall and Marshall 1976; Haimoff 1984; Geissmann 1993, 1995, 2002b, 2003). Generally, song bouts are produced in the early morning and last approximately 10–30 min. Species-specific song characteristics in gibbons are thought to have a strong genetic component (Brockelman and Schilling 1984; Geissmann 1984; Tenaza 1985; Marshall and Sugardjito 1986; Mather 1992; Geissmann 1993). It has previously been demonstrated that gibbon song characteristics are useful for assessing systematic relationships on the level of the gibbon genus, species and local population, and for reconstructing gibbon phylogeny (Haimoff et al. 1982; Haimoff 1983; Creel and Preuschoft 1984; Haimoff et al. 1984; Marshall et al. 1984; Geissmann 1993, 2002a, b; Konrad and Geissmann 2006; Dallmann and Geissmann this volume).

The Kloss's gibbon (*Hylobates klossii*) is endemic to the Mentawai Islands (Fig. 4.1), which lie 85–135 km off the west coast of central Sumatra in Indonesia (Whitten 1982). The species is sexually monochromatic, with a black pelage and skin color (Geissmann 1995). Kloss's gibbons produce male solo song bouts, which usually occur in the pre-dawn hours, and female solo song bouts, which occur post-dawn (Tenaza 1976; Whitten 1980, 1982, 1984a, b; Haimoff and Tilson 1985). This species is unusual among gibbons because mated pairs do not duet. The lack of duets and the temporal segregation of male and female songs are derived features shared only with Javan

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Fig. 4.1 Map of the Mentawai Islands showing location of study sites. Inset map: location of the Mentawai Islands in Southeast Asia

silvery gibbons (*H. moloch*) (Geissmann 1993, 2002b) and suggest a sister taxon relationship of these two species (Geissmann 2002a, b). This finding was recently supported by molecular data (Takacs et al. 2005; Whittaker et al. 2007).

The Mentawai Islands contain high levels of endemism and have been separated from the mainland for at least 500,000 years (Batchelor 1979). Four nonhuman primates are endemic to the Mentawai Islands: the Kloss's gibbon, the Mentawai macaque (*Macaca pagensis*), the Mentawai langur (*Presbytis potenziani*), and the pig-tailed langur or simakobu (*Simias concolor*). For each primate except the Kloss's gibbon, one subspecies is described as being endemic to the northernmost island of Siberut, and a second subspecies is described as being distributed across the three remaining islands of Sipora, North Pagai, and South Pagai (Chasen and Kloss 1927; Groves 2001; Roos et al. 2003).

The fact that the other three primates all exhibit taxonomic separations at the same boundary suggests that an analogous taxonomic organization could occur in the sympatric Kloss's gibbon. Moreover, many Old World monkeys including macaques and several species of leaf monkeys are known to enter water while foraging and traveling (Kawai 1965; Kawabe and Mano 1972; Kurland 1973; Zeeve 1985; Bennett and Sebastian 1988; Watanabe 1989; Steenbeek 1999; Agoramoorthy et al. 2000; Boonratana 2000; Dudgeon 2000; Pfeyffers 2000; Nikolei 2003). In contrast, wild gibbons have not been reported to enter water. Even shallow moats can prevent zoo gibbons kept on islands from escaping (Delacour 1961; Dathe 1972), and the distribution ranges of different gibbon taxa are often separated by rivers (Parsons 1940; Morris 1943; Marshall and Sugardjito 1986). As a result, the separation between Siberut and the remaining Mentawai islands may present a more serious distribution barrier for gibbons than for macaques and leaf monkeys. Consequently, the gibbon should be the Mentawai primate most likely to have diverged on Siberut and the southern islands.

Originally, the taxonomic distinction between the monkeys of Siberut and those of the three remaining islands was proposed based on differences in fur coloration, specifically darker coloration for Siberut subspecies (Chasen and Kloss 1927; Groves 2001). However, the pelt of the Kloss's gibbon is completely black and, therefore, does not offer any visual cues by which subspecies can be distinguished. Analyses of mitochondrial DNA sequences failed to find evidence for the occurrence of more than one taxon within Kloss's gibbons; however, the small sample size that led to this conclusion means it warrants further investigation (Whittaker 2005a, this volume).

In order to further examine the subspecific taxonomy of Kloss's gibbons, the present study spectrographically and statistically analyzed vocal data from male and female Kloss's gibbons to assess interpopulation diversity. We compared the vocal diversity of wild Kloss's gibbons at four localities (two on Siberut and one each on Sipora and South Pagai) to assess whether vocal differences among populations indicate the occurrence of a distinct subspecies on Siberut, correspond to geographic distance or follow any other recognizable pattern. If the data suggest the existence of more than one taxon, there will be implications for conservation strategies. The Kloss's gibbon is an endangered species with an estimated total population size of 20,000–25,000 individuals (Whittaker 2005b). Currently, only one substantial protected area, Siberut National Park, exists within the range of Kloss's gibbons. Detection of a second taxon on the remaining three islands would indicate a need for the establishment of a second protected area on one of these islands.

Materials and Methods

Field Methods

The gibbon songs included in the present study were recorded by SAK and MSW in four different localities on the Mentawai Islands in 2005. The localities are mapped in Fig. 4.1; coordinates and recording dates are listed in Table 4.1. Field site selection was based on accessibility, the presence of gibbons, and recommendations of previous researchers (Paciulli 2004; Whittaker 2005a). On Siberut, where we sampled more than one population, we selected sites that

Table 4.1 List of field sites where Kloss's gibbons were recorded, with coordinates and recording dates

Locality	Coordinates	Survey and recording date
Simabuggai, Siberut National Park, central Siberut Island	01°22'30.6"S, 098°56'35.2"E	05–14 June 2005
Sikabei, southern Siberut Island	01°37'04.3"S, 099°15'41.5"E	03–14 July 2005
Saureinu, Sipora Island	02°07'15.5"S, 099°38'04.1"E	07–19 August 2005
Malakopa logging concession, South Pagai Island	02°58'00.9"S, 100°17'15.5"E	19–30 July 2005

were >20 km apart to ensure that different populations were sampled. Three to six listening posts were used per study site.

Data Collection

Vocalizations were recorded with a Sony TCM-450DV cassette recorder and a Sennheiser ME66 short directional microphone. The tape recordings were digitized with a sampling rate of 44.1 kHz and a sample size of 16 bits. Sonograms (time versus frequency displays) of the sound material were generated using the Raven version 1.2.1 software (Cornell Laboratory of Ornithology). The sonograms were computed by *Fast-Fourier-Transformation* (FFT). The FFT size of the sonograms was 512 points, using the window function = Hann and a 3dB filter bandwidth of 124 Hz. The time resolution was 256 points with an overlap of 50%, the frequency resolution was 512 points with a frequency grid spacing of 86.1 Hz (Charif et al. 2004).

The variables that were used to measure the great call and the male trill phrase are described in detail in the Appendix.

Kloss's Gibbon Song Structure

The acoustic terminology used in the present study largely follows that proposed by Haimoff (1984). The most relevant terms for the present study are defined below. A *note* is any single continuous sound of any distinct frequency or frequency modulation, which may be produced during either inhalation or exhalation. A *phrase* is a single vocal activity consisting of a larger or looser collection of notes. These parts may be produced together or separately. A *great call* is the most stereotyped and most easily identifiable phrase of the gibbon song, produced by the adult females of all gibbon species. A *song* is "a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time." (Thorpe 1961: p. 15). A *song bout* is all song notes of a gibbon group separated by periods of silence of less than 10 min. A *solo song bout* is a song bout produced by one individual (male or female) alone.

Male Song Structure

A male song bout exhibits a progressive elaboration of call structure from simple notes to more complex phrases. Roughly, the following three stages can be identified: (1) the song bout starts with single "hoo" notes and progresses to short phrases with simple "hoo's"; this stage lasts up to 25 min; (2) the second stage is composed of longer phrases of "hoo" note combinations; and (3) the progression stabilizes with fully developed phrases that exhibit a trill (called trill phrases in the following text). Trill phrases consist of an initial pre-trill, a trill, and a final post-trill part (Fig. 4.2a).

Female Song Structure

The song structure of female Kloss's gibbons consists of an introductory sequence of single-frequency build-up notes, followed by repeated great call phrases. Similar to fully developed male trill phrases, each complete great call phrase consists of an initial pre-trill, a trill, and concluding post-trill phase (Fig. 4.2b). The male trill phrases are much shorter (5–14 s), however, than female great call phrases (22–39 s).

The great call phrase begins with the pre-trill part encompassing a single rising note, followed by single-frequency notes. The trill part consists of rapid notes for a period of approximately 8–12 s. The post-trill part has notes that gradually increase in duration while decreasing in frequency and amplitude. The entire great call usually lasts in the region of 20–30 s. In this study only the first two parts of the great call were analyzed because post-trill notes were often lost from recordings due to inaudibility.

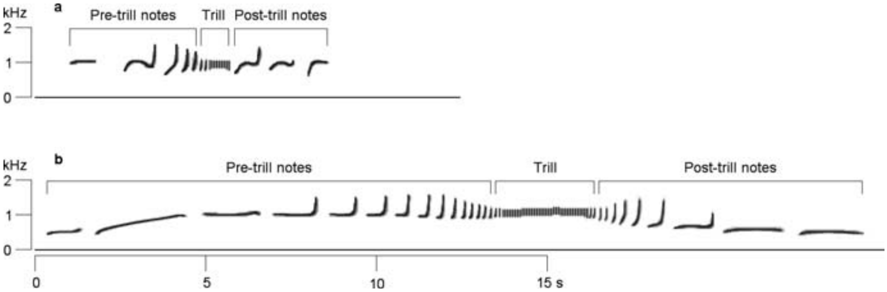

Fig. 4.2 Stylized sonograms of male and female song phrases. (**a**) fully expressed male trill phrase from the stable part of the male solo song. (**b**) female great call phrase

Sample Size of Tape-Recorded Gibbon Songs

We analyzed a total of 137 great call phrases from 24 different females (mean ± SD; 5.7±2.0, range 3–11 great calls per female) and 224 trill phrases from 27 different males (8.3±6.1, range 2–21 phrases per male). All songs are from wild, non-habituated gibbons.

As the actual distribution of the group territories was unknown and the gibbon groups or individuals were generally out of sight while being recorded, we deduced the identity of the tape-recorded individuals from indicators such as position of the singer, simultaneous singing of distinct groups, group composition (e.g., number of singers), or individual vocal characteristics. When in doubt

Table 4.2 The number of song bouts recorded and analyzed at each locality for male and female Kloss's gibbons

	Individual		Song bouts analyzed		Song phrases recorded		Song phrases analyzed	
Location	Female	Male	Female	Male	Female	Male	Female	Male
Central Siberut, Simabuggai	1	1	1	1	7	23	7	20
	2	2	1	1	7	8	7	8
	3	3	1	1	7	8	7	5
	4	4	1	1	5	8	4	8
	5	5	1	1	4	4	4	4
	6	6	1	1	4	6	4	5
	7	7	1	1	5	4	4	4
Southern Siberut, Sikabei	1	1	1	1	6	22	6	21
	2	2	1	1	7	8	6	2
	3	3	1	1	8	2	3	2
	4	4	1	1	5	13	5	9
	5	5	1	1	6	12	6	11
	6	6	1	1	5	5	5	4
	7	7	1	1	9	4	9	4
		8		1		22		19
Sipora, Saureinu	1	1	1	2	9	9	9	6
	2	2	1	1	11	21	11	18
	3	3	1	1	6	19	6	5
	4	4	1	1	6	13	5	13
	5	5	1	1	6	17	6	6
		6		1		9		6
		7		1		8		7
South Pagai, Malakopa	1	1	1	2	10	22	7	21
	2	2	1	1	4	21	3	5
	3	3	1	1	3	10	3	4
	4	4	1	1	7	4	6	4
	5	5	1	1	6	7	4	3
Total	24	27	24	29	153	309	137	224

about whether two recorded songs were produced by the same gibbon or by two distinct gibbons, we excluded the recording of inferior sound quality from the analysis. Table 4.2 lists the number of gibbons recorded at each locality whose recorded songs were found to be suitable for analysis.

Acoustic Analysis

In order to quantify acoustic characteristics of the male and the female phrases, we defined 31 variables with structural parameters consisting of note counts and the frequency or time dimensions (19 for male and 12 for female phrases), which we determined from the sonograms of each phrase. The variables are listed in the Appendix.

Statistical Analysis

All statistical analyses were conducted using the statistical software package SPSS 12.0.1. Data from each female were paired with data from the male that was believed to be of the same group, based on corresponding calling localities. Although there is no guarantee that all pairs were correctly matched, perfect matching is not required to determine the vocal affinities of the four gibbon populations. For three of the 27 study males, songs of the (assumed) female partner could not be recorded in sufficient quality for inclusion in our analyses. Most multivariate statistical analyses cannot be conducted on data sets with a missing value. Therefore, the missing values in the data matrix were replaced by the overall mean for that particular song variable to allow for inclusion of the complete sample (i.e., all 27 assumed gibbon pairs).

Discriminant Function Analysis

We used stepwise discriminant function analysis (DFA) to identify the differences between vocalizations from our four study populations (i.e., central Siberut, southern Siberut, Sipora, and South Pagai). This multivariate method allows the study of group differences with respect to several variables simultaneously. Redundancy among the independent variables is avoided by a tolerance test, which measures the degree of linear association between variables. Variables determined to be redundant are then excluded from the analysis. For the stepwise procedure we determined Wilks' Lambda as the criterion for variable selection. To test the significance of the change in the selection criterion when a variable was entered or removed from the model, we used the probability of *F* with *p-to-enter* = 0.05 and *p-to-remove* = 0.10. This allowed us to screen out variables that were less efficient discriminators and to identify the combination of song features that best discriminated among the study populations. Based on these selected variables, three linear functions (discriminant functions) were formed – one fewer than the number of groups (i.e., study populations). These functions in turn were used for the classification procedure that assigned each gibbon group to its appropriate population (correct assignment) or to another population (incorrect assignment). We used the percentage of correct assignments as an indicator of how reliably a population could be discriminated, and calculated Cohen's κ to test whether the resulting classification significantly differed from chance (Siegel and Castellan 1998). The model derived from this analysis was cross-validated by the *leaving-one-out method* (Norusis 1994). This method involves leaving out each of the cases in turn, calculating the functions based on the remaining *n–1* cases, and then classifying the left-out case.

Multidimensional Scaling

We used multidimensional scaling (MDS) with ALSCAL and Euclidean distances to visualize (and further analyze) the vocal similarities or dissimilarities (distances) between the recorded gibbon groups and populations. Variables were standardized on a scale of 0–1. MDS plots are better suited to visualize multivariate relationships in two-dimensional plots than discriminant functions, because the resulting plots exhibit a much lower degree of distortion (Sneath and Sokol 1973; Manly 1994). Therefore, we used MDS plots in order to estimate "vocal distances" among gibbon populations.

Results

Figures 4.3 and 4.4 show representative sonograms of male trill phrases and female great call phrases, respectively. Calls of two individuals from each locality are shown in order to exemplify the variability occurring among localities. Two calls from one selected gibbon are also included in each figure in order to depict intra-individual variability.

Discriminant Function Analysis

The discriminant function analysis model used 8 out of 31 submitted variables to create three functions. Seven of them describe the male song (Variables 2, 3, 5, 8, 13, 18, 19), and one describes the female song (Variable 31). This subset of variables was most efficient in distinguishing among the songs of the four gibbon populations. The standardized canonical discriminant function

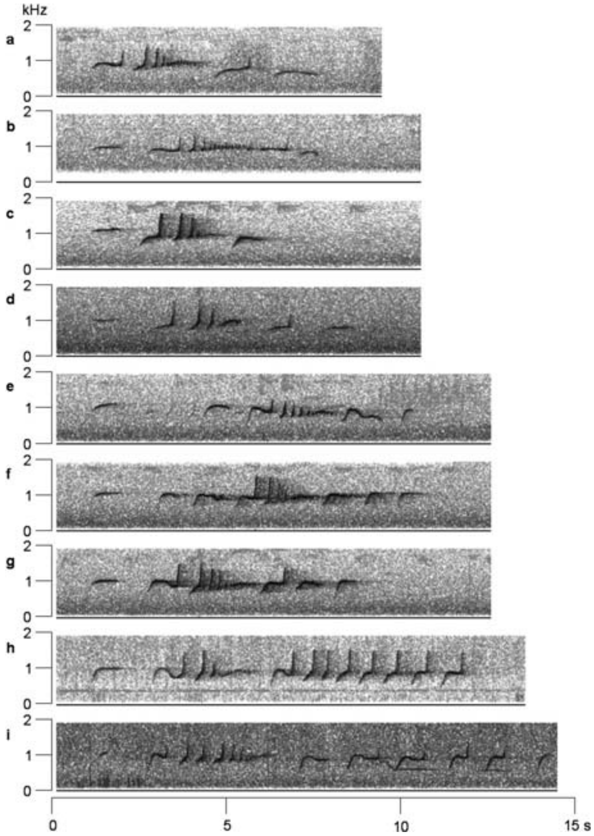

Fig. 4.3 Sonograms of male trill phrases, including two different males from each recording locality: (**a**) and (**b**) central Siberut; (**c**) and (**d**) southern Siberut; (**e–g**) Sipora; and (**h**) and (**i**) South Pagai. Sonograms (**f**) and (**g**) are from the same male in order to show individual variability

coefficients (listed in Table 4.3) of these key variables estimate the relative contribution of a given variable to the three discriminant functions, i.e., the reclassification of gibbon groups into populations. High absolute values represent a large relative contribution.

The discriminant functions represent differing percentages of variance in the populations and, therefore, differing amounts of discriminatory power. The first function normally has the highest discriminatory power and the last function the lowest. This discriminatory strength can be expressed by the percentage of between-group variability attributable to a specific function. Function 1 made the highest contribution to separating the four gibbon populations by explaining 64.5% of the total variability, whereas functions 2 and 3 contributed progressively less (27.6 and 7.8%, respectively).

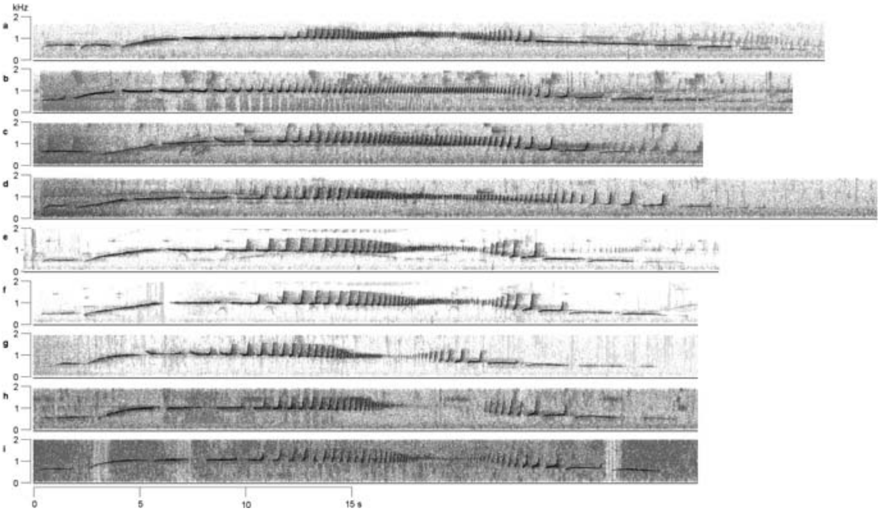

Fig. 4.4 Sonograms of female song phrases, including two different females from each recording locality: (**a**) and (**b**) central Siberut; (**c**) and (**d**) southern Siberut; (**e–g**) Sipora; and (**h**) and (**i**) South Pagai. Sonograms (**e**) and (**f**) are from the same female in order to show individual variability

Table 4.3 Standardized canonical discriminant function coefficients

		Function		
Variable number	Song variable	1	2	3
2	Number of male phrase notes	−2.741	0.347	−0.212
3	Minimum frequency of male phrase	−0.927	0.986	0.507
5	Number of male pre-trill notes	1.514	−0.983	−0.500
8	Maximum frequency of male pre-trill	2.589	0.241	−0.297
13	Minimum frequency of male trill	−1.635	1.167	0.271
18	Minimum frequency of male post-trill	2.361	−1.347	−0.643
19	Maximum frequency of male post-trill	0.266	−0.441	1.055
31	Notes/second in female trill	−1.051	0.186	−0.177

Figure 4.5 is a two-dimensional plot of all gibbon groups according to their discriminant scores for the first and the second discriminant functions and illustrates the degree of separation among the overall mean scores for each gibbon population. The discriminant function 1 mainly contributes to separating the Southern Siberut and Sipora populations from the Central Siberut and South Pagai populations (it also discriminates fairly well between the latter two populations), whereas discriminant function 2 elucidates differences between the population from Sipora and all other populations. Clearly, the separation between Siberut and the other islands is less pronounced than the separation between Southern Siberut and Sipora on

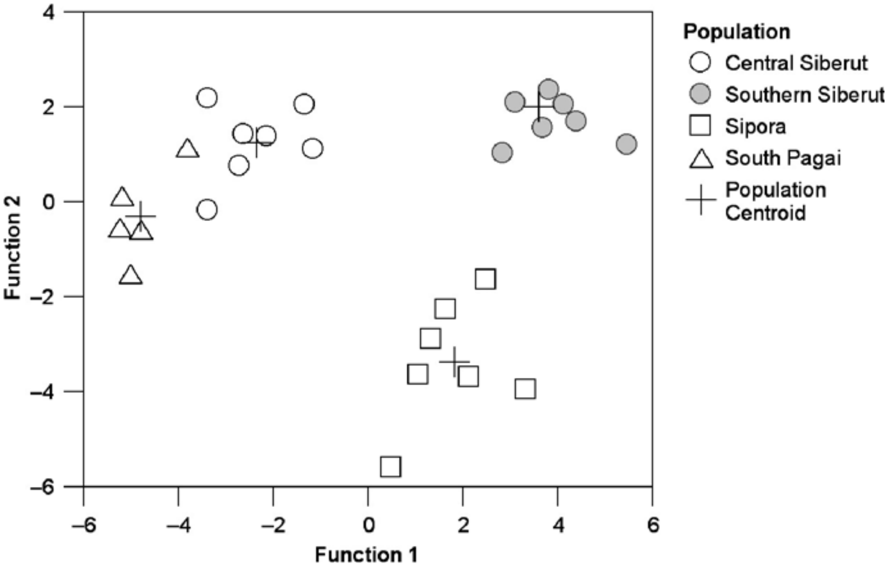

Fig. 4.5 Discriminant scores (*dot symbols*) of all gibbon groups. Different populations are identified with different symbol shapes. *Crosses* indicate population centroids

one hand and Central Siberut and South Pagai on the other. In addition, the two populations from Siberut appear to differ more from each other than the two islands Sipora and South Pagai.

The results of the reclassification procedure are shown in Table 4.4. All gibbon groups (100%) were correctly assigned to their population prior to cross-validation, a result that differed significantly from chance (Cohen's $\kappa = 1.000$, $p < 0.001$). The results of our multivariate analysis of vocal characteristics show that local gibbon populations have their own vocal "identities" and can clearly be distinguished from each other.

Classifications were cross-validated using the "leave-one-out" method, which involves taking each single observation in turn (e.g., song bout or individual) and using this to validate the models derived from the rest of the sample. This process greatly improves the accuracy of the classifications, making for a more realistic result. In the cross-validated classification, 85.2% of groups were correctly assigned, which is 14.8% lower than for the original classification.

The accuracy of classification of gibbon groups to populations ranged from 80% for the South Pagai population to 87.5% for the population from southern Siberut. Incorrectly classified groups originally from central Siberut were assigned to South Pagai, and all incorrectly classified groups from other populations were assigned to central Siberut. Despite the lower classification accuracy in the cross-validation, the classification results still differed significantly from chance (Cohen's $\kappa = 0.801$, $p < 0.001$).

Table 4.4 Classification results of discriminant analysis using all song material (male and female phrases)[a]

	Population	Predicted groups assigned to population				Total number of pairs
		Simabuggai	Sikabei	Saureinu	S. Pagai	
Original classification	Simabuggai	7	0	0	0	7
	Sikabei	0	8	0	0	8
	Saureinu	0	0	7	0	7
	S. Pagai	0	0	0	5	5
%[b]	Simabuggai	100.0	0.0	0.0	0.0	100.0
	Sikabei	0.0	100.0	0.0	0.0	100.0
	Saureinu	0.0	0.0	100.0	0.0	100.0
	S. Pagai	0.0	0.0	0.0	100.0	100.0
Cross-validated classification	Simabuggai	6	0	0	1	7
	Sikabei	1	7	0	0	8
	Saureinu	1	0	6	0	7
	S. Pagai	1	0	0	4	5
%[c]	Simabuggai	85.7	0.0	0.0	14.3	100.0
	Sikabei	12.5	87.5	0.0	0.0	100.0
	Saureinu	14.3	0.0	85.7	0.0	100.0
	S. Pagai	20.0	0.0	0.0	80.0	100.0

[a] The original classification was obtained when groups were classified by the functions derived from all groups (*n*). In the cross-validation, each group was classified by the functions derived from all groups other than that group (*n*–1).

[b] 100.0% of original grouped cases correctly classified.

[c] 85.2% of cross-validated grouped cases correctly classified.

Multidimensional Scaling

Figure 4.6 shows a two-dimensional representation of the vocal similarities among the recorded gibbon groups resulting from the MDS procedure (Stress = 0.266). Points that are close together represent gibbon groups that exhibit strong vocal similarity, and large distances on the map indicate gibbon groups that exhibit strong vocal dissimilarity. The position of the population centroids and the amount of overlap among the population polygons represent the degree of similarity among the four study populations. The plot demonstrates that distances between the two populations on the same island (Central and Southern Siberut) are equivalent to or exceed distances between the islands (Siberut, Sipora, South Pagai). The two southern islands overlap with each other to a greater degree than they overlap with the two Siberut populations, an observation that is strongly supported by the position of the southern island populations' centroids.

Vocal Versus Geographic Distance

Geographic distance was measured as the minimum distance between the coordinates of the recording sites. The position of each population was

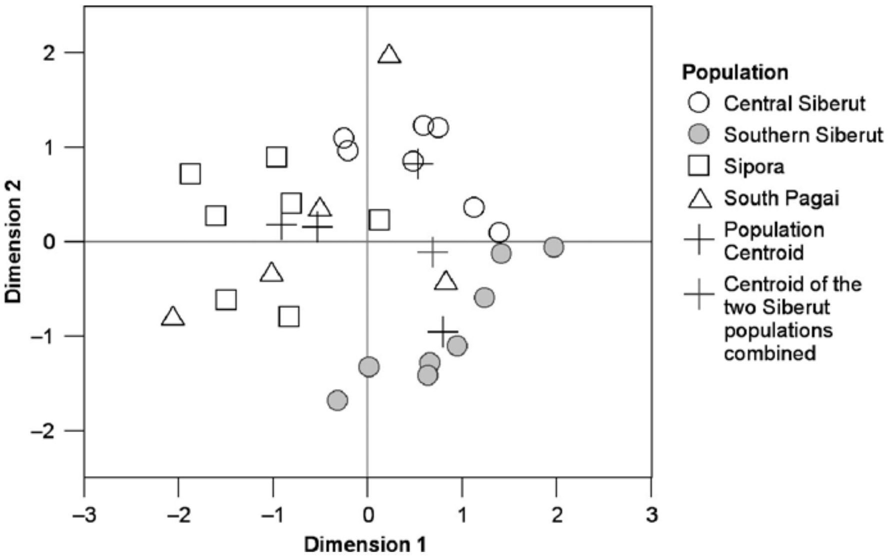

Fig. 4.6 Two-dimensional display representing similarity, as determined by multidimensional scaling (MDS). *Dot symbols* represent individual gibbon groups. Different populations are identified with different symbol shapes. *Crosses* indicate population centroids

represented with the coordinates of one particular recording position. The small distances between the recording positions used when recording gibbon groups in the same population were disregarded. Vocal distance between gibbon populations was measured as the distance between the respective centroids of these populations on the plot of the MDS analysis (Fig. 4.6). No significant correlation was found between geographic and vocal distances (Pearson Correlation: $n = 6, r = -0.402, p = 0.429$) (Fig. 4.7).

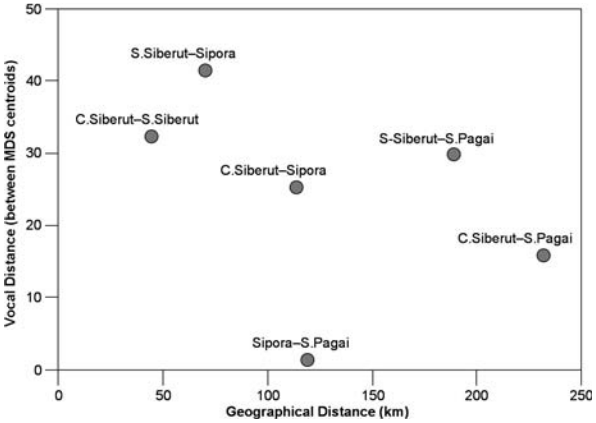

Fig. 4.7 Vocal distance (corresponding to distances between MDS centroids in Fig. 4.6) versus geographic distance (km) between all study populations

Discussion

Both female and male calls of Kloss's gibbons differ among localities and can be correctly assigned to their locality approximately 85% of the time using discriminant analysis. This result is similar to those of studies on Cambodian crested gibbons (genus *Nomascus*) and female Javan silvery gibbons, which were also able to discriminate among localities (Konrad and Geissmann 2006; Dallmann and Geissmann this volume).

In the other primates endemic to the Mentawai Islands (*Macaca pagensis*, *Presbytis potenziani*, and *Simias concolor*), the population of the northernmost island, Siberut, appears to differ from the populations of the other three islands in fur coloration and in DNA sequences, although the latter have been less studied. Based on these differences, distinct subspecies of *Simias concolor* and *Presbytis potenziani* (Groves 2001; Brandon-Jones et al. 2004) and distinct species of *Macaca* (Kitchener and Groves 2002; Roos et al. 2003) are recognized: one taxon for the Siberut population (*Macaca siberu*; *Simias concolor siberu*; *Presbytis potenziani siberu*) and one taxon for populations of the more southern islands (*Macaca pagensis*; *Simias concolor concolor*; *Presbytis potenziani potenziani*) of the Mentawais.

The Kloss's gibbon is also endemic to the Mentawai Islands, but so far, no taxonomic split has been proposed for this species. This is surprising, as water courses and sea channels are thought to represent a more substantial barrier for gibbons than macaques and leaf monkeys.

The results of this study suggest that vocal differences among Kloss's gibbon populations exhibit no apparent relationship to geographic distances. This is not surprising as some of the islands are a further geographic distance from other landmasses than others. However, a larger sample of populations would be required to explore the relationship between geographic and vocal distances fully.

In contrast to expectations, however, vocal differences between the two localities on Siberut are at least as pronounced as those between Siberut and localities on other islands. Affinities among the populations are of comparable degrees and, therefore, recognition of a distinct Siberut subspecies is not warranted. The conclusion drawn from our vocal data is supported by results from a study of the molecular diversity in wild Kloss's gibbons (Whittaker this volume). In contrast, this finding does not reflect the patterns observed in other Mentawai primates. We propose three possible explanations for why the situation in Kloss's gibbons may differ from that observed in the sympatric macaques and leaf monkeys.

(1) Gibbons may have spread across the Mentawai islands at a considerably later date than did other nonhuman primates. During the mid-Pleistocene glaciations, sea levels fluctuated dramatically (Batchelor 1979), repeatedly dropping to 230 m below current levels, exposing the whole Sundaland area as a connected land mass, and then rising again to submerge low-lying areas,

fragmenting the land mass into islands. Whereas the sea channels between the individual Mentawai islands are less than 50 m deep, the Mentawai Islands are separated from Sumatra by deep basins reaching depths of up to 1500 m (Karig et al. 1980; Moore et al. 1980; Whitten et al. 2000).

The Batu Islands to the north of the Mentawai chain provide a link with the Sunda shelf and Sumatra via a periodically exposed land bridge (Batchelor 1979; Dring et al. 1990). Any moderately forested land bridge linking the Mentawais to Sumatra may initially have allowed leaf monkeys and macaques to populate the Mentawai Islands, whereas gibbons would have required a closed-canopy forest for dispersal to the Mentawais. A subsequent rise in sea levels may have resulted in the isolation of the whole island chain from Sumatra and, later, in isolation of Siberut from the remaining islands. This separation may have promoted the evolution of endemic species of these Mentawai primates and the divergence of the southern island and Siberut populations.

Kloss's gibbons may have colonized the Mentawais during a more recent glacial period, and the subsequent isolation of the individual islands by rising sea levels may not have been of sufficient duration to produce taxonomic distinctiveness within the species.

Batchelor (1979) and Milliman and Emory (1968) estimate that the Mentawai Islands were last separated from Sumatra 1.0–0.5 million years ago, whereas the most recent separation among the Mentawai Islands may be as recent as 7000 years (Whittaker 2005a). This very recent divergence date is consistent with the lack of vocal or genetic divergence within the Kloss's gibbon species. However, if these estimates are correct, then the short time frame available for within-Mentawai divergence also raises questions about the validity of taxonomic divisions for the sympatric Mentawai monkeys.

(2) It is also possible that the taxonomic distinctiveness of the three species of Mentawai monkeys on Siberut and the southern islands has been overestimated. The proposed classification for the simakobu subspecific classifications is based on a very small sample size (four individuals from Sipora, three individuals from Siberut), and the main feature purported to establish the distinctiveness of the Siberut subspecies (*Simias concolor siberu*) is its being, "...like *S. concolor* from Sipora island, but darker, especially on the rump" (Chasen and Kloss 1927). The authors acknowledge that the Siberut female specimen cannot be distinguished from the Sipora specimens.

Roos et al. (2003) propose classifying Mentawai macaques as two distinct species: one on Siberut and one on Sipora and the Pagais, as a result of morphological and genetic analyses (Kitchener and Groves 2002; Roos et al. 2003). The genetic analysis utilized mtDNA loci. Use of mtDNA is problematic in phylogeographic analyses involving macaques due to female philopatry (Evans et al. 2003). However, only 5 of the 12 "Siberut" specimens were actually sampled on Siberut. The rest of the sample was collected from the Bukittinggi Zoo and

Padang (presumably from pets), on the Sumatran mainland (Whittaker 2005a). As accurate records of origin are not generally kept for pets, and the dubious conditions in the Bukittinggi Zoo (pers. obs.) raise questions about animal husbandry practices there, the provenance of these animals must be described as questionable. Furthermore, Roos et al. (2003) describe the Siberut macaque *(Macaca siberu)* as being more genetically similar to the Sumatran pig-tailed macaque *(Macaca nemestrina),* which suggests the possibility that the origin of the "Siberut" sample found on mainland Sumatra may not be the Mentawais. Alternatively, genetic mixing between captive macaques may have occurred, thus obscuring their distinctiveness. Morphological evidence, although compelling, must come with a caveat because it is based on a small sample size (Kitchener and Groves 2002). Therefore, ESUs for all Mentawai monkey species need further research to substantiate proposed taxonomic distinctiveness of the Siberut and southern taxa of the Mentawai monkey species.

(3) The estimated generation time for captive gibbons (mean 7.82 years, range 5.18–9.33 years) is almost twice as long as that of macaques (mean 4.57 years, range 3–5.54 years) and Asian colobines (mean 3.97 years, range 3.42–4.58 years) (Harvey et al. 1987; Ross 1992; Kappeler and Pereira 2003). Field studies are rarely of sufficient duration to document even a single generation span, much less produce a meaningful average value for a gibbon taxon. But if we accept the captive data as a first approximation, they suggest that under genetic isolation, macaque and Asian leaf monkey populations should diverge genetically almost twice as fast as gibbon populations.

The study was affected by a number of methodological limitations. For example, we collected a smaller sample of recordings from females than expected, due to a lower-than-expected female calling rate. Whitten (1982) reported that females sing every 3–4 days, whereas during the sampling period, females sang less frequently (pers. obs.). Future research should take this unpredictability in singing behavior into account.

It is also possible that increasing the number of variables measured would reveal more differences or similarities between populations. In particular, future research should have an increased focus on the female song. The use of a larger sample would also be helpful, because it is clear that vocal diversity is high within this species (Keith 2005; Waller 2005). In addition, the exclusion of young adults might reduce the effects of developmental variables (or "practice") on vocal characteristics.

Finally, although previous studies suggest that robust species and subspecies-level taxonomic inferences may be drawn from vocal data (Geissmann 1984, 1993, 1995; Zimmermann et al. 2000; Geissmann 2002a; Merker and Groves 2006), it is unclear to what extent vocal variation at the population level is attributable to the genetic signal.

To summarize, the results of our study on vocal diversity of Kloss's gibbons produced conclusions identical to those of an independent parallel study on molecular diversity of the same species (Whittaker this volume). Although the analysis of DNA produces more characters (base-pairs) than vocalizations for analysis and involves characters that are related to genetic evolution in a more direct manner, vocal data have certain benefits. Vocal data can be collected without approaching or directly observing the calling gibbons, and thus may impose less stress on unhabituated study animals. In addition, vocal data is cheaper to analyze than genetic data. Future studies of gibbon systematics could, therefore, benefit from inclusion of vocal data. This study also demonstrates the validity of using discriminant function analysis as a means for determining the origin of individual Kloss's gibbons based on their vocal characteristics, and suggests that this method has the potential for use in studies of other gibbon species.

Our results suggest that the Kloss's gibbon can be treated as a single Evolutionary Significant Unit (ESU). However, management strategies must also account for high levels of habitat fragmentation and the possibility of incipient divergence on the different islands. Treatment of the species as just one ESU may lead managers to focus on the larger, presumably more viable, Siberut population at the cost of the other island populations.

Without conservation throughout the Mentawai Islands, the Kloss's gibbon will lose genetic variation and subsequently reduce its adaptation potential. This genetic depletion restricts a taxon's ability to cope with future challenges such as climate change. Range shifts to track changing environmental conditions are not generally possible for island species (Mimura et al. 2007), making genetic adaptation the only response available to the Kloss's gibbon. Therefore, we implore the relevant authorities and conservation agencies to strive to maintain the genetic diversity of the Kloss's gibbon.

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Appendix: List of Vocal Variables

Trill Phrase of the Male

1. Duration of entire male phrase (s).
2. Total number of notes in male phrase.
3. Minimum frequency of phrase (Hz).
4. Maximum frequency of phrase (Hz).
5. Number of pre-trill notes.
6. Duration of pre-trill part of male phrase (s).
7. Minimum frequency of pre-trill notes (Hz).
8. Maximum frequency of pre-trill notes (Hz).

9. Frequency modulation (from minimum to maximum) from start to end of second note (Hz).
10. Frequency modulation from start to end of third note (Hz).
11. Number of trill notes.
12. Duration of trill (s).
13. Minimum frequency of trill (Hz).
14. Maximum frequency of trill (Hz).
15. Frequency modulation from start to end of first post-trill note (Hz).
16. Number of post-trill notes.
17. Duration of post-trill part of male phrase (s).
18. Minimum frequency of post-trill notes (Hz).
19. Maximum frequency of post-trill notes (Hz).

Great Call Phrase of the Female

20. Total duration of pre-trill and trill part of female great call (s).
21. Frequency range of pre-trill and trill part of female great call (Hz).
22. Duration of first great call note (s).
23. Frequency modulation from start to end of first great call note (Hz).
24. Duration of second great call note (s).
25. Dominant frequency of second great call note (Hz).
26. Number of pre-trill notes.
27. Duration of pre-trill part of great call (s).
28. Number of pre-trill notes per second.
29. Trill duration (s).
30. Number of trill notes.
31. Number of trill notes per second.

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Chapter 5

Phylogeography of Kloss's Gibbon (*Hylobates Klossii*) Populations and Implications for Conservation Planning in the Mentawai Islands

Danielle J. Whittaker

Introduction

The Kloss's gibbon (*Hylobates klossii*) has long been recognized as distinct among the members of the genus *Hylobates* due to its small size and completely black pelage with no markings. Unlike most other gibbon species, the male and female do not duet; instead, neighboring males chorus before dawn, while the females sing after dawn. The only other gibbon to share these behavioral characteristics is the closely related Javan silvery gibbon (*H. moloch*) (Takacs et al. 2005; Geissmann and Nijman 2006; Whittaker et al. 2007). The Kloss's gibbon is endemic to the Mentawai Islands, located off the west coast of Sumatra in Indonesia, and is endangered as a result of continuing deforestation and hunting (Whittaker 2006). Since the 1970s, researchers have advocated increasing protection of this unusual species (McNeely 1978; World Wildlife Fund 1980; Tenaza 1988; Fuentes 1996/1997; Kobold et al. 2003; Paciulli 2004; Whittaker 2005a, 2006), but conservation planning has suffered from a lack of knowledge about intraspecific variation throughout the Mentawais.

There are four endemic primates in the Mentawai Islands, which have a total landmass of less than 7,000 km^2. The four Mentawai Islands are not connected to neighboring Sumatra: during the Tertiary period, the force of the subduction of the Indian plate under the Sunda plate pushed up this chain of islands from the ocean floor. The Mentawais have long been isolated from mainland Sundaland by the 1,500-m deep Mentawai Basin, except for brief periods when sea levels were at their lowest, the last occurring between one million and 500,000 years ago (Batchelor 1979; Karig et al. 1980; Moore et al. 1980; Whitten et al. 2000). This long history of isolation likely accounts for the islands' high level of endemism: 65% of non-volant mammals in the Mentawai Islands are endemic at the genus or species level (World Wildlife Fund 1980).

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There are four Mentawai Islands: Siberut, Sipora, North Pagai, and South Pagai. The largest and northernmost island of Siberut is home to the only protected area in the Mentawais, Siberut National Park, which at 1,926 km^2 comprises nearly half of the island. Logging concessions and oil palm plantations make up much of the area outside the park (Whittaker 2005b, 2006). Sipora is the most developed of the four islands and is home to the regency capital, Tua Pejat. Only 10–15% of this island's forest cover remains (Fuentes 1996/1997). Much of the interior of the Pagai Islands is a large logging concession (83,330 ha) that has been controlled since 1971 by PT Minas Pagai Lumber Corporation; this company practices selective logging and replanting, and many patches of forest appear to be suitable habitat for primates (Paciulli 2004; Whittaker 2005a, b, 2006).

The other three primate species in the Mentawai Islands are the simakobu monkey (*Simias concolor*), the Mentawai langur (*Presbytis potenziani*), and the Mentawai macaque (*Macaca pagensis*). Each of these species currently includes two different subspecies: one subspecies in Siberut (*S. concolor siberu*, *P. potenziani siberu*, and *M. pagensis siberu*) and one in the three southern islands (*S. c. concolor*, *P. p. potenziani*, and *M. p. pagensis*). Researchers have based these classifications primarily on pelage differences, as all three Siberut populations have darker coloration (Chasen and Kloss 1927; Whitten and Whitten 1982). Recent studies of morphological differences (Kitchener and Groves 2002) and mitochondrial variation (Roos et al. 2003) in Mentawai macaques suggest that the two populations are actually different species, *M. pagensis* in the south and *M. siberu* in Siberut. However, the level of genetic differentiation observed (5.9%) is not dramatically different from the range of estimated mtDNA sequence divergence found between rhesus macaque populations (0.2–4.5%), even without physical isolation (Melnick and Hoelzer 1992).

Kloss's gibbon populations have no subspecific designations, because they exhibit no obvious phenotypic variation: all Kloss's gibbons have completely black fur with no markings. Furthermore, to date researchers have conducted behavioral studies on the island of Siberut only, so behavioral differences among populations are unknown. However, the four Mentawai primate species presumably share the same biogeographic history, and thus distribution of genetic variation in Kloss's gibbons should follow the same pattern as morphological variation in the Mentawai monkeys. This study tests the hypothesis that the Siberut population of Kloss's gibbons is genetically distinct from the southern population on Sipora and the Pagais.

All four species of Mentawai primates are threatened by legal and illegal logging, hunting for meat, and the illegal pet trade. As noted above, the only protected area in the Mentawai Islands is Siberut National Park. In recognition of the possibly unique subspecies of primates living in the southern islands, researchers have suggested a few sites in the Pagai Islands for protected area status: Sinakak islet in South Pagai, and Betumonga in North Pagai (Tenaza 1987, 1988; Fuentes 1996/1997; Paciulli 2004). Unfortunately, both areas have been logged in recent years.

Conservation planning aims to preserve genetic diversity within a species. If genetically distinct units are identified within a species, ideally conservation strategies should consider each unit. "Evolutionarily Significant Units" (ESUs) are defined as genetically, ecologically, or morphologically distinct lineages (Vogler and DeSalle 1994). In this study, I test the hypothesis that populations of *Hylobates klossii* have diverged into multiple ESUs. The results are applicable to conservation planning: if there are multiple units within the species, multiple conservation areas should be set aside for their protection.

Methods

Sampling

I visited the Mentawai Islands from January to May 2001 and August to December 2003 and non-invasively collected fecal samples from 31 wild gibbon groups at five sites on all four islands (Fig. 5.1, Table 5.1). I stored the fecal

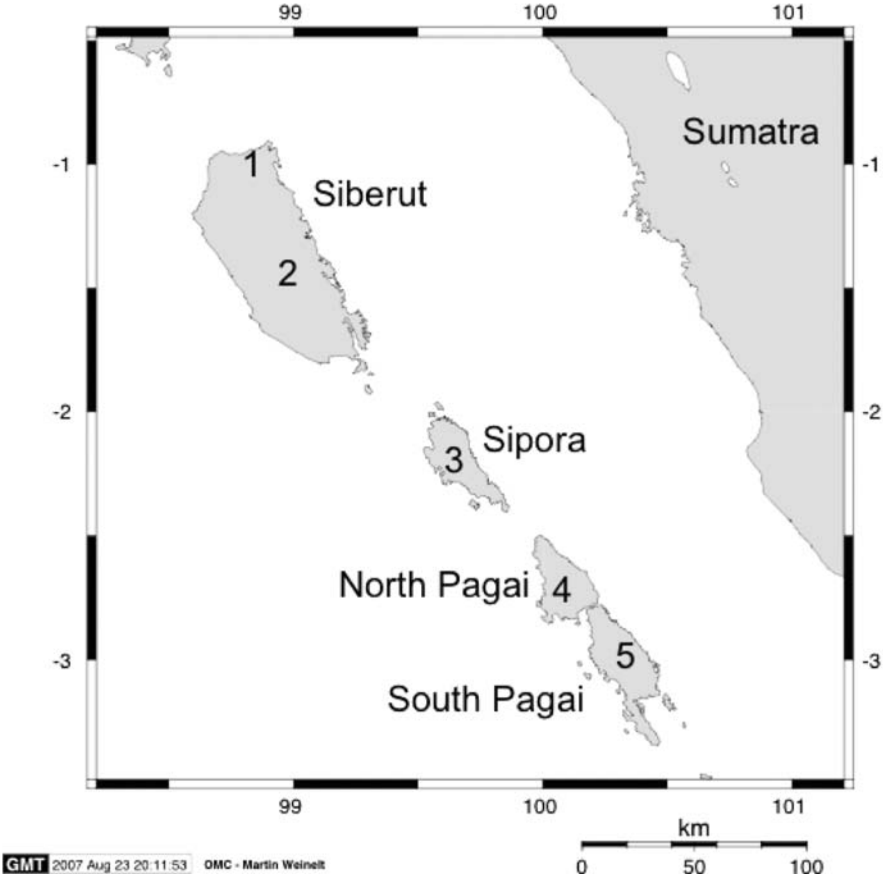

Fig. 5.1 Map of the Mentawai Islands, showing sampling sites (created using online map creation at http://www.aquarius.ifm-geomar.de/). Numbers correspond to sites listed in Table 5.1

Table 5.1 List of samples collected and sequenced

Site	Sample code	Groups sampled	Individuals sequenced
1. Peleonan forest, North Siberut	PL, CA	8	3
2. Simabuggai, Siberut National Park	SB	5	4
3. Saureinu, Sipora	SR	2	2
4. Betumonga and Muntei, North Pagai	NP	8	5
5. South Pagai	SP	8	7
Total		**31**	**21**

samples at room temperature in RNA*later*® (Ambion) until I returned to the United States, where I stored them at –20°C. I extracted DNA from these samples using Qiagen Stool Kits® and the manufacturer-supplied protocols.

DNA Sequencing

Rapidly evolving loci are necessary to examine intraspecific relationships. I chose the hypervariable region I (HV-I) of the mitochondrial D-loop, which evolves more quickly than any other part of the primate mitochondrial genome (Avise 2000). Researchers have used this locus to examine genetic variation within *H. moloch* (Andayani et al. 2001) and *H. lar* (Woodruff et al. 2005). I amplified and sequenced the HV-I region of the D-loop as described in Whittaker (2005b) and Whittaker et al. (2007), using the following gibbon-specific primers: GIBDLF3 (5′ CTT CAC CCT CAG CAC CCA AAG C 3′) and GIBDLR4 (5′ GGG TGA TAG GCC TGT GAT C 3′) (Andayani et al. 2001), which correspond to the human primers L15996 (Vigilant et al. 1989) and H16498 (Kocher et al. 1989). I deposited all sequences in GenBank (accession numbers EF363486 through EF363506).

Phylogenetic Inference

I examined phylogenetic relationships among the populations using the neighbor-joining algorithm and bootstrap replications in PAUP* 4.0 (Swofford 2002). I chose neighbor-joining for this study because it can tolerate high levels of saturation as might be expected in a quickly mutating locus. This algorithm groups taxa based on overall genetic distance, rather than individual evolutionary changes (Saitou and Nei 1987). I used the distance calculated by the evolutionary model that best fit the data, as chosen by the program MODELTEST 3.6 (Posada and Crandall 1998).

I also conducted a Bayesian analysis using Mr. Bayes 3.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). A Bayesian analysis uses

Markov Chain Monte Carlo simulations to consider various genealogies and calculate the posterior probability of each tree topology, producing a credibility score for each node based on a likelihood model. I used MODELTEST to choose the parameters for this likelihood model.

I used sequences from *H. pileatus* and *Hoolock hoolock* as outgroups for the analysis (Roos and Geissmann 2001; Whittaker et al. 2007). Several recent analyses have suggested that *Hoolock* is likely basal to the hylobatid radiation, and that *H. pileatus* is the basal taxon of the genus *Hylobates* (Zehr 1999; Takacs et al. 2005; Whittaker et al. 2007).

Phylogenetic Species Concept

In contrast to the Biological Species Concept (BSC), which defines a species as a group of actually or potentially interbreeding populations, a concept that can be difficult to operationalize, the Phylogenetic Species Concept (PSC) focuses on how to recognize a species and defines a species as the smallest diagnosable unit on the basis of fixed, or reciprocally monophyletic, character states (Platnick 1979; Cracraft 1983; Nixon and Wheeler 1990). Under the BSC, geographically isolated populations that display phenotypic differentiation are often considered subspecies. No criteria are established that specify what level of differentiation is sufficient to designate populations as subspecies, and some systematists have argued that this largely subjective system should either be abandoned entirely or replaced with a more careful system of defining "evolutionarily significant units" (ESUs), particularly for the purpose of making conservation decisions (Ryder 1986; Vogler and DeSalle 1994). In practice, ESUs are defined as genetically, ecologically, or morphologically distinct lineages; this definition also meets the requirements for the PSC, and the PSC can be used to identify populations for conservation. In the present study, I focus on identifying whether populations are genetically distinct under the PSC.

Population aggregation analysis (PAA) is a character-based method that identifies genetically distinct lineages by analyzing patterns of distribution of genetic variation. Under this method, one creates a profile for each population describing the presence or absence of each attribute in each individual. Only attributes that are fixed in populations are informative for this analysis. The analysis then groups together populations based on these attributes. After successive rounds of grouping local populations together, the result is either one group with no diagnosable units or two or more distinct populations that under the PSC could be considered species (Davis and Nixon 1992). The units identified by PAA have likely been isolated long enough that different characters have become fixed in each population. Thus, the identification of these units suggests a historical absence of gene flow between the populations (Davis and Nixon 1992; Goldstein et al. 2000). I conducted a PAA using MacClade 4.0 (Maddison and Maddison 2000).

Population Genetics

To examine patterns of current gene flow, I conducted an analysis of molecular variance (AMOVA) at three levels: within local populations, among local populations within island groups, and among island groups of populations (Excoffier et al. 1992). I defined the island groups as: (1) Siberut, including North Siberut and Siberut National Park; (2) Sipora; and (3) the Pagais, including North and South Pagai. From these data, I also calculated F_{ST}, which describes the proportion of total genetic variance accounted for by variation among populations. I used Arlequin 2.0 (Schneider et al. 2000) for both of these analyses.

Results

I sampled a total of 31 gibbon groups. Because of their preferred height in the canopy, gibbons' feces are usually splattered by the time they reach the ground. DNA is present in the epithelial cells shed from the lining of the intestinal tract, and these cells are found on the outer surface of the fecal bolus. However, many of the gibbon samples had been badly splattered and the portions collected may not have had enough epithelial cells present to give a sufficient amount of gibbon DNA. I successfully sequenced only 21 individuals, yielding a 479 base-pair region of the mitochondrial D-loop. In this sample, 15 haplotypes were found, with 37 polymorphic sites. Of these, 35 were transitions, one a transversion, and one an insertion/deletion.

According to MODELTEST, the nucleotide substitution patterns observed in the data correspond to the HKY + G model (Hasegawa et al. 1985). This model assumes that transitions are more likely than transversions, that purine and pyrimidine transitions are equally likely, and that the substitution rate is heterogeneous across sites, following a gamma distribution (shape parameter for this dataset: 0.3740). I constructed the neighbor-joining tree using the HKY85 distance measure, which in addition to total nucleotide differences incorporates base frequencies and treats transitions and transversions differently (Hasegawa et al. 1985). This tree (Fig. 5.2) shows no resolution and no separation of populations, with individuals from Siberut and the Pagais found throughout the tree.

I ran the Bayesian analysis with four chains for 300,000 generations, sampling every 100th generation, with a burn-in percentage of 25% or 750 samples. The Bayesian tree, like the neighbor-joining tree, also fails to separate different populations into different clades (Fig. 5.3).

Table 5.2 presents pairwise nucleotide sequence divergence estimates, using both uncorrected p distance (the total number of nucleotide differences divided by the total number of sites) and the HKY85 distance (Hasegawa et al. 1985; Swofford et al. 1996). Within-population divergences (p) range from 0% to

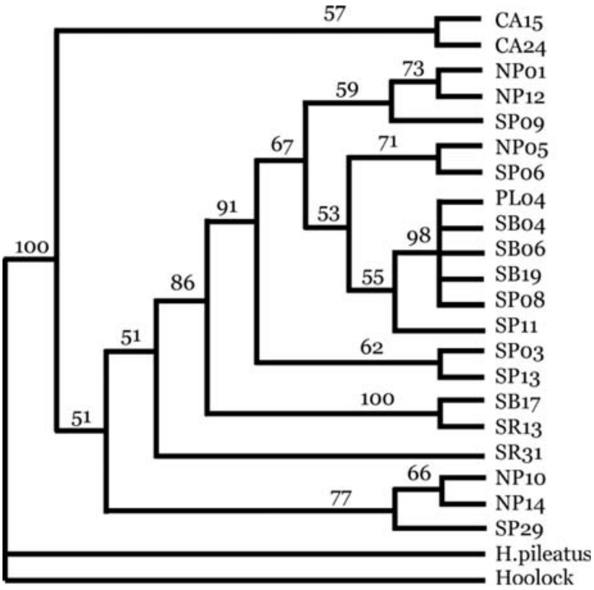

Fig. 5.2 Neighbor-joining tree, with 1,000 bootstrap replications

4.3% (HKY distance: 0–5.3%), while between-population divergences range from 0% to 4.5% (HKY: 0–5.8%).

In the PAA, I examined polymorphic sites to determine whether populations display any fixed character differences. Table 5.3 shows the 37 polymorphic

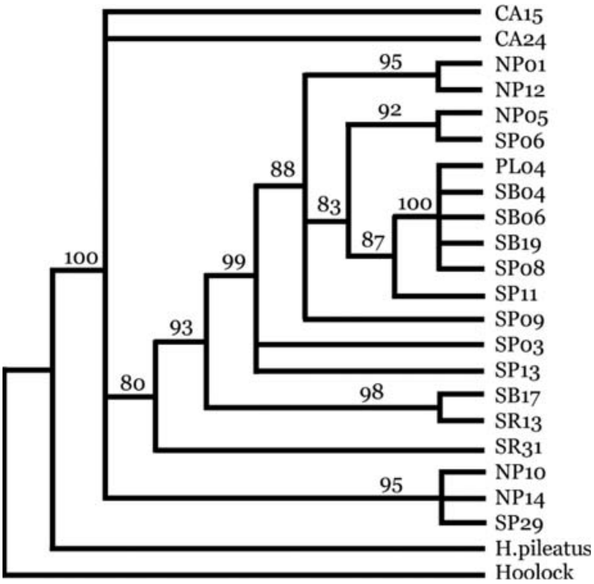

Fig. 5.3 Bayesian tree, showing clade credibility values

Table 5.2 Molecular pairwise distance matrix. Figures above diagonal are uncorrected *p* distance; those below the diagonal are HKY85 distances. Within-population distances are highlighted for the five populations (from left to right: North Siberut, Siberut National Park, Sipora, North Pagai, and South Pagai)

	CA15	CA24	PL04	SB04	SB06	SB17	SB19	SR13	SR31	NP01	NP05	NP10	NP12	NP14	SP03	SP06	SP08	SP09	SP11	SP13	SP29	pileatus	Hoolock
CA15		0.0082	0.0389	0.0389	0.0389	0.0327	0.0389	0.0286	0.0082	0.0368	0.0389	0.0184	0.0368	0.0184	0.0286	0.0368	0.0389	0.0348	0.0409	0.0307	0.0204	0.1432	0.1892
CA24	0.0085		0.0429	0.0429	0.0429	0.0327	0.0429	0.0286	0.0123	0.0409	0.0429	0.0184	0.0409	0.0184	0.0327	0.0409	0.0429	0.0389	0.0450	0.0348	0.0204	0.1453	0.1954
PL04	0.0476	0.0539		0.0000	0.0000	0.0348	0.0000	0.0307	0.0307	0.0143	0.0164	0.0368	0.0143	0.0368	0.0184	0.0143	0.0000	0.0123	0.0102	0.0164	0.0348	0.1657	0.1932
SB04	0.0476	0.0539	0.0000		0.0000	0.0348	0.0000	0.0307	0.0307	0.0143	0.0164	0.0368	0.0143	0.0368	0.0184	0.0143	0.0000	0.0123	0.0102	0.0164	0.0348	0.1657	0.1932
SB06	0.0476	0.0539	0.0000	0.0000		0.0348	0.0000	0.0307	0.0307	0.0143	0.0164	0.0368	0.0143	0.0368	0.0184	0.0143	0.0000	0.0123	0.0102	0.0164	0.0348	0.1657	0.1932
SB17	0.0391	0.0391	0.0416	0.0416	0.0416		0.0348	0.0082	0.0245	0.0286	0.0348	0.0307	0.0286	0.0307	0.0286	0.0327	0.0348	0.0266	0.0328	0.0266	0.0286	0.1576	0.1931
SB19	0.0476	0.0539	0.0000	0.0000	0.0000	0.0416		0.0307	0.0307	0.0143	0.0164	0.0368	0.0143	0.0368	0.0184	0.0143	0.0000	0.0123	0.0102	0.0164	0.0348	0.1657	0.1932
SR13	0.0334	0.0334	0.0358	0.0358	0.0358	0.0085	0.0358		0.0204	0.0245	0.0307	0.0266	0.0245	0.0266	0.0245	0.0286	0.0307	0.0225	0.0287	0.0225	0.0245	0.1535	0.1891
SR31	0.0085	0.0131	0.0358	0.0358	0.0358	0.0280	0.0358	0.0228		0.0286	0.0348	0.0184	0.0286	0.0184	0.0204	0.0327	0.0307	0.0266	0.0328	0.0225	0.0204	0.1473	0.1933
NP01	0.0450	0.0512	0.0153	0.0153	0.0153	0.0334	0.0153	0.0280	0.0334		0.0102	0.0389	0.0000	0.0389	0.0082	0.0082	0.0143	0.0020	0.0082	0.0061	0.0368	0.1596	0.1933
NP05	0.0481	0.0545	0.0177	0.0177	0.0177	0.0420	0.0177	0.0362	0.0420	0.0108		0.0368	0.0102	0.0368	0.0143	0.0061	0.0164	0.0082	0.0103	0.0123	0.0348	0.1576	0.1891
NP10	0.0203	0.0203	0.0445	0.0445	0.0445	0.0363	0.0445	0.0307	0.0203	0.0481	0.0451		0.0389	0.0000	0.0307	0.0389	0.0368	0.0368	0.0389	0.0327	0.0020	0.1433	0.1972
NP12	0.0450	0.0512	0.0153	0.0153	0.0153	0.0334	0.0153	0.0280	0.0334	0.0000	0.0108	0.0481		0.0389	0.0082	0.0082	0.0143	0.0020	0.0082	0.0061	0.0368	0.1596	0.1933
NP14	0.0203	0.0203	0.0445	0.0445	0.0445	0.0363	0.0445	0.0307	0.0203	0.0481	0.0451	0.0000	0.0481		0.0307	0.0389	0.0368	0.0368	0.0389	0.0327	0.0020	0.1433	0.1972
SP03	0.0334	0.0391	0.0201	0.0201	0.0201	0.0334	0.0201	0.0280	0.0228	0.0085	0.0154	0.0362	0.0085	0.0362		0.0123	0.0184	0.0061	0.0123	0.0020	0.0286	0.1555	0.1933
SP06	0.0450	0.0512	0.0153	0.0153	0.0153	0.0391	0.0153	0.0334	0.0391	0.0085	0.0063	0.0481	0.0085	0.0481	0.0131		0.0143	0.0061	0.0082	0.0102	0.0368	0.1596	0.1892
SP08	0.0476	0.0539	0.0000	0.0000	0.0000	0.0416	0.0000	0.0358	0.0358	0.0153	0.0177	0.0445	0.0153	0.0445	0.0201	0.0153		0.0123	0.0102	0.0164	0.0348	0.1657	0.1932
SP09	0.0420	0.0481	0.0130	0.0130	0.0130	0.0307	0.0130	0.0254	0.0307	0.0021	0.0085	0.0450	0.0021	0.0450	0.0063	0.0063	0.0130		0.0062	0.0041	0.0348	0.1575	0.1913
SP11	0.0513	0.0579	0.0107	0.0107	0.0107	0.0391	0.0107	0.0335	0.0391	0.0086	0.0108	0.0482	0.0086	0.0482	0.0131	0.0086	0.0107	0.0064		0.0103	0.0369	0.1638	0.1934
SP13	0.0362	0.0420	0.0177	0.0177	0.0177	0.0307	0.0177	0.0254	0.0254	0.0063	0.0131	0.0391	0.0063	0.0391	0.0021	0.0108	0.0177	0.0042	0.0108		0.0307	0.1575	0.1913
SP29	0.0228	0.0228	0.0416	0.0416	0.0416	0.0335	0.0416	0.0280	0.0228	0.0450	0.0421	0.0021	0.0450	0.0021	0.0334	0.0450	0.0416	0.0420	0.0452	0.0362		0.1453	0.1993
Hpileatus	0.3131	0.3231	0.4320	0.4320	0.4320	0.3884	0.4320	0.3653	0.3332	0.3982	0.3874	0.3139	0.3982	0.3139	0.3755	0.3987	0.4320	0.3869	0.4246	0.3869	0.3238		0.2074
Hoolock	0.4061	0.4373	0.4214	0.4214	0.4214	0.4254	0.4214	0.4054	0.4265	0.4246	0.4050	0.4473	0.4246	0.4473	0.4253	0.4050	0.4214	0.4150	0.4257	0.4150	0.4585	0.4979	

Table 5.3 Population Aggregation Analysis of *H. klossii* D-loop sequences, showing only variable sites

	16	17	25	96	113	122	133	140	142	144	145	153	159	161	166	167	170	185	213	221	222	226	253	287	303	304	306	311	329	340	341	357	360	361	366	436	449
PL04	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
CA15	A	G	G	G	C	A	A	A	T	A	C	G	A	A	C	C	A	A	A	C	T	T	A	T	-	C	A	C	A	T	A	G	T	T	C	T	T
CA24	A	G	G	G	C	A	A	A	T	A	C	G	A	A	C	C	A	A	A	T	T	T	A	T	-	C	A	C	A	C	A	G	T	T	C	T	C
SB04	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SB06	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SB17	A	G	A	G	C	A	A	G	C	A	T	A	A	A	C	T	A	A	A	C	C	T	A	C	-	C	A	T	G	C	G	G	C	C	C	C	C
SB19	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SR13	A	G	G	G	C	G	A	A	C	A	T	A	A	A	C	T	A	A	A	C	C	T	A	C	-	C	A	T	G	C	A	G	C	C	C	C	C
SR31	A	G	G	G	C	A	A	A	T	A	C	G	A	A	C	T	A	A	A	C	C	T	A	T	-	C	A	C	A	T	A	G	T	C	C	T	C
NP01	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	G	A	A	C	C	T	G	C	-	C	A	T	A	T	A	A	C	C	T	T	C
NP05	G	G	G	A	T	A	A	A	C	G	T	A	G	A	C	C	A	A	A	C	C	C	G	C	-	C	G	T	A	T	A	A	C	C	T	T	C
NP10	G	A	G	A	C	A	A	A	C	A	C	G	A	A	C	C	A	G	A	C	C	T	A	T	-	C	A	C	A	C	A	G	T	T	C	C	C
NP12	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	G	A	A	C	C	T	G	C	-	C	A	T	A	T	A	A	C	C	T	T	C
NP14	G	A	G	A	C	A	A	A	C	A	C	G	A	A	C	C	A	G	A	C	C	T	A	T	-	C	A	C	A	C	A	G	T	T	C	C	C
SP03	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	A	A	A	C	C	T	G	C	-	C	A	C	A	T	A	A	T	C	C	T	C
SP06	G	G	G	A	T	A	A	A	C	G	T	A	G	A	C	T	A	A	A	C	T	T	G	C	-	C	G	T	A	T	A	A	C	C	T	T	C
SP08	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SP09	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	A	A	A	C	C	T	G	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SP11	G	G	G	A	T	A	A	A	C	G	T	A	G	A	T	T	A	A	A	C	C	T	G	C	T	T	A	T	A	T	A	A	C	C	T	T	C
SP13	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	A	A	A	C	C	T	G	C	-	C	A	T	A	T	A	A	T	C	C	T	C
SP29	G	A	G	A	C	A	A	A	C	A	C	G	A	A	C	C	A	G	A	C	C	T	A	C	-	C	A	C	A	C	A	G	T	T	C	C	C
JP97	A	G	G	G	C	A	G	G	C	A	T	A	A	A	C	T	A	A	A	C	T	T	A	C	-	C	A	T	G	C	G	G	C	C	C	C	C
JP103	A	G	G	G	C	A	A	A	C	A	T	A	A	A	C	T	A	A	A	C	C	T	A	C	-	C	A	T	G	C	A	G	C	C	C	C	C

Siberut	A/G	G	A/G	A/G	C/T	A	A	A/G	C/T	A/G	C/T	A/G	A/G	A/G	C/T	C/T	A	A	A/C	C/T	C/T	T	A	C/T	-	C	A	C/T	A/G	C/T	A/G	A/G	C/T	C/T	C/T	C/T	C/T
Others	A/G	A/G	G	A/G	C/T	A/G	A	A	C/T	A/G	C/T	A/G	A/G	A/G	C/T	C/T	A/G	A/G	A/C	C	C/T	C/T	A/G	C/T	-/T	C/T	A/G	C/T	A/G	C/T	A	A/G	C/T	C/T	C/T	C/T	C
PAA	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T

Table 5.4 Results of AMOVA

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation
Among islands	2	19.714	0.51157 Va	8.17
Among populations within islands	2	14.910	0.46909 Vb	7.49
Within populations	16	84.519	5.28244 Vc	84.34
Total	20	119.143	6.26310	

sites in the *H. klossii* DNA sequences. "Characters" are nucleotide differences that are fixed in each population; those that are not fixed are "traits." In this dataset, every site is a trait, not a fixed character, and no population has any fixed nucleotide differences. Therefore, under this criterion, *H. klossii* is a single phylogenetic species.

Individuals PL04 from North Siberut, SB04, SB06, and SB19 from Simabuggai, and SP08 from South Pagai all share an identical, divergent haplotype that is differentiated from other haplotypes by four substitution sites, including the only transversion seen in the data.

The detailed results of the AMOVA are given in Table 5.4. Eight percent of diversity is partitioned among islands, and 7.5% among populations within islands. The majority of the variation (84%) is due to variation within populations.

F_{ST} based on the sequence data is 0.157 ($p = 0.07$), which falls within the range considered to indicate *great* genetic differentiation (Wright 1978). However, this result is not significant at the $p < 0.05$ level, which suggests that despite the high F_{ST} value, it is not significantly different from zero and may be due to chance. Thus, these data suggest that the populations are not differentiated.

Discussion

The mitochondrial data suggest that there is no significant differentiation among *Hylobates klossii* populations, and none of the analyses identified any diagnosable intraspecific units. Thus, this study does not support the hypothesis that *H. klossii* has genetically differentiated lineages, rather the Kloss's gibbon is a single phylogenetic species.

Between-population divergence (average 2.9%, range 0–5.8%) does not fall outside the range seen within populations (average 2.4%, range 0–5.3%). In other gibbon species for which divergent populations have been identified, the observed sequence divergence is higher between populations than within populations. For example, the reported average within-population divergence for the western clade of *H. moloch* was 1.3%, and 3.1% for the central clade; the average divergence between these populations was 3.5% (Andayani et al. 2001) For different populations of *H. agilis*, divergence was as high as 8.9% (Whittaker et al. 2007).

The data show shared haplotypes between Siberut and South Pagai. In particular, a haplotype with four distinct substitution sites including a transversion (making it unlikely that the similarity is due to homoplasy) was found in north Siberut, central Siberut, and South Pagai. One cannot infer differentiation among these localities.

Analysis of ESUs typically strives to avoid Type I statistical errors, or the recognition of distinct units where there are none. Much of the discussion in the literature focuses on the sample size needed to sample an acceptable proportion of the genetic variation in the population; estimates of minimum sample size range from 20 to 59 individuals (Crandall et al. 2000; Walsh 2000). This study, with 21 individuals, falls into the lower end of that range. However, Type II errors, or false acceptance of the null hypothesis of no differentiation, can lead to inappropriate conservation management (Moritz et al. 1995; Taylor and Dizon 1999). Additional sampling of Kloss's gibbons is not likely to reveal differentiation at the D-loop locus, as divergent haplotypes are found throughout the range of the species. However, analysis of nuclear loci such as microsatellites may give a better estimate of current genetic population structure, which should reveal a lack of gene flow among islands. Indeed, I attempted such an analysis, but amplifying nuclear DNA from gibbon feces proved extremely problematic due to low DNA concentration (Whittaker 2005b).

The fast mutation rate of the mitochondrial D-loop makes it an ideal locus for identifying intraspecific variation, and the results presented here were surprising. However, a recent study on variation in Kloss's gibbon vocalizations also supports this conclusion (Keith et al., this volume). Possible explanations for a lack of differentiation within this species include: (1) recent gene flow, either natural or human-mediated; (2) historical gene flow; and (3) incomplete lineage sorting.

Recent Gene Flow

Current or recent gene flow among the Mentawai Islands is nearly impossible. Observations suggest that gibbons rarely come to the ground, and that they never cross water. Furthermore, the water channels separating each of the islands are very dangerous, as the Indian Ocean has virtually no breaks between Madagascar and the Mentawai Islands. The resulting large waves make the Mentawais one of the most popular surfing spots in the world. Humans rarely cross the water within the Mentawai archipelago (with the exception of the short crossing between North and South Pagai), preferring the safer route of traveling across the Strait to mainland Sumatra and then back out to another island.

While gibbons are popular pets in the Mentawais, the probability that pet gibbons have been reintroduced into the wild across islands is very low. Pet gibbons, which are typically acquired as infants, rarely survive to adulthood, and reintroduction of any pet primate is difficult (Cheyne, this volume). Primates that have been reared by humans have never learned how to interact with conspecifics, avoid predators, and rear young. Even with an extensive rehabilitation and reintroduction program, primates usually cannot acquire these abilities later in life, and rehabilitated adults often are unable to raise offspring successfully (Yeager and Silver 1999). Furthermore, few Mentawai people travel between Siberut and the southern islands. The inhabitants of the Pagais and Sipora characterize the Siberut peoples as "primitive," and warn researchers against traveling there for fear of getting shot at with bows and arrows. Most Siberut peoples, on the other hand, are cash-poor and have few opportunities to travel outside of Siberut, or even outside of their own region within Siberut.

Historical Gene Flow

The Mentawai Islands have been isolated from Sumatra for 500,000 to one million years by the 1,500-m deep Mentawai Strait (Whitten et al. 2000). However, sea levels between the individual Mentawai Islands are currently only 10–25 m deep, as shown in nautical maps (London Admiralty 1993). Eustatic sea levels were about 25 m lower than current levels approximately 7,000 years ago (Milliman and Emory 1968), which would have been low enough to connect all four Mentawai Islands into a single landmass. Gene flow could thus have occurred among the Mentawai primate populations as recently as 7,000 years ago, resulting in the genetic pattern seen here.

Incomplete Lineage Sorting

Genetic differentiation of mtDNA between populations occurs when ancestral lineages are "pruned" so that each population consists of descendants of different lineages, resulting in reciprocal monophyly (Avise 2000). Such pruning occurs much later than the physical separation of the populations. Thus, despite a geographic separation, the Kloss's gibbons of Siberut and of the southern islands may have retained ancestral mtDNA haplotypes. Since the Mentawais may have been a single landmass as recently as 7,000 years ago, enough time may not have passed to allow lineage sorting.

Implications for the Other Mentawai Primates

If Kloss's gibbons show no significant genetic differentiation, the subspecific taxonomy of the Mentawai colobines and macaque may also be questioned. As discussed in the Introduction, the designations rely on small differences in coat color in the colobines and, for the macaques, differentiation in the mitochondrial genome is not much greater than that seen between populations of other macaque species, due to the extreme female philopatry of macaques. Even so, Kitchener and Groves (2002) argue that the two macaque populations are morphologically very distinct, suggesting full species-level separation.

Due to different generation times, it is possible that the other Mentawai species may display genetic differentiation while the gibbons do not. Gibbons have longer life histories and longer generation times than macaques and colobines. Generation time is equal to the length of time from the birth of a female to her age at first birth. While life history data are not available for all species, members of the same genus or family tend to have similar characteristics. Average generation time has been estimated at 54 months (range 46–65) for macaque species (Harvey et al. 1987), and 51 months (range 48–55) for Asian colobines (including *Nasalis larvatus*, the closest relative of *Simias concolor*) (Harvey et al. 1987; Ross 1992). The estimated generation time for hylobatids is twice as long, at 110 months (range 108–112) (Harvey et al. 1987). For every 1,000 years of separation, 222 generations would have passed for the macaques and leaf monkeys, and only 110 for the gibbons. In this way, the different Mentawai primates could have the same biogeographic history but different levels of genetic differentiation, due to lineage sorting in the colobines and macaques but not in the gibbons.

Conservation Planning

The 2008 IUCN Red List listed the Kloss's gibbon as Endangered IUCN 2008. Based on the mitochondrial data presented here and the analysis of vocalizations presented elsewhere in this volume (Keith et al.), conservationists should manage the species *H. klossii* as a single unit. Despite this conclusion, multiple reserves may be preferable for long-term conservation. The "single large or several small" (SLOSS) debate has focused on just this problem. Large reserves are generally agreed to be better than small reserves, but multiple reserves regardless of size may be able to preserve more genetic variation within a single species or a higher number of species. Furthermore, reliance on multiple reserves may reduce loss due to disease or environmental stochasticity such as earthquakes or fires. However, isolated small reserves that cannot exchange individuals and genes with other reserves are less likely to succeed over the long term (Shafer 1990).

A number of efforts have been made to set aside areas for conservation in the Pagais, all of which have been unsuccessful thus far (Tenaza 1987, 1988; Fuentes 1996/1997; Paciulli 2004). The largest population of Kloss's gibbons is found in Siberut National Park, where there are 13,000–15,000 gibbons

(Whittaker 2005a). Although this area has formal protection, there are a number of problems such as lack of enforcement of hunting laws, insufficient personnel, and encroachment of surrounding logging operations (Whittaker 2006). This large population has the greatest chance of surviving, as long as it is not neglected. Conservation efforts should focus on enforcing the existing laws to protect this population, rather than attempting to create new conservation areas.

However, because the other Mentawai primates do exhibit differences in the southern islands, conservation plans should not ignore these populations. Additionally, mitochondrial DNA and vocal analyses may be overlooking differentiation among Kloss's gibbon populations. Although efforts to set aside areas for conservation in the Pagais have been unsuccessful, potentially viable primate populations exist within the selectively logged and regenerating areas of the PT Minas Pagai Lumber logging concession (Paciulli 2004; Whittaker 2006). In addition to this 130 km^2 of "Limited Production Forest," the company has set aside about 78 km^2 of Buffer Zone and Conservation Areas to preserve genetic diversity of the tree stocks. Collaborating with this company to reduce hunting within the logging concession may be the best way to preserve the primates in the Pagai Islands (Whittaker 2006).

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Chapter 6
Individual and Geographical Variability in the Songs of Wild Silvery Gibbons (*Hylobates Moloch*) on Java, Indonesia

Robert Dallmann and Thomas Geissmann

Introduction

The present study focuses on the great-call phrases of wild female silvery gibbons (*Hylobates moloch*). The aim of this study is to answer the following questions: (1) To what degree is great-call variability within a species useful for both individual and population identification? (2) Do vocal differences among local populations correspond to geographical distances or do they show evidence for genetic isolation among populations? (3) Can vocal data be used to test the validity of subspecific taxon boundaries suggested by previously reported genetic data?

Compared with bird vocalizations, primate vocalizations, in general, and inter-population differences in these vocalizations, in particular, are rarely analyzed (but see Green 1975; Hodun et al. 1981). As Hodun et al. (1981) point out, however, there are several good reasons for studying vocalizations in more than one population of a species. Firstly, vocal differences can be used to assess affiliations among taxa and to reconstruct their phylogenies, similar to the more frequently used morphological and molecular differences (Haimoff et al. 1982; Oates and Trocco 1983; Haimoff et al. 1984; Gautier 1988, 1989; Geissmann 1993; Macedonia and Stanger 1994; Stanger 1995; Geissmann 2002a; Takacs et al. 2005). Secondly, vocal differences can be used to estimate the degree of divergence between populations and the positions of taxonomic and biogeographic boundaries between populations, as suggested by studies on birds, tree frogs, and gibbons (Baker 1974, 1975; Ralin 1977; Konrad and Geissmann 2006). Unfortunately, most studies compare no more than two different samples (e.g., Maeda and Masataka 1987; Mitani et al. 1992; Arcady 1996; Fischer et al. 1998; Hafen 1998;

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Mitani et al. 1999), which makes it difficult to assess the relevance of the vocal differences.

The gibbons or small apes are distributed throughout the tropical rain forests of Southeast Asia (Chivers 1977; Marshall and Sugardjito 1986; Geissmann 1995). They usually live in socially monogamous territorial family groups typically consisting of an adult pair and 1–3 immature offspring (Chivers 1977; Leighton 1987; Chivers 2001). All species of gibbons are known to produce elaborate, loud, long and stereotyped patterns of vocalization often referred to as "songs" (Marshall and Marshall 1976; Haimoff 1984; Geissmann 1993, 1995, 2000). Typically, song bouts are produced in the early morning and last about 10–30 min. In most species, mated pairs utter their songs in the form of well-coordinated duets. In addition to duet song bouts, gibbons of the genus *Hylobates* also produce male solo songs. Female solo songs are common and duet songs are apparently absent in only two species (*Hylobates klossii* and *H. moloch*; Tenaza 1976; Kappeler 1981, 1984a; Geissmann 1993, 2002b; Geissmann and Nijman 2006). Due to the rarity of male singing in *H. moloch* (Kappeler 1981; Geissmann and Nijman 2006), adult females of this species appear to be the vocal "representative of the family" (Kappeler 1984b: 388).

In this study, we focus on the great-call, which has been identified as the most conspicuous and stereotyped phrase of the female song repertoire (Marshall and Marshall 1976; Geissmann 1995). In the silvery gibbon, a typical female song bout consists of several great-calls, which are usually introduced by series of so-called *wa*-phrases and single *wa*-notes (Geissmann 1993, 1995; Geissmann and Nijman 2006). Variability and syntax of the silvery gibbon male song is described elsewhere (Geissmann et al. 2005).

Species-specific song characteristics in gibbons are largely genetically determined (Brockelman and Schilling 1984; Geissmann 1984; Tenaza 1985; Marshall and Sugardjito 1986; Mather 1992; Geissmann 1993, 2000), which makes gibbon song vocalizations particularly suitable for the reconstruction of the phylogenetic relationships among species (Geissmann 2002a). The apparent lack of vocal learning constitutes a fundamental difference to songbirds, where vocal dialects of the song can be learned (Thorpe 1958; Nottebohm 1968; Marler 1970; Mundinger 1982; Slater 1986; Marler and Peters 1987; Catchpole and Slater 1995; Whaling 2000; Tchernichovski et al. 2001; Yamaguchi 2001). To date, there is no evidence that any vocal differences between gibbon populations are learned.

Although gibbon great-calls are remarkably stereotypic, they clearly exhibit some degree of variability, even within the same song bout (Kappeler 1981, 1984b; Dallmann and Geissmann 2001a, b). Although it has been reported that gibbon great-calls exhibit individual-specific characteristics (Kappeler 1981, 1984b; Haimoff and Gittins 1985; Haimoff and Tilson 1985; Mitani 1985), great-call variability has only been quantified for three species (*H. agilis*: Haimoff and Gittins 1985; *H. klossii*: Haimoff and Tilson 1985; *H. moloch*: Dallmann and Geissmann 2001a, b). In earlier studies on *H. moloch*, we demonstrated that inter-individual differences in most great-call variables are statistically significant (Dallmann and Geissmann 2001b). In addition, we found that inter-individual variability of great-calls is significantly higher than intra-individual variability. Furthermore, we demonstrated that variability is significantly lower within one population than among any two populations (Dallmann and Geissmann 2001a).

The silvery gibbon is endemic to Java (and is therefore also called the Javan gibbon). It occurs only in relatively few, isolated forest patches (Fig. 6.1). A viability analysis carried out in 1994 estimated that approximately 400 gibbons were left in Java (Gurmaya et al. 1994). In their most recent report, the IUCN Species Survival Commission (IUCN 2008) recognized the species as Endangered. Although we know now that the gibbon population in Java is much larger than 400 individuals (Asquith et al. 1995; Nijman 2004), the species is in any case more endangered than any species of great ape (Geissmann 2002c).

Although the silvery gibbon has traditionally been regarded as a monotypic species (Groves 1972; Marshall and Sugardjito 1986; Geissmann 1995; Groves 2001), a few recent publications recognize two distinct taxa: a western subspecies (*H. moloch moloch*) and a Central Javan subspecies (*H. moloch pongoalsoni*; Hilton-Taylor 2000; Supriatna and Wahyono 2000). Evidence for pronounced differences in great-call characteristics between any two of our sample sites could help to locate a possible subspecies boundary and thus be of importance in population management and conservation strategies for this species.

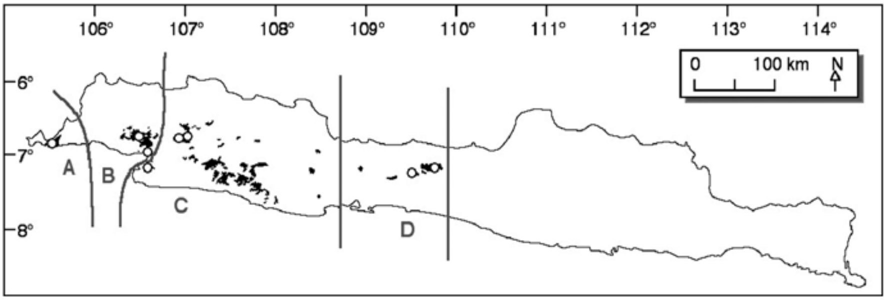

Fig. 6.1 Map of Java showing the forest areas inhabited by gibbons in *black* (gibbon distribution after Kappeler 1984a; Asquith et al. 1995; Nijman 1995; Andayani et al. 1998; V. Nijman pers. comm.). *Circles* indicate the localities where gibbon songs were recorded. *Gray bars* and letters indicate the major gibbon populations identified in this paper: A = Ujung Kulon complex (including localities Kalejetan and Tereleng); B = Gunung Halimun complex (including localities Pelabuhanratu and Gunung Halimun); C = Gunung Pangrango complex (including localities Ciletu, Cibodas, and NW-Gunung Pangrango); D = Central Java (including localities Gunung Lawét and Linggo Asri)

Methods

Study Animals

We analyzed a total of 373 great-calls from 38 different *H. moloch* females. Tape-recordings were carried out by Markus Kappeler in 1976 and 1978, one of us (TG) in September 1998, and Björn Merker in 2000. Tape-recording localities are shown in Fig. 6.1, and sample sizes (number of individuals and great-calls) are listed in Table 6.1. Tape-recordings from eight different localities were available for this study, covering most of the current distribution of the silvery gibbon. We divided our sample into four distinct populations by pooling localities in the same forest system or mountain complex; all populations are divided by major rivers (Table 6.1 and Fig. 6.1). These populations are (A) the Ujung Kulon complex (including localities Kalejetan and Tereleng); (B) the Gunung Halimun complex (including localities Pelabuhanratu and Gunung Halimun); (C) the Gunung Pangrango complex (including localities Ciletu, Cibodas, and NW-Gunung Pangrango); and (D) Central Java (including localities Gunung Lawét and Linggo Asri). All available great-calls were analyzed if the recording quality was good enough for analysis (i.e., depending on the amount of background noise and the distance of the calling animal).

Recording and Analysis Equipment

Field recordings were made with a SONY WM–D6C cassette recorder and a JVC MZ–707 directional microphone by T. Geissmann, with a UHER REPORT 4200 tape recorder and a NIVICO IVC directional microphone by M. Kappeler, and with a SONY TDC-D8 DAT recorder and two SONY electret condenser ECM 150 microphones with plastic parabolic reflectors by B. Merker.

The recordings were digitized with a sample rate of 11 kHz and a sample size of 16 bits. Time versus frequency displays (sonograms) of the sound material were generated using the Canary version 1.2.4 on a Power Macintosh G3 (Charif et al. 1995). The FFT size of the sonograms was 2048 points with an overlap of 75% and a frame length of 1024 points (time resolution = 11.5 msec, frequency resolution = 5.371 Hz).

Acoustic Analysis

The female song bout of *H. moloch* consists mainly of two different acoustic components: (1) great-call phrases, which are uttered at intervals of about two minutes, and (2) single *wa*-notes and phrases of *wa*-notes, which are produced before, after, and between the great-calls. Whereas *wa*-phrases are of variable

Table 6.1 Origin, number of individuals, number of great-calls per locality, and individual and recording information of the sound material analyzed in this study

			Number of great-calls		Number of song-bouts	
Population	Locality* (abbreviation)	*N* (individuals)	Total	Median (range) calls/ individual	Total	Median (range) bouts/individual
A	Kalejetan[1] (*ka*)	9	100	9 (3–26)	11	1(1–2)
	Tereleng[1] (*te*)	3	14	3 (2–9)	3	1
B	Gn. Halimun[5] (*ha*)	6	43	5.5 (3–15)	7	1(1–2)
	Pelabuhanratu[2] (*pe*)	1	10	10	1	2
C	Cibodas[2] (*cb*)	1	12	12	1	1
	Ciletu[3] (*ci*)	2	3	1.5 (1–2)	2	1
	Gn. Pangrango[3] (*pa*)	3	67	30 (5–32)	3	1
D	Gunung Lawét[2] (*la*)	2	3	1.5 (1–2)	1	1
	Linggo Asri, Dieng[4] (*as*)	11	121	6 (2–37)	20	1(1–5)
Total		38	373	6 (1–37)	49	1(1–5)

*Code to sources of tape-recordings: [1]Markus Kappeler (1976); [2]Markus Kappeler (1978); [3]Marshall and Marshall (1976); [4]Thomas Geissmann (1998); [5]Björn Merker (2000).

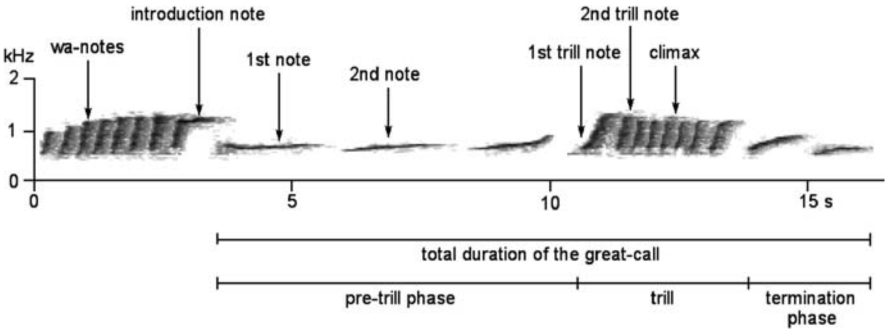

Fig. 6.2 Sonogram of a great-call phrase produced by a female silvery gibbon, illustrating the three main phases (i.e., pretrill phase, trill phase, and termination phase), which are typical features of this species' great-calls, and some of the variables measured

organization even within the same song bout, great-call phrases are highly stereotypic and species-specific (Kappeler 1981; Haimoff 1984; Kappeler 1984b; Dallmann and Geissmann 2001a). Like most previous studies on songs of female gibbons, we analyze the great-call exclusively because it is the longest and most standardized part of the female's song repertoire (Haimoff and Gittins 1985; Haimoff and Tilson 1985). Figure 6.2 shows a sonogram of a typical great-call phrase of a female silvery gibbon. The great-call is usually about 15 s in duration and the fundamental frequency ranges between 0.5 and 1.5 kHz. The great-call can be divided into three main parts: (1) a slow pre-trill phase with long howling notes, (2) an accelerando-decelerando of *wa*-notes that is commonly named a trill, and, finally, (3) a termination phase, during which notes slow down in speed and frequency. In order to quantify acoustic characteristics of the great-call, we defined 39 variables, as defined in Table 6.2.

Table 6.2 Descriptions of the variables analyzed in this study

No.	Variable (Unit)	Description
1	Total great-call duration (s)	Time interval between start of the first note until the end of the last note of the great-call
2	Total great-call duration excluding termination phase (s)	No. 1 minus No. 38
3	Duration of trill (s)	No. 1 minus (No. 11 plus No. 38)
4	Number of notes of entire great-call	Number of notes between first and last note of great-call
5	Frequency range of entire great-call (Hz)	No. 7 minus No. 9
6	Number of note with max. frequency	The number of the note with the highest frequency
7	Maximum frequency (Hz)	The highest frequency in the entire great-call

Table 6.2 (continued)

No.	Variable (Unit)		Description
8	Number of note with min. frequency		The number of the note with the lowest frequency
9	Minimum frequency (Hz)		The lowest frequency in the entire great-call
10	Number of pre-trill phase notes		Number of notes between first note and last note before trill
11	Duration pre-trill phase (s)		Time between start of first note and start of first trill note
12	Introduction note	Duration (s)	Duration of the introduction note
13		Frequency range (Hz)	No. 15 minus No. 14
14		Min. frequency (Hz)	The lowest frequency of the introduction note
15		Max. frequency (Hz)	The highest frequency of the introduction note
16	1. note	Duration (s)	Duration of the first note of the great-call
17		Frequency range (Hz)	No. 19 minus No. 18
18		Min. frequency (Hz)	The lowest frequency of the first note of the great-call
19		Max. frequency (Hz)	The highest frequency of the first note of the great-call
20	2. note	Duration (s)	Duration of the second note of the great-call
21		Frequency range (Hz)	No. 23 minus No. 22
22		Min. frequency (Hz)	The lowest frequency of the second note of the great-call
23		Max. frequency (Hz)	The highest frequency of the second note of the great-call
24	1. trill note	Duration (s)	Duration of the first trill note
25		Frequency range (Hz)	No. 27 minus No. 26
26		Min. frequency (Hz)	The lowest frequency of the first trill note
27		Max. frequency (Hz)	The highest frequency of the first trill note
28	2. trill note	Duration (s)	Duration of the second trill note
29		Frequency range (Hz)	No. 31 minus No. 30
30		Min. frequency (Hz)	The lowest frequency of the second trill note
31		Max. frequency (Hz)	The highest frequency of the second trill note
32	Number of trill notes		No. 4 minus (No. 10 plus No. 39)
33	Number of notes before climax		Number of notes from first note until the climax note (climax note included)
34	Number of notes after climax		No. 33 minus No. 4

Table 6.2 (continued)

No.	Variable (Unit)	Description
35	Min. frequency at end of a trill note (Hz)	The lowest frequency at an end of a trill note
36	Min. frequency range in trill (Hz)	The minimal frequency bandwidth of a trill note
37	Max. note speed in trill (s)	The minimal time needed for three consecutive trill notes
38	Duration of termination phase (s)	The time from start of the first termination phase note until the end of the last termination phase note
39	Number of termination phase notes	The number of notes in the termination phase

Statistics

All data for each variable were standardized with a mean of 0 and a standard deviation of 1 in order to allow comparison of the variability among variables and individuals. Because our variables were highly correlated, we conducted a factor analysis, and all subsequent statistics were performed with the principle components derived from this procedure. We discarded all factors with an eigenvalue below one, and hence retained 10 factors, which explained 84.2% of the total variation. On the retained components, the highest-loaded variables were as follows: Factor 1 (Variable 7), Factor 2 (Variable 21), Factor 3 (Variable 32), Factor 4 (Variable 39) Factor 5 (Variable 26), Factor 6 (Variable 11), Factor 7 (Variable 28), Factor 8 (Variable 14), Factor 9 (Variable 36), and Factor 10 (Variable 17). All retained factor loadings were above 0.8.

Differences within and between individuals were analyzed using cluster analysis and multidimensional scaling, described in Sneath and Sokal (1973) and Guttman (1968), respectively. Cluster analysis was carried out using unweighted pair group average linking with squared Euclidean distances.

The aim of multidimensional scaling (MDS) is to build, in a small dimensional space, a pictorial mapping of the distances (or dissimilarities) of a group of objects. To build an optimal representation, the MDS algorithm minimizes a criterion called stress or distortion. The closer the stress is to zero, the better the representation. Each dimension (scale) represents a separate bipolar standard of comparison. The similarity matrix for our MDS analysis was also computed using squared Euclidean distances. The starting configuration for MDS was Guttman-Lingoes and two was chosen as the number of dimensions.

Finally, discriminant function analyses were conducted to compare the quality of different a priori classifications of our populations. This type of analysis automatically determines some optimal combination of variables so that the first function provides the most overall discrimination between groups; the second provides the second most, and so on. The functions are independent; that is, their contributions to the discrimination between groups will not overlap. Computationally, the analysis performs a canonical correlation analysis that will determine the successive functions and canonical roots (the term root refers to the eigenvalues that are associated with the respective canonical function). The models derived from this analysis have been cross-validated.

The three different statistical methods mentioned above were used to first reveal intra- and inter-individual differences (cluster analyses) and, second, to determine the amount of difference within the populations (MDS). Finally, we tested our data set for the proposed existence of two subspecies. Here, we used discriminant analyses because of the necessary a priori assumption of two subspecies, which could not be incorporated using the first two methods.

Statistical analyses were performed on a Windows PC using the STATISTICA (Kernel 5.1) software. All procedures were carried out according to the STATISTICA manual (StatSoft Inc. 1998).

Results

To illustrate the variability of the great calls, Fig. 6.3 shows the representative examples of two great-calls from one individual (a), a second individual from the same population (b), and individuals from all other populations (c–e).

Variability Within and Between Individuals

In Fig. 6.4, a tree plot of a cluster analysis using 53 great-calls from 7 different females from Gunung Halimun (population B) is shown. In this analysis, 47 great-calls (88.7%) fall into individual-specific clusters; only five great-calls (four of female *pe* and one of female *ha2*) fall into other clusters. This shows that similarity among great-calls of the same individual is higher than that among the great-calls of different individuals, suggesting that individual females can be distinguished by their great-calls.

Cluster analysis of great-calls of the other gibbon populations (A, C and D) produced similar results. Individual-specific clusters were found in 97 of 114 great-calls (85.1%) of population A, in 79 of 82 great-calls (96.3%) of population C, and in 106 of 124 great calls (85.5%) of population D. Individual differences in all time and frequency variables are larger than the respective time and frequency resolutions of our sonograms.

The results of the multidimensional scaling for the whole data set are shown in Fig. 6.5. Each dot represents one great-call. Calls by each individual form more or less well-defined clusters that are surrounded in the figure by the minimum polygons. Polygon overlap between individuals varies. In the plot for the population from Gunung Halimun (Fig. 6.5b), for example, only the

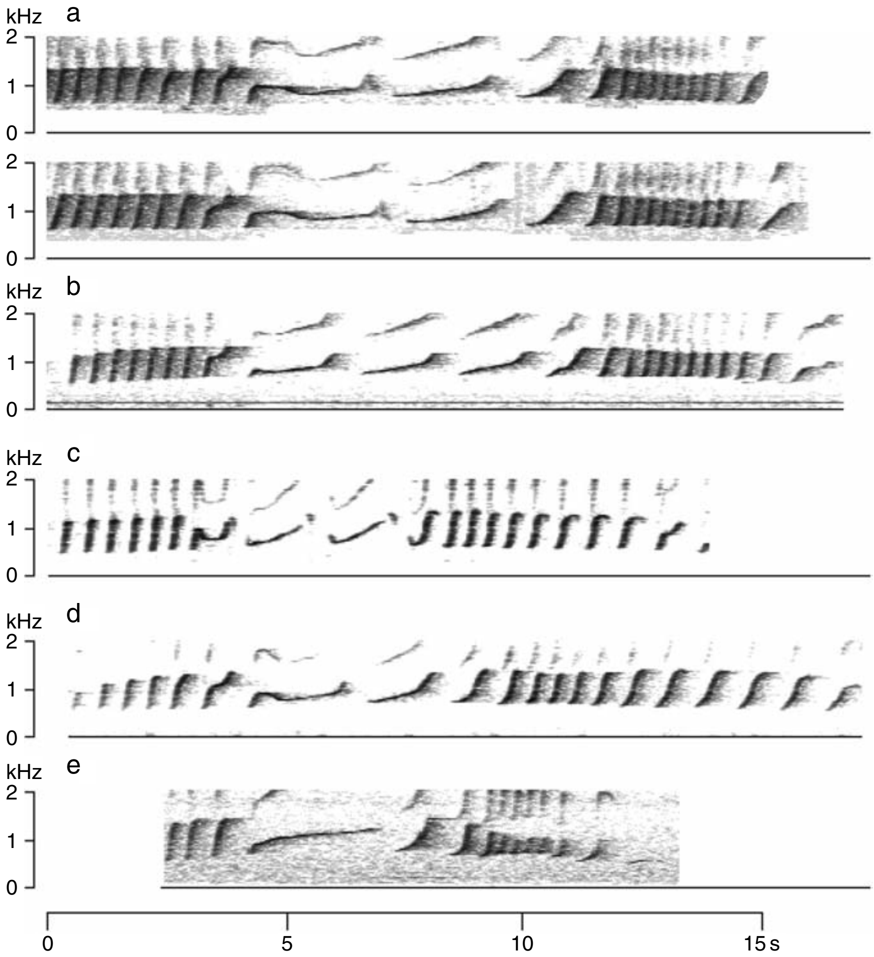

Fig. 6.3 Representative *Hylobates moloch* great-calls: (**a**) two calls of the same individual (*ka2*) from population A, (**b**) call of a different individual (*ka8*) from the same population, and (**c–e**) one call each of a female from populations B (*pe1*), C (*ci1*), and D (*as10*), respectively

polygons of two individuals (*ha1* and *ha6*) show some overlap, which, moreover, includes only one great-call of each individual. In the females from the Gunung Pangrango complex (Fig. 6.5c), overlap is slightly higher, and the females from Kalejetan (Fig. 6.5a) and Linggo Asri (Fig. 6.5d) show even more overlap. In many cases, overlap results from outliers of the respective cluster of dots. This is particularly obvious in Fig. 6.5c, where a single great-call of female *pa2* is solely responsible for the extensive polygon overlap between *pa1* and *pa2*. Similarly, in Fig. 6.5d, the overlap between *as1* and *as2* mostly results from one outlier in the *as2* cluster. We assume that these outliers are

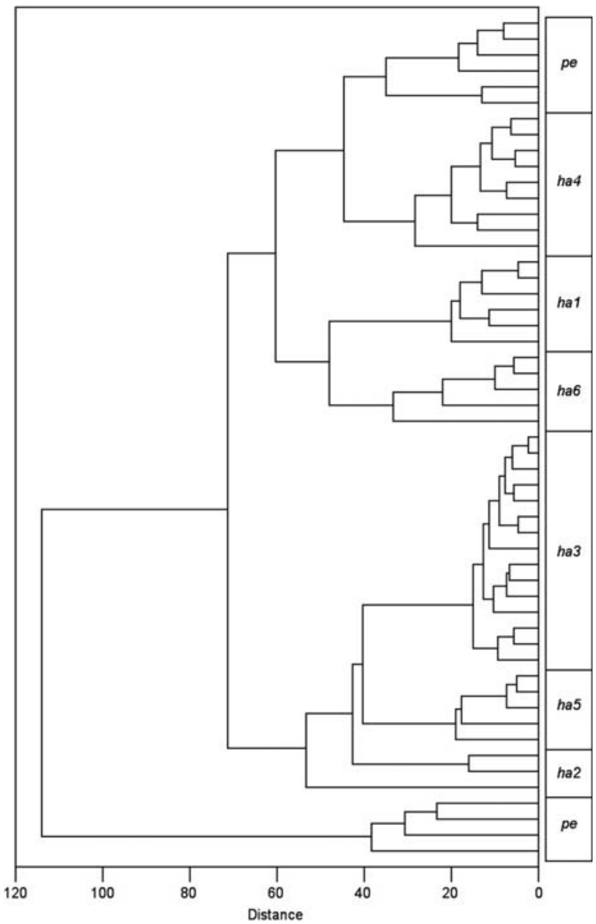

Fig. 6.4 Cluster analysis of seven individuals from the Gunung Halimun population (population B). Each terminal branch represents one of 53 great-calls. Branch length is plotted as squared Euclidian distance

atypical great-calls. Individuals do occasionally produce atypical calls within otherwise typical song bouts. The reasons why they do so are unknown. Our impression is that sometimes, in the middle of a great-call, a gibbon may suddenly become aware of a neighboring call, and while trying to make out what and where the other gibbon is calling, the singer may sometimes draw out one note or one interval of the great-call longer than usual. It is also our impression that great-calls may require a great deal of energy from the singer and that occasionally individuals sound as if they had a throat problem in the middle of a great-call.

As demonstrated by these results, individual females can be fairly well distinguished by the great-call variables measured in the present study.

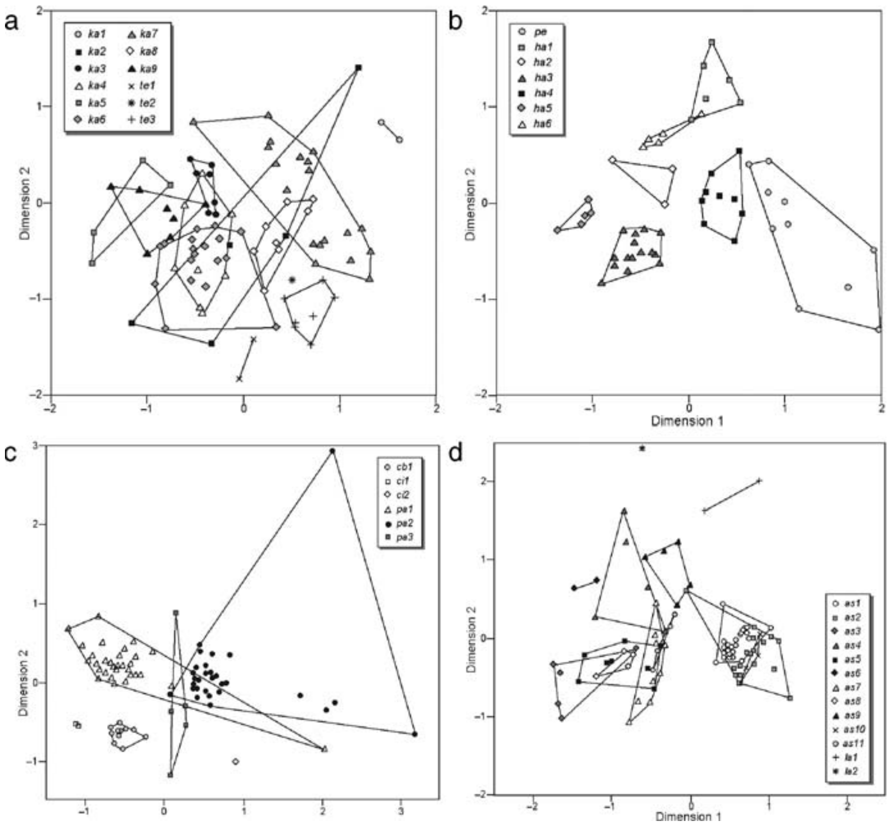

Fig. 6.5 Multidimensional scaling analysis of all 373 great-calls from all populations. Each *dot* represents a single great-call. Different individuals are identified by different symbol shapes. (**a**) Population A (*ka* = Kalejetan, *te* = Tereleng), (**b**) Population B (*ha* = Gunung Halimun, *pe* = Pelabuhanratu), (**c**) Population C (*cb* = Cibodas, *ci* = Ciletu, *pa* = Gunung Pangrango), Population D (*as* = Linggo Asri, *la* = Gunung Lawét)

Variability Between Populations

The results of the discriminant analyses are shown in Table 6.3. Our total sample of 373 great-calls was randomly divided into two subsets of about equal size (with subset *a* consisting of 187 great-calls, and *b* of 186 great-calls). Using subset *a* in a first run of the discriminant analysis, 88.2% of the great-calls were correctly assigned to their respective population (Table 6.3a). In order to validate the calculated model equation, we used the discriminating function to classify the second subset *b*. Here, 83.3% of all great-calls were correctly assigned (Table 6.3b).

Figure 6.6 shows a plot of the two best separating roots computed in the discriminant analysis. In this analysis, Root 1 is most strongly correlated

Table 6.3 Results of discriminant analyses for populations using all individual great-calls. The data were randomly split in two subsets of about equal size: (a) which served to determine the discriminant function (learning sample), and (b) which served to evaluate the derived function (test sample); *n* = number of great-calls

	Great-calls assigned to					
	A	B	C	D	% correctly assigned great-calls	Total great-calls
Subset (a)						
A	53	1	3	0	93.0	57
B	0	24	3	0	88.9	27
C	7	0	34	0	82.9	41
D	3	3	2	54	87.1	62
Total	**63**	**28**	**42**	**54**	**88.2**	**187**
Subset (b)						
A	53	3	1	0	81.2	57
B	0	24	2	0	80.0	26
C	8	2	31	0	70.7	41
D	3	4	1	54	85.5	62
Total	**64**	**33**	**35**	**54**	**83.3**	**186**

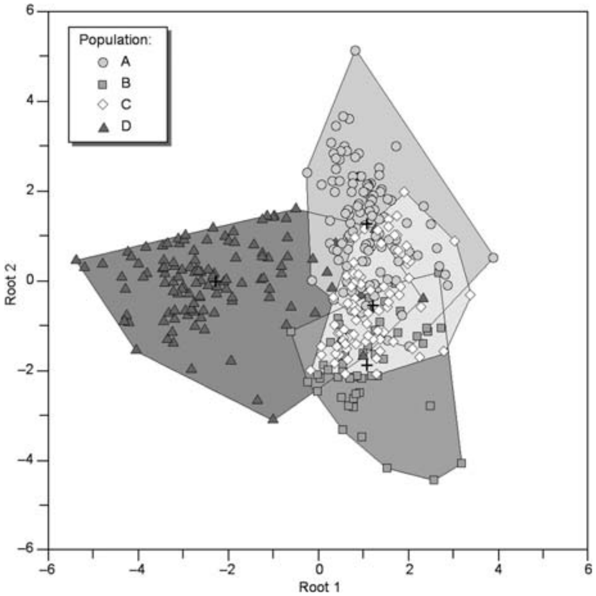

Fig. 6.6 Discriminant analysis of all great-call data. Each dot represents a single great-call. Different populations are identified by different symbol shapes, and population clusters are surrounded by minimum polygons. Heavy crosses identify population centroids. For a definition of "roots" see the Methods section. Populations are: A = Ujung Kulon complex (including localities Kalejetan and Tereleng); B = Gunung Halimun complex (including localities Pelabuhanratu and Gunung Halimun); C = Gunung Pangrango complex (including localities Ciletu, Cibodas, and NW-Gunung Pangrango); D = Central Java (including localities Gunung Lawét and Linggo Asri)

($r = -0.43$) with Factor 1 (highest loading: Variable 7), whereas Root 2 is most strongly correlated ($r = 0.44$) with Factor 7 (highest loading: Variable 28). Each population forms a clearly distinguishable cluster, with the exception of the population from the Gunung Pangrango complex (C), which almost completely overlaps with the other clusters. In West Java, at least, the distances between the clusters do not appear to correspond to the geographical distances between the populations. In the discriminant analysis, the gibbons from Gunung Pangrango (C) take an intermediate position between those of Ujung Kulon (A) and those from the Gunung Halimun complex (B). As shown in Fig. 6.1, this arrangement clearly inverses the actual geographical relationships among the three populations.

To test whether uneven sample sizes for each individual influenced our results, we repeated the discriminant analysis using only mean values for each individual instead of every great-call. The results of this procedure are identical to those described above, and the relationships of the populations in the plot remain as those shown in Fig. 6.6.

We also do not think that the differences we found are due to the recording equipment, because more than one set of recording equipment was used in most populations and none of our analyses group the individuals according to recording equipment. In addition, the two populations (C and D) that were sampled, in part, using the same equipment do not exhibit any particular affinities (Fig. 6.6). Instead, C exhibits the most similarities to A, judging by the number of incorrectly assigned great-calls in the discriminant analyses (Table 6.3).

Possible Taxonomic Boundary

In a discriminant analysis comparing two clusters of gibbon populations corresponding to those proposed by Andayani et al. (2001) (i.e., comparing populations A and B *vs*. C and D), 81.6% of the great-calls of our study animals are correctly assigned to their respective clusters. If the same analysis is repeated comparing two clusters corresponding with biogeographic groupings found in other taxa (Brandon-Jones 1995a, b, 1996; i.e., comparing populations A, B, and C vs. D), we obtain a better separation: in this case, 97.4% of all great-calls are correctly assigned to their respective clusters. Table 6.4 shows the results of this discriminant analysis in more detail.

Discussion

Sody (1949) first described "*Hylobates lar pongoalsoni*" as a gibbon subspecies which occurred in Central Java and which differed from West Javan gibbons in fur coloration. These differences were, however, not confirmed in later studies (Groves 1972; Kappeler 1981), and no subspecies of *H. moloch* have been

Table 6.4 Results of discriminant analyses comparing two different locations of a hypothetical subspecies boundary: (a) boundary located between populations B and C, and (b) boundary located between populations C and D

	Great-calls assigned to			
(a)	A & B	C & D	% correctly assigned great-calls	Total great-calls
A & B	145	22	86.8	167
C & D	27	179	86.9	206
Total	172	201	**86.9**	373
(b)	A & B & C	D		
A & B & C	249	0	100.0	249
D	18	106	85.5	124
Total	267	106	**95.2**	373

recognized in any revisions of gibbon systematics in the past 30 years (e.g., Groves 1972; Marshall and Sugardjito 1986; Geissmann 1995; Groves 2001).

Recent studies comparing mitochondrial DNA sequences of captive silvery gibbons suggested the presence of two genetically distinct lineages: a “western” lineage represented by the gibbons of the Gunung Halimun complex, and a “central” lineage comprising all populations east of the Gunung Halimun complex, including gibbons of the Gunung Pangrango complex and of Central Java (Andayani et al. 1998; Supriatna et al. 1999; Andayani et al. 2001). Apparently based on these reports, several authors appear to recognize two subspecies of *H. moloch* (Hilton-Taylor 2000; Supriatna and Wahyono 2000), although subspecies are not explicitly mentioned in the molecular studies cited above.

Interestingly, the border between the two genetically differentiated lineages was reported to be located between two neighboring mountain complexes, the Gunung Halimun and Gunung Pangrango, which both are situated in West Java (Andayani et al. 2001). This would correspond to the genetic boundary between populations B and C in Fig. 6.1.

A comparison with other Javan mammals suggests, however, that a more likely biogeographical boundary is located between West and Central Java, not in West Java. This boundary appears to be located somewhere between the Gunung Pangrango complex and the Gunung Lawét (i.e., between populations C and D on our map, Fig. 6.1). A similar location of taxonomic boundaries reportedly occurs in other Javanese primates, such as *Trachypithecus auratus* (separating the subspecies *T. a. auratus* and *T. a. mauritius*) and *Presbytis comata* (separating the subspecies *P. c. comata* and *P. c. fredericae*; Brandon-Jones 1995a, b, 1996; Groves 2001). Incidentally, the specimen localities that Sody (1949) mentioned for his two silvery gibbon subspecies suggest exactly such a location of the subspecies boundary.

Molecular and biogeographic data thus provide conflicting evidence on the location of the hypothetical subspecies boundary. Based on vocal evidence, we suggest that if two subspecies exist, the boundary between them is located somewhere between the Pangrango complex and Central Java, as indicated by independent biogeographic evidence, and not between the Pangrango and the Halimun complex, as suggested by Andayani et al. (1998, 2001) and Supriatna et al. (1999).

Our study includes a median of 9.5 individuals per population (range 6–13 individuals), and a median of 98 calls per population (range 53–124 calls, see Table 6.1). This may be one of the largest studies on wild gibbon calls of a single species ever published. Comparable molecular studies on gibbons usually work with much smaller samples of about 1–5 individuals per species (Garza and Woodruff 1992; Hayashi et al. 1995; Hall et al. 1998; Roos and Geissmann 2001), and the largest DNA study on any single gibbon species with the same goal as ours (Andayani et al. 2001) used data from 31 captive Javan gibbons. In comparison, we sampled 38 wild gibbons with exact locality information. Because of the highly stereotyped structure of the gibbon great-calls we studied (Dallmann and Geissmann 2001a, b), these sample sizes should be adequate to accurately represent each individual and population.

It should be stressed that we do not make any statements as to whether subspecies do exist in *Hylobates moloch* or not. Our results offer no conclusive evidence on that question, because we have no comparative data that allow us to decide how large the "vocal distance" should be in order to qualify as evidence for a subspecies difference.

Conclusions

First, we show that individuals can be distinguished by their great-calls. In addition, some, but not all, populations can be distinguished by their great-calls. Vocal distances between populations, however, are not consistent with geographical distances. Our results suggest that if two gibbon subspecies exist on Java, the boundary between them is located somewhere between West and Central Java, and not in West Java, as suggested by molecular evidence.

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Chapter 7
The Fossil Record of Gibbons

Nina G. Jablonski and George Chaplin

Modern gibbons of the family Hylobatidae are distinguished from other living apes by a suite of shared-derived characteristics (synapomorphies) related to their unique mode of overhead suspensory locomotion and territorial defense. These characteristics include a greatly elongated and highly mobile forelimb, greatly reduced or nonexistent sexual dimorphism in body and canine tooth size, a predominantly monogamous social organization, and stereotyped vocalizations that function to establish and maintain boundaries between family groups. In recent years, there has been considerable debate as to whether gibbons so defined are an ancient lineage with roots well back into the middle Miocene or whether they are of more recent origin. Here, one immediately confronts the difficulty that identification of true gibbons in the fossil record is limited to characters of the skeleton and dentition and, thus, only assays half of the features that define the Family.

In this chapter, we first update and review what is known of the fossil record of the Hylobatidae. We include in this review a discussion of the changes in distribution of gibbons through time, which can be inferred from the fossil record. This is done with reference to the environmental history of Southeast Asia, paying special attention to the patterns of sea-level change and to the development of paleorivers that would have affected gibbon evolution. Second, we then propose a scenario of deployment for the gibbons based on the fossil record and the environmental history of Southeast Asia, which is consistent with current understanding of the phylogeny of the group. Finally, we discuss the biological and ecological factors that influenced the distribution of gibbons through time.

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The Nature of the Fossil Record of Gibbons and Gibbon-Like Primates

Until the widespread adoption of molecular genetic and auditory sonagraphic methods, knowledge of the evolutionary history of gibbons rested largely on the interpretation of controversial fossil evidence. Although Hylobatidae were once regarded as the best-documented evolutionary lineage of primates (Simons and Fleagle 1973), considerable controversy exists as to which taxa belong to or were ancestral to the Hylobatidae. The Miocene fossil record of Eurasia and East Africa is filled with small apes including members of the families Propliopithecidae (*Propliopithecus*), Pliopithecidae (*Pliopithecus*), and Proconsulidae (*Micropithecus*, *Dendropithecus*, *Limnopithecus*, *Dionysopithecus*, and *Platodontopithecus*) that have been nominated as possible gibbon ancestors because of their small size and simple molar cusp morphology (Simons and Fleagle 1973). These genera are now generally viewed as early catarrhines or early hominoids, whose primitive characteristics do not ally any of them with modern gibbons (Harrison 1987; Tyler 1993; Fleagle 1999; Harrison 2002). It is more likely that modern hylobatids are not the descendants of small Miocene apes, but are instead phyletic dwarfs descended from larger Asian hominoids of the middle Miocene (Tyler 1993). In contrast to the upsizing that occurred in many mammalian lineages when species faced increasing environmental seasonality, downsizing was common among later Miocene hominoids. In these moderately to highly encephalized mammals, smaller body sizes worked to reduce the total energy intake required to maintain health and reproductive fitness.

Of all the Miocene species that have been suggested as candidates for gibbon ancestry or sister taxon status, the Chinese fossil species *Laccopithecus robustus* from approximately 8 myr old deposits at Lufeng, Yunnan (Wu and Pan 1984, 1985, 1994), is the most persuasive contender. *Laccopithecus* is distinguished from modern hylobatids in its possession of an extreme amount of canine tooth dimorphism (Pan et al. 1989), but the rest of its cranial and dental anatomy is very similar to that of modern gibbons. The only identified postcranial element of *Laccopithecus*, a proximal fifth phalanx, is similar to the modern siamang (Meldrum and Pan 1988). This evidence sways us to support the tentative placement of *Laccopithecus* within the Hylobatidae rather than the Pliopithecidae (Tyler 1993), but other workers have disagreed and have classified it as a pliopithecid (Harrison et al. 2002). Further evidence of the highly diagnostic ear region and postcrania is required for a definitive assignment. *Laccopithecus robustus* is excluded from our compilation of fossil Hylobatidae for these reasons, but it should be noted that one of the two Pliocene localities for fossil Hylobatidae is also at Lufeng, Yunnan.

Unequivocal evidence of true Hylobatidae in the fossil record is known from deposits of latest Miocene or earliest Pliocene age onward (i.e., 6–5 Ma), with most fossils deriving from the Late Pleistocene and Holocene (Hooijer 1960; de Vos 1983; Gu 1986, 1989; Ciochon and Olsen 1991; Zong et al. 1991; Wu and

Poirier 1995; Ciochon et al. 1996; Harrison 1998; Jablonski et al. 2000; Tougard 2001; van den Bergh et al. 2001; Storm et al. 2005; Zeitoun et al. 2005; Harrison et al. 2006). From a taphonomic perspective, gibbons are rare elements of the fossil record because their preference for forested habitats, their relatively small bodies (<10 kg), and gracile bones militate against long-term preservation. The known fossil localities for the Hylobatidae are presented in Table 7.1, where they are generalized to a scale of 1 M:1. Locality data were compiled from the original reports cited above, in which the ages of fossil-producing deposits were determined mostly by faunal correlation. The geological ages of fossil localities are, thus, given only as epochs or sub-epochs. We did not inspect or compare most of the gibbon fossils discussed in this paper because they are held in widely dispersed repositories with restricted access in Asia. Most of the gibbon fossils reported in the literature are isolated molar teeth or small portions of jaws with teeth, and diagnosis of such remains to the species level is uncertain because gibbons, with the exception of *Symphalangus*, are not strongly differentiated by their dental morphology. Most of the features that distinguish the species of gibbons today are integumentary and behavioral; the skeletal and dental differentiation that exists is extremely subtle and difficult to detect in the fossil record. The species names and ages of fossils provided in Table 7.1 are those derived from the original published descriptions of the fossils. The names provided in the original reports must be treated with caution, because in many cases species assignments were given on the basis of geographical propinquity of fossil localities to sites of living populations, not on thorough comparisons of morphology. The conventions for genus designations within Hylobatidae are those followed throughout this volume. Fossils not originally assigned to species are here attributed to "Hylobatidae gen. et sp. indet."

The Distribution of Fossil Gibbons in Relation to Changing Sea Levels and Landforms

The date of the great ape-gibbon split is widely regarded as 15 Ma (Tyler 1993; Chatterjee 2006), based on molecular clock estimates. The absence of informative fossils marking the origin of the gibbon lineage led Chatterjee to undertake further molecular clock analyses to estimate the origin of the gibbon radiation at about 10.5 Ma (Chatterjee 2006, this volume). No fossils unequivocally attributed to Hylobatidae are known before the terminal Miocene, and the early fossil record of the Family is particularly sparse. This account complements the summary of the paleontological record of gibbons provided by Chatterjee (this volume), by emphasizing the distribution of gibbon fossil sites relative to the physiographic features that would have influenced gibbon distributions through time.

Since the estimated time for the beginning of the gibbon radiation, fluctuating sea levels have influenced the configuration and connectivity of land masses

Table 7.1 Occurrences of fossil Hylobatidae, collected from the literature (see body of text for citations)

Genus	Species (original and current equivalent)	Locality	Province	Country	Latitude	Longitude	Period
Hylobatidae gen. indet.	sp.	Hudieliangzi	Yunnan	China	25° 55′ N	101° 46′ E	Pliocene
Hylobatidae gen. indet.	sp.	Lufeng	Yunnan	China	25° 3′ N	102° 4′ E	Pliocene
Nomascus	*sericus* (= *concolor*)	Wanxian	Sichuan	China	30° 25′ N	108° 10′ E	Early Pleistocene
Hylobatidae gen. indet.	sp.	Baojing	Hunan	China	28° 42′ N	109° 40′ E	Early Pleistocene
Nomascus	*concolor*	Xinshuishan Cave	Guangxi	China	22° 52′ N	107° 14′ E	Middle Pleistocene
Nomascus	*concolor*	Tham Khuyen	Lang Song	Vietnam	21° 51′ 17 N	106° 28′ 15 E	Middle Pleistocene
Hylobates	*hoolock*	Daxin	Guangxi	China	22° 52′ N	107° 13′ E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Ban Fa Suai	Chiang Dai	Thailand	19° 29′ 8 N	97° 59′ 35 E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Hang Hum	Hoang Lien Son	Vietnam	21° 51′ N	104° 50′ 30 E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Keo Leng	Lang Song	Vietnam	21° 58′ 30 N	106° 33′ 20 E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Tham OM	Nghetinh	Vietnam	19° 34′ 25 N	105° 8′ 5 E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Lang Trang	Ba Thuoc	Vietnam	20° 40′ N	105° 0′ E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Bama	Guangxi	China	24° 10′ N	107° 15′ E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Daxin	Guangxi	China	23° 20′ N	110° 25′ E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Tongzi	Guizhou	China	28° 15′ N	106° 45′ E	Middle Pleistocene
Nomascus	*sericus* (= *concolor*)	Yanjingkou	Sichuan	China	30° 35′ 40 N	108° 25′ 40 E	Middle Pleistocene
Nomascus	*concolor*	Baise	Guangxi	China	23° 55′ N	106° 37′ E	Late Pleistocene
Nomascus	*concolor*	Guilin	Guangxi	China	25° 14′ N	110° 17′ E	Late Pleistocene
Nomascus	*concolor*	Lingyan Cave	Guangxi	China	24° 15′ N	109° 25′ E	Late Pleistocene
Nomascus	*concolor*	Lipu	Guangxi	China	24° 30′ N	110° 24′ E	Late Pleistocene
Nomascus	*concolor*	Shanglin	Guangxi	China	23° 27′ N	108° 34′ E	Late Pleistocene
Nomascus	*concolor*	Yangshuo	Guangxi	China	24° 43′ N	110° 29′ E	Late Pleistocene

Table 7.1 (continued)

Genus	Species (original and current equivalent)	Locality	Province	Country	Latitude	Longitude	Period
Nomascus	*concolor*	Qiongzhong	Hainan	China	19° 5′ N	109° 50′ E	Late Pleistocene
Nomascus	*concolor*	Liujiang	Sichuan	China	24° 15′ N	109° 25′ E	Late Pleistocene
Nomascus	*concolor*	Baoshan	Yunnan	China	25° 5′ N	99° 5′ E	Late Pleistocene
Nomascus	*concolor*	Jiangcheng	Yunnan	China	22° 40′ N	101° 53′ E	Late Pleistocene
Nomascus	*concolor*	Jingdong	Yunnan	China	24° 35′ N	102° 39′ E	Late Pleistocene
Nomascus	*concolor*	Luchun	Yunnan	China	22° 55′ N	102° 23′ E	Late Pleistocene
Nomascus	*concolor*	Mengla	Yunnan	China	21° 27′ N	101° 30′ E	Late Pleistocene
Nomascus	*concolor*	Shangyong	Yunnan	China	21° 38′ N	101° 38′ E	Late Pleistocene
Nomascus	*concolor*	Shuangbai	Yunnan	China	24° 38′ N	101° 25′ E	Late Pleistocene
Nomascus	*concolor*	Xinping	Yunnan	China	24° 2′ N	101° 57′ E	Late Pleistocene
Nomascus	*concolor?*	Du′an	Guangxi	China	23° 17′ N	106° 30′ E	Late Pleistocene
Hylobates	*hoolock*	Lipu	Guangxi	China	24° 30′ N	110° 24′ E	Late Pleistocene
Hylobates	*hoolock*	Baoshan	Yunnan	China	25° 5′ N	99° 5′ E	Late Pleistocene
Hylobates	*hoolock*	Lianghe	Yunnan	China	24° 55′ N	98° 0′ E	Late Pleistocene
Hylobates	*hoolock*	Tengchong	Yunnan	China	25° 4′ N	98° 7′ E	Late Pleistocene
Hylobates	*hoolock*	Yingjiang	Yunnan	China	24° 40′ N	97° 8′ E	Late Pleistocene
Hylobates	*leuciscus* (= *moloch*)	Punung	Java	Indonesia	8° 8′ 28 S	111° 1′ 48 E	Late Pleistocene
Hylobates	*muelleri*	Niah Cave	Sarawak	Malaysia	3° 46′ N	113° 42′ 20 E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Baojiyan	Guangxi	China	25° 13′ N	109° 50′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Bose	Guangxi	China	23° 56′ N	106° 34′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Du′an	Guangxi	China	23° 57′ N	108° 6′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Liuzhou	Guangxi	China	24° 20′ N	109° 26′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Longlin	Guangxi	China	24° 45′ N	105° 20′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Shanzhongmen	Guangxi	China	24° 15′ N	109° 10′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Taipingyan	Guangxi	China	25° 22′ N	110° 24′ E	Late Pleistocene

Table 7.1 (continued)

Genus	Species (original and current equivalent)	Locality	Province	Country	Latitude	Longitude	Period
Hylobatidae gen. indet.	sp.	Xichou	Guangxi	China	24° 22′ N	109° 25′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Yishan Cave	Guangxi	China	24° 30′ N	108° 40′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Tongzi	Guizhou	China	28° 15′ N	106° 45′ E	Late Pleistocene
Symphalangus	*syndactylus*	Gunung Dawung	Java	Indonesia	8° 7′ 33 S	110° 59′ 15 E	Late Pleistocene
Symphalangus	*syndactylus*	Punung	Java	Indonesia	8° 8′ 28 S	111° 1′ 48 E	Late Pleistocene
Symphalangus	*syndactylus*	Lida Ayer	Sumatra	Indonesia	0° 19′ 19 S	100° 29′ 7 E	Late Pleistocene
Symphalangus	*syndactylus*	Sibrambang	Sumatra	Indonesia	0° 36′ 56 S	100° 38′ 6 E	Late Pleistocene
Hylobates	*muelleri*	Madai	Sabah	Malaysia	4° 40′ 46 N	118° 7′ E	Holocene
Hylobates	*muelleri*	Bua	Sarawak	Malaysia	1° 19′ 16 N	110° 8′ 30 E	Holocene
Hylobates	*muelleri*	Gua Sireh	Sarawak	Malaysia	1° 5′ 57 N	110° 26′ 23 E	Holocene
Hylobatidae gen. indet.	sp.	Fuzhou	Fujian	China	26° 4′ N	119° 15′ E	Holocene
Hylobatidae gen. indet.	sp.	Dian Bai	Guangdong	China	21° 27′ N	111° 0′ E	Holocene
Hylobatidae gen. indet.	sp.	Gaozhou	Guangdong	China	21° 52′ N	110° 52′ E	Holocene
Hylobatidae gen. indet.	sp.	Luoding	Guangdong	China	22° 42′ N	111° 31′ E	Holocene
Hylobatidae gen. indet.	sp.	Maoming	Guangdong	China	21° 36′ N	110° 52′ E	Holocene
Hylobatidae gen. indet.	sp.	Heng County	Guangxi	China	22° 41′ N	109° 17′ E	Holocene
Hylobatidae gen. indet.	sp.	Nanning	Guangxi	China	22° 47′ N	108° 20′ E	Holocene
Hylobatidae gen. indet.	sp.	Yulin	Guangxi	China	22° 37′ N	110° 7′ E	Holocene
Hylobatidae gen. indet.	sp.	Ding′an	Hainan	China	19° 39′ N	110° 20′ E	Holocene
Hylobatidae gen. indet.	sp.	Ling Shui	Hainan	China	18° 31′ N	110° 0′ E	Holocene
Hylobatidae gen. indet.	sp.	Qiongshan	Hainan	China	19° 58′ N	110° 20′ E	Holocene
Hylobatidae gen. indet.	sp.	Wen Chang	Hainan	China	19° 38′ N	110° 40′ E	Holocene
Hylobatidae gen. indet.	sp.	Wuzhi Shan	Hainan	China	18° 47′ N	109° 40′ E	Holocene
Hylobatidae gen. indet.	sp.	Anxiang	Henan	China	29° 24′ N	112° 8′ E	Holocene
Hylobatidae gen. indet.	sp.	Cili County	Henan	China	29° 24′ N	111° 7′ E	Holocene

Table 7.1 (continued)

Genus	Species (original and current equivalent)	Locality	Province	Country	Latitude	Longitude	Period
Hylobatidae gen. indet.	sp.	Dayong	Henan	China	29° 10′ N	110° 28′ E	Holocene
Hylobatidae gen. indet.	sp.	Li Xian	Henan	China	29° 39′ N	111° 43′ E	Holocene
Hylobatidae gen. indet.	sp.	Linli County	Henan	China	29° 27′ N	111° 37′ E	Holocene
Hylobatidae gen. indet.	sp.	Shimen	Henan	China	29° 36′ N	111° 22′ E	Holocene
Hylobatidae gen. indet.	sp.	Guangnan	Yunnan	China	24° 3′ N	105° 7′ E	Holocene
Hylobatidae gen. indet.	sp.	Longling	Yunnan	China	24° 35′ N	98° 2′ E	Holocene
Hylobatidae gen. indet.	sp.	Luxi County	Yunnan	China	24° 28′ N	103° 47′ E	Holocene
Hylobatidae gen. indet.	sp.	Pu′er	Yunnan	China	23° 3′ N	101° 4′ E	Holocene
Hylobatidae gen. indet.	sp.	Yuanjiang	Yunnan	China	23° 30′ N	102° 0′ E	Holocene
Hylobatidae gen. indet.	sp.	Anji	Zhejiang	China	30° 39′ N	119° 42′ E	Holocene
Hylobatidae gen. indet.	sp.	Tianmu Shan	Zhejiang	China	30° 20′ N	119° 30′ E	Holocene

Boundary dates for the geological epochs are as follows: Pliocene-Early Pleistocene: 1.8 Ma; Early Pleistocene- Middle Pleistocene: 0.78 Ma; Middle Pleistocene – Late Pleistocene: 0.13 Ma; Late Pleistocene – Holocene: 0.001 Ma (10 Ka). Locality data generalized to 1 million: 1.

in Southeast Asia. The study of sea level changes requires an understanding of variations in the structure and volume of oceans, the conformation of ocean basins, and changes in the vertical dimensions of coasts. Readers should appreciate that these details are beyond the scope of this report and that further information should be sought from the relevant primary geological reports (Haq et al. 1987; Fleming et al. 1998; Hall 2001, 2002). Alternating periods of exposure and inundation of portions of the Sunda Platform and Sunda Shelf dramatically affected the distribution of gibbons through time by the creation and elimination of land bridges.

The distribution and dispersal of gibbons in the past was also constrained by the courses of large rivers: the Yangzi to the north, and – at different times – the Mekong, Salween, and Irrawaddy (or Ayeyarwady) successively to the west (Geissmann 2002). These rivers are ancient waterways that share upper reaches in the eastern Himalaya and Heng Duan Mountains, where they have carried large volumes of water through erosion-resistant rocks for tens of millions of years (Chaplin 2005). The trenchant gorges scoured by the rivers have created durable geographic barriers to the dispersal of most terrestrial species and particularly to gibbons who are committed arborealists almost incapable of locomoting on the ground. Through time, gibbons came to occupy more river drainages within Southeast Asia and successively lower-altitude habitats as the animals moved distally along river courses. Changing sea levels and large rivers created opportunities for dispersal and vicariance as well as invasion, extirpation, and reinvasion.

Prior to the estimated origin of the gibbon radiation, sea levels as reconstructed by Haq (Haq et al. 1987) were considerably higher than those at present, and dispersal of mammals into Sundaland was prevented by consistently high sea-level stands. These levels ranged from a low of + 41 m at 16.4 Ma to a high of + 143 m at 15 Ma. By the estimated time of origin of the gibbon radiation, 10.5 Ma, the inundation of large areas of modern coastal Southeast Asia and the Sunda Platform had given way to a major sea-level recession of −80 m, and then another transgression to + 1 m at 9.1 Ma. A sequence of sea-level recessions and transgressions followed in the terminal Miocene and earliest Pliocene: −24 m at 7.9 Ma, + 14 m at 7.0 Ma, and + 90 m at 4.5 Ma. The widely used plate tectonic reconstructions of Southeast Asia by Hall emphasized the movement and deformation of plate blocks (Hall 1996, 1997, 2001, 2002), and all but discounted the importance of changes in sea level (Hall 2002: p. 371) that would have determined the habitability of Sundaland for terrestrial mammals. When these changes are taken into account, what emerges is the picture of a shifting patchwork of forests corridors and coastlines from the latest Miocene onward, which made increasingly southward dispersal of gibbons possible.

Most of the history of gibbons, in particular the early differentiation of the major gibbon sublineages, is not traced by the fossil record. Of the 81 known fossil localities for gibbons, two are from the latest Miocene or earliest Pliocene, two from the Early Pleistocene, 12 from the Middle Pleistocene, 37 from the Late Pleistocene, and 28 from the Holocene. The distribution of fossil gibbon localities is shown in Fig. 7.1.

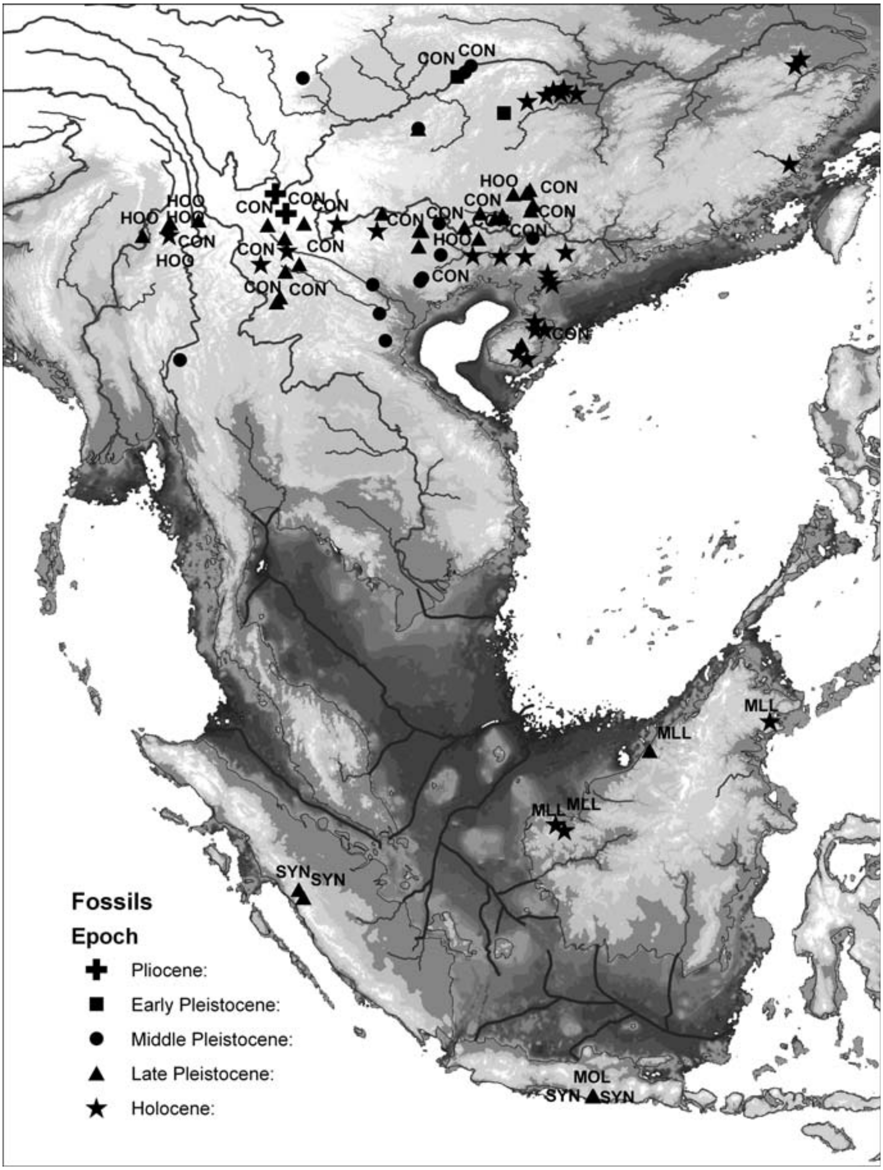

Fig. 7.1 The distribution of fossil hylobatids through time. Genus and species are indicated as follows: SYN = *S. syndactylus*, HOO = *Hoolock hoolock*, CON = *N. concolor*, MLL = *Hylobates muelleri*, MOL = *Hylobates moloch*; fossils that could not be assigned to genus and species are indicated with markers only. Sea levels were modeled at +40 m to −120 m, which are conservative estimates for the extremes of sea-level fluctuation from the later part of the Pliocene to the present

The two earliest hylobatid fossils are of latest Miocene or earliest Pliocene age and were derived from two localities south of the eastward bend of the Yangzi River, north of the Pearl and Red Rivers and east of the Mekong in Yunnan Province of China. They were not assigned to species in their original descriptions. We concur with Chatterjee (2006, this volume) that this region is probably the area of origination for the lineage. This area occupies the middle to southern part of the Yunnan Plateau. Through the later Tertiary, it was an ecologically stable area of moderate elevation (approximately 1000 m) of moist evergreen broad leaf forests that saw high amounts of endemism produced by both refugia and vicariance (Chaplin 2005). Difficult access to the region prevented encroachment from invasives, and also inhibited dispersal (Chaplin 2005). Molecular clock and phylogeographic studies suggest that differentiation of gibbons at the generic level occurred in this area at the end of the Miocene. The sequence and timing of cladogenesis in the gibbon lineage reconstructed by Chatterjee (this volume) is based on a synthesis of molecular studies (Roos and Geissmann 2001; Geissmann 2002; Chatterjee 2006) and shows that crested gibbons (genus *Nomascus*) were the first to branch off the main gibbon lineage, followed by siamangs (genus *Symphalangus*), followed by the genus *Hoolock*, and then *Hylobates*. The details of the likely vicariant events that led to this differentiation are not known, but it is important to note that early lineage-splitting events in gibbon history were not accompanied by long-distance dispersal because most of Sundaland was inundated at this time. The first expansion of the ancestral gibbon range was to the east between the Pearl and Yangzi Rivers, and possibly also between the Pearl and the Red Rivers. Early gibbons probably did not occupy low-altitude, wet evergreen forests.

The first bifurcation of the gibbon lineage was relative to the Paleo-Mekong. The proto-*Nomascus* group spread east of the Mekong and eventually radiated into the southern China and Indochina Bioprovinces, maintaining a distribution initially only east of the Mekong. The gibbons west of the Mekong were the common ancestral stock of *Symphalangus*, *Hoolock*, and *Hylobates*. A gap of over three million years separates the late Tertiary gibbon fossils from two Early Pleistocene hylobatid fossils. One of these comes from a site just south of the Yangzi River in Sichuan Province. This fossil was originally named *Bunopithecus sericus* (Matthew and Granger 1923), but was assigned to *Hylobates* (= *Nomascus*) *concolor* by Gu after a more thorough comparative study (Gu 1989). The other Early Pleistocene fossil is from nearby Hunan.

The Middle Pleistocene saw the westward expansion of gibbons across the headwaters of the Mekong and Salween Rivers into what is now referred to as the Three Rivers Region of northwestern Yunnan Province in China and northeastern Myanmar. Other Middle Pleistocene localities fall immediately south of the Yangzi River in Sichuan Province of China and along the main channel and tributaries of the Pearl River in China and the Red River in Vietnam. One Middle Pleistocene locality is known from north of the Yangzi, and marks the northernmost documented occurrence of a fossil hylobatid. Most Middle Pleistocene gibbons have not been diagnosed to the species level. The expansion of gibbon distributions at this time was made possible by a combination of factors, including environmental amelioration brought about by interglacial climate and changes in the conformation of rivers. Sudden shifts in the courses of rivers and quake dams brought about by tectonic disturbances in this highly seismically active area would have made it possible for gibbons to disperse across rivers and tributaries that previously could not have been crossed.

The gibbons that dispersed west of the Paleo-Salween were *Hoolock hoolock*. This species eventually dispersed north of the headwaters of the Irrawaddy into northern Myanmar, eastern India, and Bangladesh. No gibbon fossils have been found west of the Irrawaddy. The gibbons remaining in the narrow region were constrained by the Salween to the west and the Mekong to the east. This group included the ancestors of *Symphalangus syndactylus* and *Hylobates* spp. These animals began to disperse southward as climatic conditions deteriorated and falling sea levels exposed more of the Sunda Shelf and Sunda Platform. This is attested by a fossil locality lying just east of the Salween River in Thailand. Expansion of the range of gibbons occurred first along the western side of the Mekong in Thailand, and eventually along a forest corridor into the Malay Peninsula and Sumatra. By the end of the Middle Pleistocene and earliest Late Pleistocene, depressed sea levels made possible the colonization of Java and Borneo.

"Sundaland" or the Sunda Shelf is depicted in various configurations on maps of the Pleistocene topography of Asia. At its brief maximum extent, it comprised the area between Borneo, Sumatra, Java, and the south of Indochina (Voris 2000) and covered various geological provinces. The Sunda Platform geologic province extends from north of Natuna Island across to Singapore and the east coast of southern Sumatra to just south of Bangka Island; it then crosses back eastwards to Belitung Island and into southern Borneo, incorporating most of that island's western and central districts (Bishop 2000a, b; Doust and Noble 2008). The Sunda Platform geologic province is more stable than adjacent areas. Between the Sunda Platform and Java are the North Java Basin and East Java Basin. North of the Sunda Platform are the West Natuna, Panjang, Cardomomes, Mekong, Cuulong, Vung Tau, Malay, and Thai Basins. Unlike the Sunda Platform, these basins have been subjected to extreme deformation. They are being compressed by the Indian and Australian tectonic plates at a rate of about 60 mm per year. The cumulative effect of this movement over the last 10–15 Ma has been hundreds of kilometers of crustal deformation and compression.

Sundaland, as exposed during most of the Late Pleistocene, was a region of low relief, covered with poorly drained forests and swamps and dissected by large rivers (Voris 2000). The course of the major paleo-rivers and land areas of Sundaland is reconstructed in Fig. 7.2. The rivers of Sundaland were large and access across them was limited. Part of northern Sundaland was drained by the Paleo-Siam-Chao Phyra river and encompassed some one million km^2, or approximately half of the area of the Yangzi or Mekong river drainage basins.

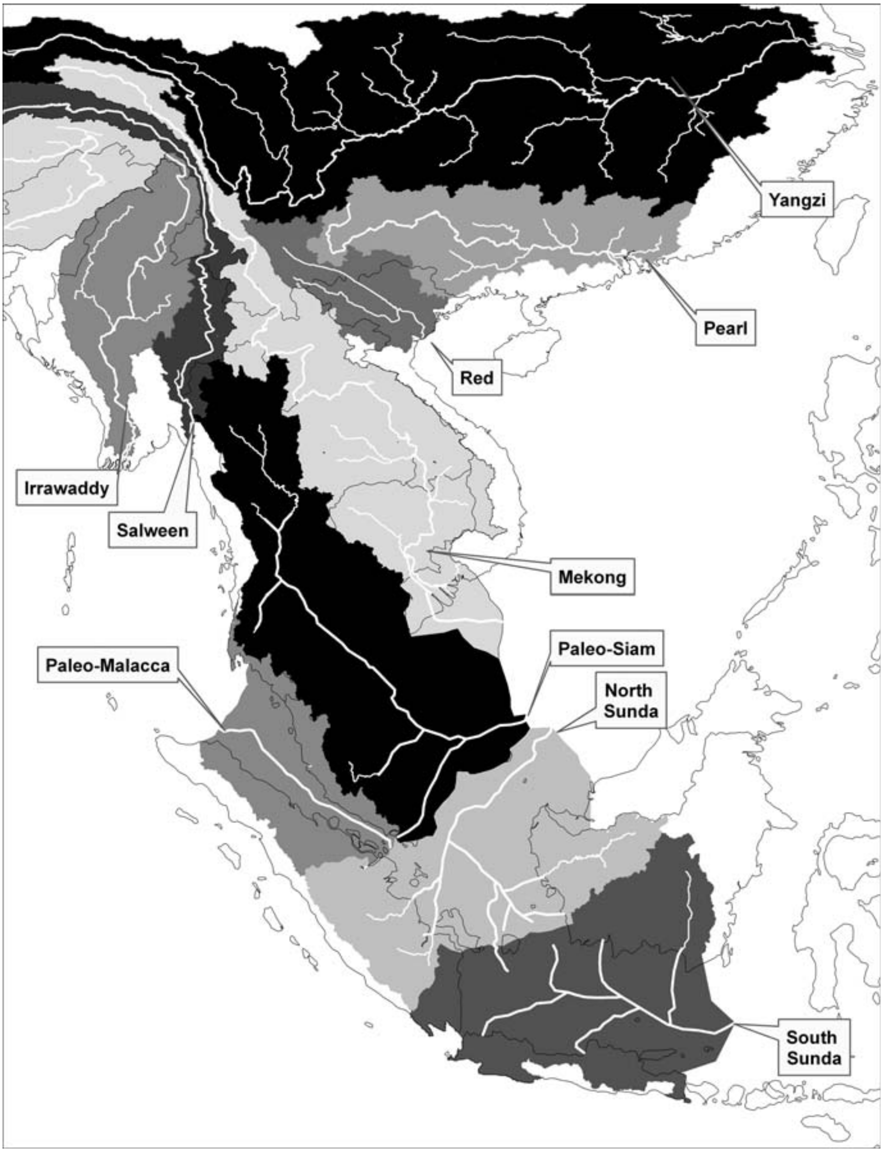

Fig. 7.2 The courses and drainages of the paleo-river of Sundaland, following the methodology and naming conventions of Voris (2000). River courses were drawn with respect to basin geometry and current bathymetry as derived from USGS ETOPO 2 data, and information derived from seismic investigations conducted in connection with oil exploration (Bishop 2000a, b; Nguyen and Hung 2004; Doust and Noble 2008). Continental river courses and catchment areas were derived from USGS HYDRO1K data

The Paleo-North Sunda river drained the remaining roughly 750,000 km^2 of the northern part of the Sunda Platform. The Paleo-South Sunda river drained the southern part of the Sunda Platform and the basin of the Java Sea, an area that encompassed 800,000 km^2. Sumatra was separated from the future Malay Peninsula by the Paleo-Malacca river, which drained an area of 350,000 km^2. Being located in areas of equatorial rainfall, these paleo-rivers carried prodigious volumes of water and would have posed formidable barriers to gibbon dispersal, even during the driest intervals of the Late Pleistocene.

By the Late Pleistocene, a large number of hylobatid fossils mostly assigned to *Nomascus concolor* are recognized within the Pearl River drainage, and thus south of the Yangzi and east of the Mekong in southeastern China. A smaller number assigned mostly to *Hoolock hoolock* were distributed between the Irrawaddy and Salween Rivers in far western Yunnan Province of China and eastern Myanmar. A few were found in the distal extremities of Southeast Asia, with the southern-most fossils attributed to *Symphalangus syndactylus* on the Indonesian islands of Java and Sumatra, *Hylobates moloch* (= *leuciscus*) on Java, and *Hylobates muelleri* on Borneo (Sarawak and Sabah, Malaysia). The pattern and timing of hylobatid dispersal into Sundaland bears similarities to those of freshwater fishes, which were equally constrained by rivers (Yap 2002).

The Holocene witnessed a re-radiation of gibbons into the northern areas along the Yangzi and an expansion of the range of gibbons into nearly all of previously occupied areas. Known Holocene occurrences of hylobatids include clusters of sites in mostly low-lying regions south of the Yangzi River – in Hunan, Guangdong, and Hainan Provinces of China – that have yielded fossils of indeterminate species. Three localities for *H. muelleri* on Borneo are also known. The *lar* group of gibbons probably originated in southern Sundaland and dispersed northward toward the Heng Duan Range, with populations constrained by the tributaries of the Mekong, Salween, and Irrawaddy Rivers. Some *lar* group gibbons eventually became sympatric with *Symphalangus syndactylus*.

Life History, Diet, and the Evolution of Gibbons

The Late Miocene witnessed dramatic changes in the diversity and primacy of catarrhine lineages in Africa and Eurasia, with a marked decline in diversity and distribution of hominoids and a gradual increase in diversity and distribution of cercopithecoids (Jablonski and Kelley 1997; Jablonski et al. 2000; Barry et al. 2002; Jablonski 2005). The radiation of gibbons was a conspicuous and important exception to this trend, but the relative success of the group relative to other hominoids demands an explanation.

Hylobatids and other hominoids are characterized by an advanced age for the onset of reproduction, long gestation periods, long weaning periods, and long interbirth intervals (Table 7.2) (Jablonski et al. 2000). Mammals with such

Table 7.2 Life history parameters of gibbons from China and Southeast Asia compared to *Macaca mulatta* and *Pongo pygmaeus*

Species	Adult mass, male (g)	Adult mass, female (g)	Neonatal mass (g)	Age at first birth	Gestation (d)	Weaning age (yr)	Interbirth interval (yr)
Hylobates lar	5940	5303	389	10	199–215	1.5–2.0	2.0–4.0
Symphalangus syndactylus	10913	10600	537	–	230–235	1.0–2.0	2.0–3.0
Pongo pygmaeus	74483	37143	1750	12.0–15.0	244	3.0–4.0	7.0–8.0
Macaca mulatta	7883	4743	475	4.0	167	0.5–1.0	1.0

Data were collected from the literature on adult body mass (Leigh 1994), neonatal body mass (Hayssen et al. 1993; Geissmann and Orgeldinger 1995), age at first birth (Hayssen et al. 1993), gestation periods (Galdikas and Wood 1990; Hayssen et al. 1993; Markham 1994), weaning age (Chivers and Raemaekers 1980; Treesucon 1984; Hayssen et al. 1993; Lappan 2005), and interbirth intervals (Galdikas and Wood 1990; Hayssen et al. 1993).

slow life histories are characterized by high parental investment in low numbers of offspring per lifetime, and a low intrinsic rate of increase of population. This pattern originally evolved under the more stable environmental conditions of the early and middle Miocene in Eurasia (Kelley 1997), characterized by low to moderate levels of seasonality and more highly predictable regimes of forest productivity (Janis 1993; Morley 2000; Morley 2002). Hominoid life history parameters were established early in the Miocene, when extensive belts of low-seasonality forests were widespread. The highest levels of diversity and the maximum total distribution area of hominoid species were attained when Miocene forests reached their areal maxima, approximately 17–12 Ma (Kelley and Pilbeam 1986; Andrews 1992). Apart from species in the human lineage, no hominoid ever significantly utilized nonforest habitats.

The subtropical and, especially, the tropical forests of the Miocene forests produced juicy fruits and leaf flush on a regular basis and this characteristic undoubtedly sustained hominoid populations living there. Anatomical evidence suggests that at least three groups of Miocene apes, in addition to the hylobatids and orang-utan ancestors, utilized suspensory postures and locomotion, primarily as an adaptation to harvest widely separated, high-quality food items (Andrews et al. 1997). The Hylobatidae took this adaptation to anatomical and behavioral extremes.

Of all the apes, hylobatids have exhibited the most flexibility in terms of abilities to survive periods of environmental change and withstand increases in seasonality. Gibbons maintained distributions in subtropical environments throughout the Pleistocene whereas the orangutan (*Pongo*) and *Gigantopithecus* did not (Jablonski et al. 2000). Large hominoids paid the metabolic penalty of a combination of larger body size and encephalization by not being able to survive in forests in which seasonality had become extreme. When tree fruiting events became so irregular and widely spaced that animals could not maintain their body weight and first female reproduction was greatly delayed, the chances of survival were greatly reduced. Marked increases in seasonality would have had a particularly adverse effect on pregnant or lactating females, who could not forage as widely for preferred foods. Gibbons largely avoided this problem with their smaller body mass and, thus, lower absolute energy requirements. Also in their favor were levels of encephalization comparable to cercopithecoids and a highly energy-efficient mode of locomotion that allowed them to travel swiftly through the forest canopy to reach available high-quality foods. Today, young leaves are a significant component of the diet of most gibbons but, as is the case with larger hominoids, ripe fruits with juicy pulps are undoubtedly their preferred food items (Chivers 1984; Elder this volume). Populations of *Nomascus concolor* inhabiting evergreen broadleaf forests in southwestern Yunnan prefer fruits when they are available, but become nearly exclusively folivorous when they are not (Lan 1993). The ability of gibbons to undertake some food-switching permits them to inhabit the higher altitudes of evergreen broadleaf forests (at approximately 1000–2000 m), but not the higher coniferous forests, which – if they are inhabited by primates at all – are the homes of colobine monkeys like the snub-nosed langurs of China. Of all the hominoids, only gibbons succeeded in subtropical forest environments where others failed, but in habitats of moderate altitude (>1500 m) their populations are stressed and their densities are low. Among the *Hylobates lar* of Khao Yai, Thailand, populations at higher altitudes exhibit lower densities, delayed onset of reproduction, and longer interbirth intervals than those at lower altitudes (Warren Brockelman, pers. comm.). Gibbon food preferences limit them to certain kinds of forest with particular types of food supply (Chivers 1984).

Despite their greater ecological flexibility relative to larger hominoids, hylobatids experienced southern compression of their range because of the episodic and severe climatic changes of the Pleistocene, and the marked fluctuations in environmental seasonality they created. Shifts in gibbon distribution tracked the southward shifts of the tropical and subtropical zones as climates deteriorated, sea levels fell, and Sundaland expanded. Natural populations of animals like gibbons respond to climatic change by latitudinal shifts in abundance or geographic range boundaries or both (Graham et al. 1996; Roy et al. 1996). Environmental changes during the Pleistocene in eastern and southeastern Asia were more marked than in other parts of the Northern Hemisphere, because the local climatic effects of the Himalayas and Qinghai-Xizang (Tibetan) Plateau magnified the orbitally induced climatic fluctuations associated with glacials and interglacials worldwide (Jablonski et al. 2000) and because of immense increases in southerly land mass resulting from exposure of the Sunda Shelf and Sunda Platform. Heightened environmental seasonality at all latitudes, increasing environmental heterogeneity and fragmentation, an increasing potential for physical isolation of populations as a result of habitat fragmentation, and changes in the configuration of biogeographic corridors were the most important consequences of these changes for mammalian populations (Ferguson 1993; Jablonski 1993).

The relatively great antiquity of the gibbon radiation begs the question as to why gibbon species exhibit so little morphological, ecological, or behavioral variation. Warren Brockelman (this volume) has proposed that the relative lack of behavioral diversity within the family Hylobatidae was due to ecological and associated morphological constraints. The fundamental constraints to gibbon diversification were those of food preference and obligate arboreality, which were heritage characteristics handed down from their Miocene ape ancestors (Jablonski and Brockelman 2003). High-quality foods such as ripe fruits and young leaves are not only preferred but also essential for normal reproduction in ape species with slow life history parameters. As for obligate arboreality, the locomotor anatomy – specifically the relatively long forelimbs and short hindlimbs – that is well suited to bridging postures and suspensory locomotion in the high forest canopy also precludes extensive terrestriality. Gibbons are truly prisoners of the forest canopy.

The most morphologically distinct member of the Hylobatidae, the siamang, is the only hylobatid that lives in sympatry with any others – with *H. lar* in peninsular Malaysia and northern Sumatra and with *H. agilis* in southern Sumatra. The distribution of other hylobatid species overlaps little because the animals' shared preference for often widely distributed juicy fruits leads to enforced allopatry. Siamangs, with their diet composed of somewhat more leaves and less fruit than smaller gibbons, have evolved the most monkey-like dental and gut adaptations of the hominoids. Their larger body evolved *pari passu*, being related to lower food quality and the need for longer gut retention times. This may have been related to their use of higher-altitude forests.

The gibbon niche is defined by small body size, energetically efficient arboreal locomotion, small group size, and territorial behavior (Jablonski and Brockelman 2003). Further, the food resource requirements and territorial behavior of gibbons have prevented sympatry between the species (excepting the siamang), and hence largely restricted adaptive radiation within the family.

Summary and Conclusions

The fossil record of the Hylobatidae is not rich, but it is informative. Although fossils representing putative Miocene Hylobatidae do not exist (with the possible exception of *Laccopithecus robustus*), gibbon fossils from the latest Miocene and earliest Pliocene indicate that gibbons probably originated on the Yunnan Plateau, in a region of moderate altitude (about 1000 m) bounded by the Yangzi River to the north, the Pearl and Red Rivers in the south, and the Mekong to the west. Differentiation of the ancestral hylobatid stock into generic lineages probably occurred in the late Miocene and early Pliocene, as suggested by molecular clock analyses, but these cladogenetic events probably were not accompanied by a marked or permanent southward dispersal of gibbons because Sundaland was inundated periodically during the late Miocene and markedly (with a +90 m sea level transgression) at 4.5 Ma. Through time, dispersal of gibbons has been restricted most strongly by rivers, with the courses of the Yangzi, Mekong, Salween, and Irrawaddy rivers confining gibbon dispersal, especially westward. The southward dispersal of gibbons into the southern parts of Sundaland probably occurred only in the Pleistocene and was confined by rivers, mirroring that of freshwater fishes.

The environmental deterioration of the Pleistocene did not affect gibbons as seriously as it did other hominoids. Hylobatids were driven into lower-altitude habitats during the Middle and Late Pleistocene, but they survived probably because of their smaller body size (and absolutely lower food requirements), relatively smaller brains, highly vagile habitus, and food-switching abilities. The gibbon niche may be a highly specialized one, but it has survived the test of time.

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Part III
Diet and Community Ecology

Chapter 8
Hylobatid Diets Revisited: The Importance of Body Mass, Fruit Availability, and Interspecific Competition

Alice A. Elder

Introduction

Hylobatid Ecology

In general, hylobatids are ripe-fruit specialists (MacKinnon and MacKinnon 1980; Chivers 2001) that use figs as fallback resources (Marshall 2004; Marshall et al. this volume). Despite the widespread assumption that siamangs (*Symphalangus syndactylus*) are true folivores, the idea that siamangs are dependent on figs to the same degree as other hylobatids is not new. Chivers and Raemaekers (1986) proposed that siamangs are more accurately described as "fig seekers," an idea supported by Palombit's (1997) research. Chivers and Raemaekers (1986) labeled small-bodied gibbons, by contrast, as fruit-pulp specialists. However, both Palombit (1997) and Marshall (2004) found that small-bodied gibbons (*H. lar* and *H. albibarbis* respectively) emphasized fig eating to the same extent as siamangs. Both siamangs and white-handed gibbons have been observed to preferentially feed on figs, even when other, more sugary fruits were available (Palombit 1997). Although nutritionally inferior to sugary fruits, figs occur in large patches, have high species diversity at individual sites and fruit asynchronously both within and between species (Raemaekers 1978b; Raemaekers et al. 1980). Thus, for gibbons, figs have the potential to provide a stable food source to meet their basic energetic requirements.

However, fruit availability differs between sites, so that the degree to which each hylobatid population depends on figs may in fact reflect fig availability (Palombit 1997). For example, fig abundance and density are higher in northern Sumatra (Palombit 1992) than in Malaysia (Raemaekers et al. 1980). At sites where figs are more plentiful, hylobatids may exploit the local fig abundance, while reducing their leaf consumption (e.g., Palombit 1997). Although Raemaekers

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(1984) argued that hylobatids living in peninsular Malaysia are at their upper metabolic limits for frugivory (i.e., 50%), nearly every subsequent study has found that both siamangs and small-bodied gibbons spend a higher percentage of feeding time on fruit (West 1982; Whitten 1982; Ungar 1995; Palombit 1997; Ahsan 2001; Nurcahyo 2001; McConkey et al. 2002; Marshall 2004). Hylobatids have also been found to be flexible in how they acquire protein. Depending on habitat conditions, gibbons may supplement their highly frugivorous diet with either insects (Whitten 1982; Palombit 1997) or young leaves (Raemaekers 1979; Lan 1993).

The Effects of Body Mass on Hylobatid Energetics

In the past, hylobatid diets have been interpreted with reference to body mass, dividing members of the family into two groups: (1) large-bodied siamangs and (2) all other smaller-bodied gibbon species (Raemaekers 1979; Raemaekers 1984). Siamangs (mean female body mass 10.7 kg), which are about twice the body mass of other hylobatids (mean female body mass 6.18 kg), are expected to be constrained less by the energy content of their diet and more by their absolute food intake (Smith and Jungers 1997). Because basal metabolic rate (BMR) scales with body mass (i.e., $\text{BMR} = \text{body mass}^{3/4}$), larger-bodied animals expend less energy and require less food per unit body mass, yet require absolutely more food than smaller-bodied organisms (Kleiber 1932). Thus, larger-bodied animals are able to rely on lower-quality foods. However, this simplistic analysis overestimates the size difference between siamangs and other hylobatids. Small-bodied gibbons in fact vary considerably in body mass, with mean female masses ranging from 5.34 to 6.58 kg in the genus *Hylobates*, 6.58–6.87 kg in *Hoolock*, and 7.32–7.79 kg in *Nomascus* (Smith and Jungers 1997).

Primates select foods based on their relative nutrient content, maximizing the intake of protein and readily available energy. In contrast to fruits, leaves are high in protein content, but low in easily metabolized carbohydrates (Waterman 1984). However, to access the protein contained in leaves, folivores must contend with structural cellulose, secondary compounds, and toxins. The longer foliage remains in the gastrointestinal tract, the more fermentation and nutrient uptake can occur (Chivers and Hladik 1980). Across the primate order, the percentage of feeding time spent on leaves has been found to be positively correlated with body mass (Clutton-Brock and Harvey 1977). Because gut passage time (i.e., volumetric dimensions of the digestive tract) increases with body mass, larger-bodied species in general are able to absorb more nutrients from foliage than smaller-bodied ones (Lambert 1998). Siamangs, therefore, are thought to be able to eat more leaves than smaller-bodied hylobatids.

Competition Between Hylobatid Species

If two species occupy the same ecological niche and geographic area, one will be competitively excluded unless the two diverge in some dimension of niche use (Brown and Wilson 1956). Previous studies of sympatric primates have upheld these predictions; in areas of overlap, species of African cercopithecines (Gautier-Hion 1980; Mitani 1991; Nakagawa 2003; Wahungu 1998), Asian cercopithecines (Eudey 1981), South American platyrrhines (Guillotin et al. 1994; Heymann and Buchanan-Smith 2000; Stevenson et al. 2000), and Malagasy strepsirhines (Ganzhorn 1989; Tan 1999; Vasey 2000; Radespiel et al. 2003) partition niche space by consuming different food items or dividing the habitat structurally. Patterns of divergence often reflect differences in energetic constraints and vary with ecological conditions (Guillotin et al. 1994; Wahungu 1998; Vasey 2000). In seasonal environments niche overlap may decrease with resource availability, reducing direct competition at crunch times (Hladik 1977; Stevenson et al. 2000).

Small-bodied hylobatid species are distributed over a broader geographic area (from as far south as Java to as far north as China) than siamangs and may either be sympatric or allopatric with siamangs (Geissmann 1995). Small-bodied gibbons are generally allopatric in distribution, with only narrow hybrid zones in Thailand, Malaysia, and Kalimantan (Brockelman and Gittins 1984; Gittins 1978; Marshall and Brockelman 1986; McConkey et al. 2002). Siamangs, on the other hand, overlap with another gibbon species (either *H. lar* or *H. agilis*) throughout their range (Geissmann 1995). Therefore, siamangs always face interspecific competition, and competition over fig resources should be especially high (Raemaekers 1978a, 1984; O'Brien et al. 2004). The large body size of siamangs is thought to play a key role in permitting the coexistence of siamangs and smaller-bodied gibbons (Raemaekers 1984). Since siamangs are expected to spend more time eating leaves than other gibbon species, the level of direct competition between hylobatids should be reduced when in sympatry.

While ecological theory predicts niche divergence among similar species living in sympatry (Brown and Wilson 1956), sympatric hylobatid species have been shown to overlap broadly in ecology, using the same part of the canopy (Raemaekers 1977; MacKinnon and MacKinnon 1980) and eating the same food species, sizes, and parts (Raemaekers 1977, 1979, 1984; Palombit 1997). Siamangs and white-handed gibbons may, however, differ in finer scale parameters of their diets. For example, in northern Sumatra both species were predominantly frugivorous, ate large quantities of figs, and acquired most of their protein from insects; but while siamangs spent more time eating young leaves (16% of siamang vs. 4% of white-handed gibbon feeding time), white-handed gibbons ate more pulpy fruits (26% of white-handed gibbon vs. 18% of siamang feeding time) (Palombit 1997). If, in fact, siamangs and small-bodied gibbons are limited by different foods (young leaves vs. pulpy fruits), then differences in their population densities may reflect variation in resource availability. O'Brien et al. (2004) point out that within the siamang distribution range, population densities increase from south to north for small-bodied gibbons, but decrease from south to north for siamangs. This pattern may emerge from a higher availability of figs and large-patch fruits in the southern areas of overlapping siamang and small-bodied gibbon habitat (Palombit 1997;

O'Brien et al. 2004). The coexistence of sympatric hylobatids may be possible due to the higher availability of large, high-quality fruit patches in habitats where siamangs live sympatrically with other species compared with habitats where small-bodied gibbons live allopatrically. Siamangs are expected to have a competitive advantage over small-bodied gibbons in exploiting these patches due to their larger body size and longer feeding bouts (Raemaekers 1978a). In contrast, the density of smaller fruit trees increases from south to north, and small-bodied gibbons may be more efficient at reaching and consuming these patchily distributed resources than siamangs (O'Brien et al. 2004).

New Ways to Understand Hylobatid Diets

A great deal of our current understanding of hylobatid diets is based on early comparisons that emphasized sites in Peninsular Malaysia (Chivers 1974; Raemaekers 1977; MacKinnon and MacKinnon 1980; Gittins 1982). These studies laid the groundwork for current gibbon research and provided testable models (e.g., Raemaekers 1984) for understanding hylobatid ecology. In the past three decades, a number of new studies have been conducted (Table 8.1), covering a much wider range of the gibbon distribution across Southeast Asia and including a larger number of taxa. These dietary and habitat data, in conjunction with more detailed estimates of body mass (Smith and Jungers 1997), may be used to examine the overarching patterns in gibbon ecology. In particular, it is now possible to quantitatively examine the variables that influence diets across the family.

In early phylogenetic reconstructions, siamangs were separated from all other hylobatids based on the differences in morphology (Creel and Preuschoft 1976; Bruce and Ayala 1979; Creel and Preuschoft 1984). More recently, however, molecular and behavioral studies have revealed that the hylobatids may be divided into four genetically and vocally distinct genera: *Symphalangus* (siamangs), *Nomascus* (crested gibbons), *Hylobates* (members of the lar group), and *Hoolock* (Brandon-Jones et al. 2004; Mootnick and Groves 2005). Genetic studies of the relationships among these four genera have suggested that siamangs in fact may be more closely related to one of the small-bodied gibbon groups (*Nomascus*) than the three small-bodied genera are to each other (Müller et al. 2003). However, these relationships are still not fully resolved (Takacs et al. 2005; Chatterjee this volume). Therefore, it is important to examine differences in gibbon diets among all four genera. Although data from several populations are available for *Symphalangus* ($N = 6$) and *Hylobates* ($N = 13$), data are extremely limited for *Nomascus* (this study $N = 2$) and *Hoolock* (this study $N = 1$). Additionally, data are only available from crested gibbons at the extreme end of their distribution in China, where they may be unusually folivorous and live at the highest altitudes and coldest temperatures of any hylobatid habitat (Bleisch and Chen 1991; Lan 1993).

Though the genetic distances among the four genera of hylobatids are equal or greater than those between *Pan* and *Homo* (Roos and Geissmann 2001), this does

Table 8.1 Data used in the analyses

Species	Site	Country	Source
Symphalangus syndactylus	Ulu Sempam	Malaysia	(Chivers 1974)
Symphalangus syndactylus	Krau Reserve, Kuala Lompat	Malaysia	Raemaekers (1977)[1]
Symphalangus syndactylus	Krau Reserve, Kuala Lompat	Malaysia	MacKinnon and MacKinnon (1980)[1]
Symphalangus syndactylus	Ketambe, Sumatra	Indonesia	Palombit (1992)
Symphalangus syndactylus	Way Canguk, B.B.S., Sumatra	Indonesia	Lappan (2005)[2]
Symphalangus syndactylus	Way Canguk, B.B.S., Sumatra	Indonesia	Nurcahyo (2001)[2]
Hylobates lar	Krau Reserve, Kuala Lompat	Malaysia	Raemaekers (1977)[3]
Hylobates lar	Krau Reserve, Kuala Lompat	Malaysia	MacKinnon and MacKinnon (1980)[3]
Hylobates lar	Ketambe, Sumatra	Indonesia	Palombit (1992)
Hylobates lar	Mo Singto, Khao Yai	Thailand	Bartlett (1999)
Hylobates lar	Tanjong Triang	Malaysia	Ellefson (1967) and Ellefson (1974)
Hylobates lar	Phu Khieo	Thailand	Umponjan (2006)
Hylobates klossii	Paitan, Siberut	Indonesia	Whitten (1982)
Hylobates agilis	Sungai Dal	Malaysia	Gittins (1982)
Hylobates albibarbis	Gunung Palung, W. Kalimantan	Indonesia	Marshall (2004) and Marshall et al. (this volume)
Hylobates muelleri X albibarbis	Barito Ulu, Kalimantan	Indonesia	McConkey et al. (2002)
Hylobates muelleri	Kutai, Kalimantan	Indonesia	Leighton (unpubl. data)
Hylobates pileatus	Khao Soi Dao	Thailand	Srikosamatara (1984)
Hylobates moloch	Turalak, Ujung Kulon, W. Java	Indonesia	Kappeler (1981, 1984)
Nomascus concolor	Wuliang & Ailao, Yunnan province	China	Sheeran (1993)
Nomascus concolor	Wuliang, Yunnan province	China	Lan (1993)
Hoolock hoolock	Lawachara & Chunati	Bangladesh	Ahsan (2001)

This table lists the gibbon species, site locations, and references for all dietary and habitat data used in this study. Mean data were used in cases where data were not independent due to overlap in study groups and locations, including data on Malaysian siamangs[1], Sumatran siamangs[2] and Malaysian white-handed gibbons[3].

not automatically translate into ecological differentiation. Even if different gibbon populations have been geographically separated for millions of years, during which time they may have undergone many genetic changes, these groups may still be very similar in behavior and ecology. Generally, selective pressure must act on a population to induce changes in behavioral ecology. Therefore, gibbons may be ecologically analogous across their distribution.

Siamangs are thought to be more folivorous than other gibbon species based on the assumption that with increased body mass, the time spent eating foliage increases (Clutton-Brock and Harvey 1977). Thus, the level of folivory can be compared between siamangs and all other smaller-bodied gibbons. Even if siamangs are not found to differ from other hylobatids in their degree of folivory, this pattern may fit for gibbons overall. However, this relationship has never been quantitatively assessed for hylobatids across their size range. If body mass is not found to significantly influence folivory, then the variance in mass across Hylobatidae may not be enough to cause differences in diet.

Resource availability may be critical in determining the food choice for hylobatids across sites. Variation in hylobatid diets may simply reflect habitat variability, and in turn may be a gauge of gibbons' ecological flexibility. One way to control for resource availability is to examine what small-bodied gibbons eat when living in sympatry with siamangs compared to their dietary choices in allopatry. That is, which are more similar, the diets of two sympatric species, or the diets of two allopatric populations of the same species? However, such an analysis is not possible for siamangs because siamangs are sympatric with small-bodied gibbons throughout their range (Geissmann 1995). A second way to examine the relationship between resource availability and hylobatid diets is with measures of actual food abundance and density for each gibbon habitat. Unfortunately, these data are not available for all locations; instead, proxies of forest productivity may be used.

Because competition between closely related, ecologically similar species is expected to result in niche segregation (Brown and Wilson 1956), the difference in ecology should be greater between sympatric hylobatid species than between allopatric ones. In particular, siamangs are expected to diverge dietarily from the smaller-bodied gibbons with which they share their habitats.

In this analysis I aim to address the following questions:

1. How folivorous are siamangs relative to all other hylobatids?
2. How well is folivory linked to body mass in gibbons?
3. How do the diets of small-bodied gibbons compare when living sympatrically vs. allopatrically with siamangs?
4. What is the relationship between resource availability and hylobatid diets?
5. What is the impact of interspecific competition on gibbon diets?

Methods

Data Collection

I compiled dietary and site data from the available literature and personal communications with researchers from 21 studies at 15 sites across the geographic distribution of the hylobatid family (Table 8.1). This data set included sites from Indonesia (Sumatra, Java, Kalimantan, and Siberut), Malaysia, Thailand, China, and Bangladesh. Data selected were restricted to studies on wild populations that were at least 11 months in duration (Table 8.2). In cases where data were collected from the same location during the same time period (i.e., Lappan 2005 and Nurcahyo 2001; Raemaekers 1977; MacKinnon and MacKinnon 1980), and therefore were not independent, I used site means in the analyses. The data used for analyses included the percentages of feeding time spent eating leaves, fruit, figs, flowers, and insects (Table 8.3), as well as the latitude and mean annual rainfall for each location (Table 8.2). Variables describing local conditions (i.e., mean annual rainfall and latitude) were included in the analyses as proxies of resource availability. Both mean annual rainfall and latitude have been shown to strongly correlate with tree density and diversity (Gentry 1988).

Although siamangs (mean female mass 10.7 kg) are the largest-bodied hylobatids, the other so-called small-bodied gibbons are not of equal mass. *Hylobates* species are the smallest (mean female mass 5.69 kg), *Hoolock* gibbons are slightly heavier (mean female mass 6.58 kg), and members of the genus *Nomascus* are the heaviest (mean female body mass 7.47 kg) (Smith and Jungers 1997). Therefore, it is critical to use more precise estimates of body mass to examine its impact on diets. Body mass data were taken from Smith and Jungers (1997), and only female means were used in the analyses. As all hylobatid species are sexually monomorphic in body size (range of male mass/female mass × 100 = 95.77–111.21), this restriction should not introduce error in the results (Smith and Jungers 1997).

Statistical Analyses

Descriptive Statistics and Mann-Whitney U tests

All statistical analyses were conducted using SPSS version 13.0. I calculated mean dietary values for (1) all hylobatids, (2) siamangs alone, (3) all small-bodied gibbons, (4) small-bodied gibbons living in sympatry with siamangs, (5) small-bodied gibbons living allopatrically, (6) all sympatric gibbon species, and (7) all allopatric gibbon species. Separate Mann-Whitney U analyses were conducted to test whether the percentages of time spent feeding on leaves and fruit (fig and nonfig) differ between (1) siamangs and small-bodied gibbons, (2) small-bodied gibbons living in sympatry and in allopatry with siamangs, and (3) sympatric small-bodied gibbons and siamangs.

Regression Analyses

Bivariate correlations were calculated to explore the strength of the relationships among dietary, body mass, and site variables. To further ascertain how food availability and body mass influence each constituent of hylobatid diets when controlling for other variables, I conducted separate Hierarchical Regression analyses for percentages of time spent eating leaves, fruit, figs, flowers, and insects. For these analyses the potential predictor variables were added in the following order: body mass, mean annual rainfall, and site latitude. The order of the analysis

Table 8.2 Site descriptions

Site	Latitude	Longitude	Rain (mm)	# Groups	# Months	Source
Ulu Sempam	3°N	102°E	1594	3	17	Chivers (1974)
Krau Reserve	3°N	102°E	1982–2000	1 siamang & 1 white-handed gibbon each	24; 7	Raemaekers (1977) and MacKinnon and MacKinnon (1980)
Ketambe	3°N	97°E	3229	2 siamang & 2 white-handed gibbon	29	Palombit (1997)
Way Canguk	5°S	104°E	3500	5	23	Lappan (2005)
Mo Singto	14°N	101°E	2695.2	2	16	Bartlett (1999)
Tanjong Triang	2°N	103°E	3226	4	21	Ellefson (1967)
Phu Khieo	16°N	101°E	1100	1	12	Umponjan (2006)
Paitan	1°S	98°E	4217	1	~24	Whitten (1982)
Sungai Dal	4°N	100°E	1422	1	12	Gittins (1982)
Gunung Palung	1°S	110°E	4500	*	25	Marshall (2004)
Barito Ulu	0°	114°E	2585	2	12	McConkey et al. (2002)
Kutai	0°	117°E		1		Leighton (unpubl. data)
Khao Soi Dao	12°N	102°E	1847	3	18	Srikosamatara (1984)
Turalak, Ujung Kulon	6°S	105°E	3249	1	15	Kappeler (1981) and Kappeler 1(984)
Wuliang & Ailao	24°N	100°E	1500–2600	1; 4	11 total	Lan (1993) and Sheeran (1993)
Lawachara & Chunati	23°N	92°E		3	24	Ahsan (2001)

This table lists site latitude, longitude and mean annual rainfall, as well as the number of groups studied and the duration of study in number of months for each site used in this analysis. *For these data individual gibbon groups were not systematically observed, but rather feeding data were gathered during standardized census walks.

Table 8.3 Dietary descriptions

% Flowers	% Insects	% Leaves	% Fruit	% Figs	Source
5	6	48	41*		Chivers (1974)
6	15	43	14	22	Raemaekers (1977)
7	13	29	28	22	Raemaekers (1977)
0.4	4.5	31.4	36	27	MacKinnon and MacKinnon (1980)
3.6	8.1	43.7	44.6*		MacKinnon and MacKinnon (1980)
1	21	17	18	43	Palombit (1992)
1	24	4	26	45	Palombit (1992)
1	9	22	47	19	Bartlett (1999)
0	0	33	67*		Ellefson (1967)
0	25	2	49	23	Whitten (1982)
3	1	39	41	17	Gittins (1982)
12	0	32	34	22	Lappan (2005)
12	0.1	25	38	25	Nurcahyo (2001)
0	15	13	45	26	Srikosamatara (1984)
1	0	38	61*		Kappeler (1984)
4	8	32	38	24	Leighton (unpubl. data).
7	1	72	21*		Lan (1993)
7	2	10	35	45	Ahsan (2001)
6	0	22	58*		Umponjan (2006)
13.4	0.8	23.8	44.7	17.3	McConkey et al. (2002)
6	0.5	3	65	23	Marshall et al. (this volume)
		43	44		Sheeran (1993)

This table lists the percentage of feeding time spent eating flowers, insects, leaves, nonfig fruit and figs for each hylobatid study used in this analysis. *In cases where only percentage of fruit is listed, the percentages of time spent eating figs vs. nonfig fruits were not treated separately by the researchers.

was chosen based on the null hypothesis that with increased body mass, primates increase the time spent eating leaves, and thus body mass should be the strongest predictor for the degree of folivory (Clutton-Brock and Harvey 1977).

Discriminant Function Analyses

Two discriminant function analyses were conducted to examine whether (1) siamangs and small-bodied gibbons and (2) sympatric and allopatric populations are discriminated accurately by diet.

Results

How Folivorous Are Siamangs Relative to All Other Hylobatids?

Overall, hylobatids across the family's distribution were found to be predominantly frugivorous (total fruit 60%; nonfig fruit 36%), to largely depend on fig fruits (26%), and to spend the rest of feeding time consuming leaves (28%), insects (7%), and flowers (4%). When siamangs were considered separately from all other species, this pattern remained. Small-bodied gibbons (all hylobatids excluding siamangs) spent 63% of their feeding time on fruit (24% on fig and 39% on nonfig), 26% on leaves, 7% on insects, and 4% on flowers, while siamangs alone spent 51% of their feeding time on fruit (29% on fig and 22% on nonfig), 33% on leaves, 10% on insects, and 6% on flowers (Fig. 8.1). Overall, no significant differences were found between small-bodied gibbons and siamangs in their time spent feeding on figs ($U = 14.00$, $p = 0.77$) and leaves ($U = 19.00$, $p = 0.31$). Non-significant trends were, however, found in both the percentage of time spent eating fig and nonfig fruits combined ($U = 12.50$, $p = 0.08$) and the percentage of time spent eating nonfig fruits alone ($U = 5.50$, $p = 0.09$), where small-bodied gibbons spent more time eating fruit than siamangs.

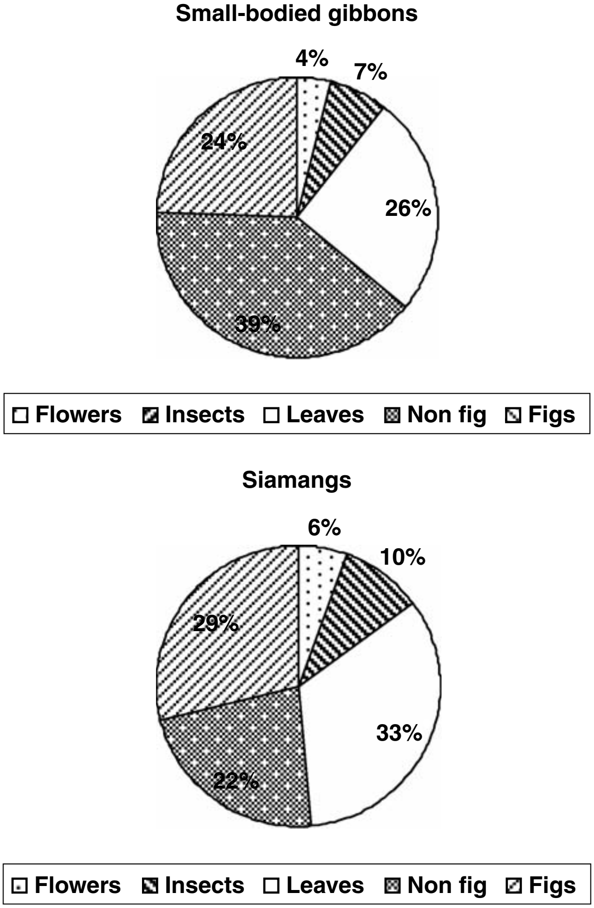


Fig. 8.1 Mean dietary proportions for “small-bodied” gibbons and siamangs based on the percentage of feeding time

Overall, dietary variables did not significantly discriminate between siamangs and small-bodied gibbons (Wilks' Lambda = 0.58, $X^2{}_5 = 5.12$, $N = 14$, $p = 0.40$). The correlations of the dietary variables with the first discriminant function were 0.69 for nonfig fruits, −0.22 for figs, −0.18 for leaves, −0.21 for flowers, and −0.13 for insects. The means of the two groups on this function were −1.50 for siamangs and 0.41 for small-bodied gibbons. Siamangs were accurately classified in 100% of cases, but small-bodied gibbons were misclassified in 27.3% of cases. When folivory and frugivory were considered alone, siamangs and small-bodied gibbons were no more accurately classified (Wilks' Lambda = 0.70, $X^2{}_3 = 3.69$, $N = 14$, $p = 0.28$). The percentages of time spent feeding on leaves, figs, and nonfig fruits correctly classified siamangs in 66.7% of cases and small-bodied gibbons in 81.8% of cases.

How Well Is Folivory Linked to Body Mass in Gibbons?

Bivariate correlations are given in Table 8.4 along with means and standard deviations for all test variables. No significant relationship was found between body mass and the percentage of time spent eating leaves across the Hylobatidae (Fig. 8.2). A significant correlation was found between body mass and the percentage of time spent eating leaves for all small-bodied gibbons ($r = 0.56$, $p < 0.05$). However, this relationship was driven by data for the genus *Nomascus* ($N = 2$), such that when crested gibbons were excluded from the data set there was no significant correlation between body mass and the percentage of feeding time small-bodied gibbons spent on foliage ($r = 0.13$, $p = 0.68$).

Table 8.4 Pearson correlations among major study variables

Variable	Body mass	% Flowers	% Insects	% Leaves	% Fruit	% Figs	Rain	Latitude
Body mass		0.43	0.04	0.36	−0.48*	0.07	−0.04	−0.13
% Flowers			−0.55*	0.20	−0.20	−0.28	−0.08	0.09
% Insects				−0.46	0.16	0.49	0.30	−0.28
% Leaves					−0.91**	−0.64*	−0.61*	0.33
% Fruit						0.54*	0.65**	−0.31
% Figs							0.36	−0.05
Rain								−0.50
Latitude								
M	7.00	4.22	7.43	27.57	59.96	25.66	2551.64	8.29
SD	2.16	3.94	8.65	17.79	15.30	11.17	1009.07	8.66

*$p < 0.05$; **$p < 0.01$

This table lists Pearson correlation values and significance values for the relationships among the major study variables. Descriptive statistics (i.e., means and standard deviations) are also listed for each variable.

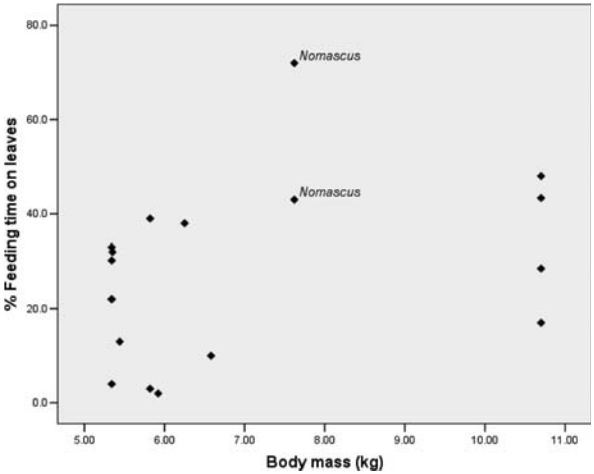


Fig. 8.2 The percentage of feeding time spent eating leaves plotted against species mean female body mass ($r = 0.36$, p is not significant)

No significant correlations were found between the body mass and the percentage of time spent by hylobatids eating figs or insects. There were, however, a significant correlation between body mass and the percentage of feeding time spent on fruit ($r = -0.48$, $p = 0.04$) and a non-significant trend between the body mass and the percentage of time spent eating flowers ($r = 0.43$, $p = 0.08$). Significant relationships were revealed between several dietary constituents. The percentage of time spent eating flowers decreased significantly with the percentage of time spent eating insects ($r = -0.55$, $p = 0.02$). Significant negative relationships were also found between the percentage of time hylobatids consumed leaves and both the percentage of time spent eating combined fig and nonfig fruits ($r = -0.91$, $p < 0.001$; Fig. 8.3) and figs separately ($r = -0.64$, $p = 0.01$).

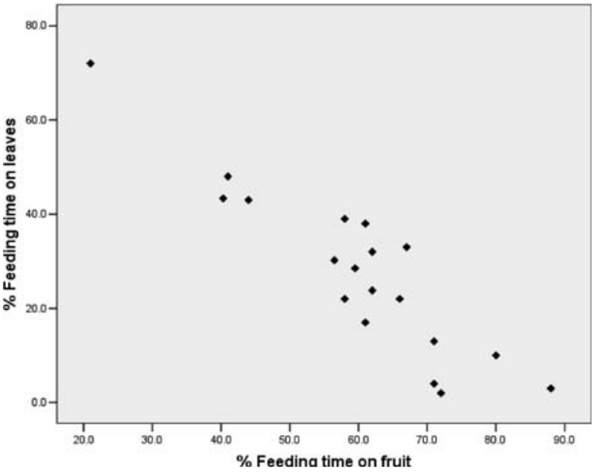


Fig. 8.3 The percentage of feeding time spent eating fruit plotted against the percentage of feeding time spent eating leaves ($r = -0.90$, $p < 0.01$)

A hierarchical regression analysis was conducted, in which potential predictor variables for the degree of folivory (i.e., percentage of feeding time spent eating leaves) were added in the following order: body mass, mean annual rainfall, and site latitude. Rainfall was the best predictor, accounting for 37.1% of the variance in the degree of folivory. Body mass accounted for an additional 15.1% of the variance, while latitude explained only 6.6% of the variance. Both rainfall ($p = 0.01$) and latitude ($p = 0.02$) added significant increments. However, body mass did not explain the variance in time spent eating leaves ($p = 0.15$). A three-variable (mass, rainfall, and latitude) prediction equation emerged as optimal from the analysis, with an overall R^2 of 0.59, $F_{3,14} = 5.24$, $p = 0.02$; the standardized regression coefficients were 0.41 for body mass, −0.45 for rainfall, and 0.30 for latitude.

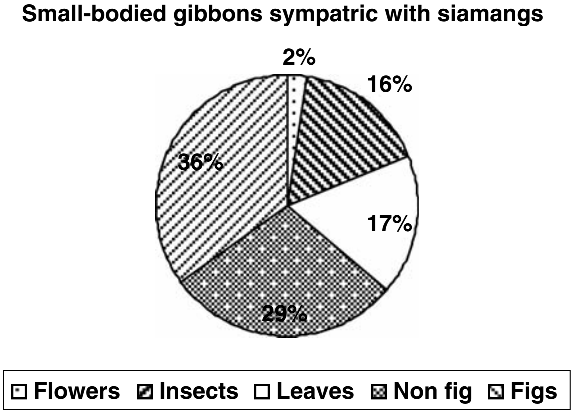
How Do the Diets of Small-Bodied Gibbons Compare When Living Sympatrically vs. Allopatrically with Siamangs?

Compared to small-bodied gibbon populations living with siamangs (36% figs, 17% leaves, 16% insects, and 2% flowers), small-bodied gibbons living without siamangs spent less time eating figs (22%), more time eating leaves (27%), and less time eating insects (5%), but differed little in the percentage of feeding time spent on flowers (4%) (Fig. 8.4). However, no statistically significant differences were found between the percentages of feeding time that small-bodied gibbons living with or without siamangs spent consuming fig and nonfig fruit combined (Fig. 8.5; $U = 11.50$, $p = 0.80$), figs (Fig. 8.5; $U = 2.50$, $p = 0.15$), nonfig fruit (Fig. 8.5; $U = 2.00$, $p = 0.15$), leaves (Fig. 8.6; $U = 9.00$, $p = 0.57$), flowers (Fig. 8.6; $U = 10.00$, $p = 0.79$), or insects (Fig. 8.6; $U = 4.00$, $p = 0.20$).

What Is the Relationship Between Resource Availability and Hylobatid Diets?

Site-specific variables that may serve as proxies for resource availability (i.e., rainfall and latitude) were found to vary significantly with hylobatid dietary variables. Mean annual rainfall was negatively correlated with the degree of folivory (Fig. 8.7; $r = -0.62$, $p = 0.01$) and positively correlated with the degree of frugivory (Fig. 8.7; $r = 0.65$, $p = 0.01$). Latitude, on the other hand, did not significantly vary with any dietary variable.

To tease apart the impacts of resource availability (i.e., mean annual rainfall and latitude) and body mass on gibbon diets, separate regression analyses were conducted for each food type. As indicated above, the results of a hierarchical regression analysis, where folivory was the dependent variable, revealed that mean annual rainfall and latitude, but not body mass, significantly predicted the percentage of time gibbons spent eating leaves.



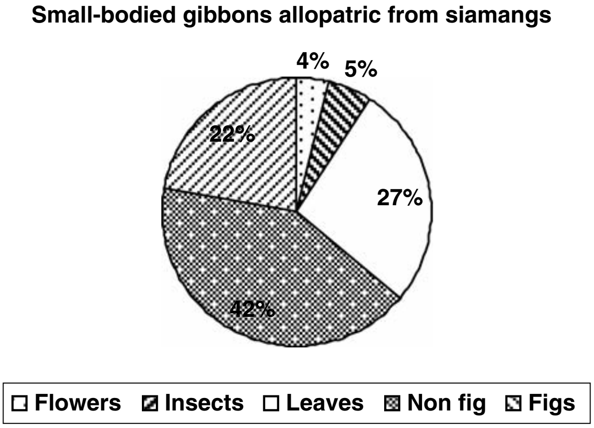


Fig. 8.4 Mean dietary proportions for small-bodied gibbons living sympatrically with siamangs and allopatrically from siamangs based on the percentage of feeding time

A hierarchical regression analysis was conducted, in which the degree of frugivory (percentage of time spent feeding on fig and nonfig fruits combined) was the dependent variable and body mass, rainfall, and latitude were added sequentially as potential predictor variables. Rainfall best predicted the degree of frugivory, accounting for 39.5% of the variance. Body mass and latitude accounted for an additional 24.3 and 9.5% of the variance in the degree of frugivory. Both rainfall ($p = 0.002$) and latitude ($p = 0.002$) added significant increments, while body mass added an increment that approached significance ($p = 0.06$). The optimal three-variable (body mass, rainfall, and latitude) prediction equation had an overall R^2 of 0.73, $F_{3,14} = 10.05$, $p < 0.002$, and the standardized regression coefficients were −0.52 for body mass, 0.44 for rainfall, and −0.36 for latitude.

A hierarchical regression analysis, where the percentage of time spent eating nonfig fruits was the dependent variable and body mass, rainfall, and latitude were added sequentially, revealed that body mass best predicted the

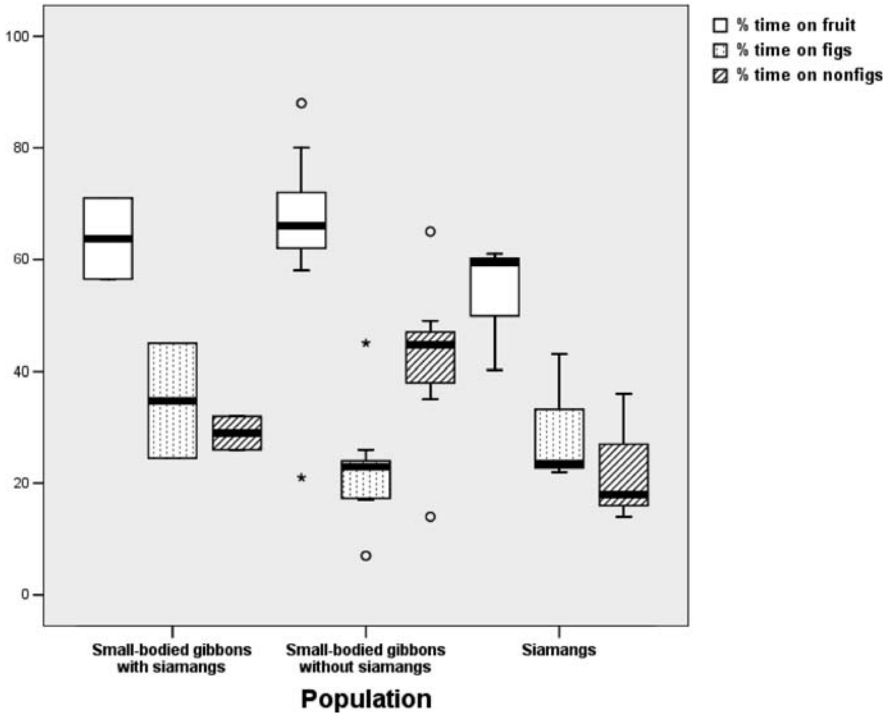


Fig. 8.5 Mean percentage of feeding time spent eating (1) combined fig and nonfig fruits, (2) figs separately, and (3) nonfig fruits separately for small-bodied gibbons living sympatrically with siamangs, small-bodied gibbons living allopatrically from siamangs and siamangs

degree of nonfig frugivory, accounting for 33.9% of the variance. Rainfall and latitude accounted for an additional 25.4 and 8.0% of the variance. However, only rainfall ($p = 0.03$) added a significant increment, while body mass ($p = 0.06$) and latitude ($p = 0.08$) added increments that approached significance. Thus, a non-significant trend was found for the percentage of time spent eating nonfig fruit alone, where the optimal three-variable prediction equation had an overall R^2 of 0.60, $F_{3,10} = 3.52$, $p = 0.08$, and the standardized regression coefficients were −0.61 for body mass, 0.46 for rainfall, and −0.11 for latitude.

Due to the apparent importance of fig availability for gibbon population densities (Marshall 2004), a separate hierarchical regression analysis was conducted for figs alone using the same predictor variables as in the analysis of frugivory as a whole. Latitude was found to best predict the percentage of time spent eating figs, accounting for 19.2% of the variance. Body mass (1.3%) and rainfall (12.1%) explained smaller portions of the variance in the percentage of time gibbons ate figs. However, none of the tested predictor variables added increments that reached the significance level of 0.05.

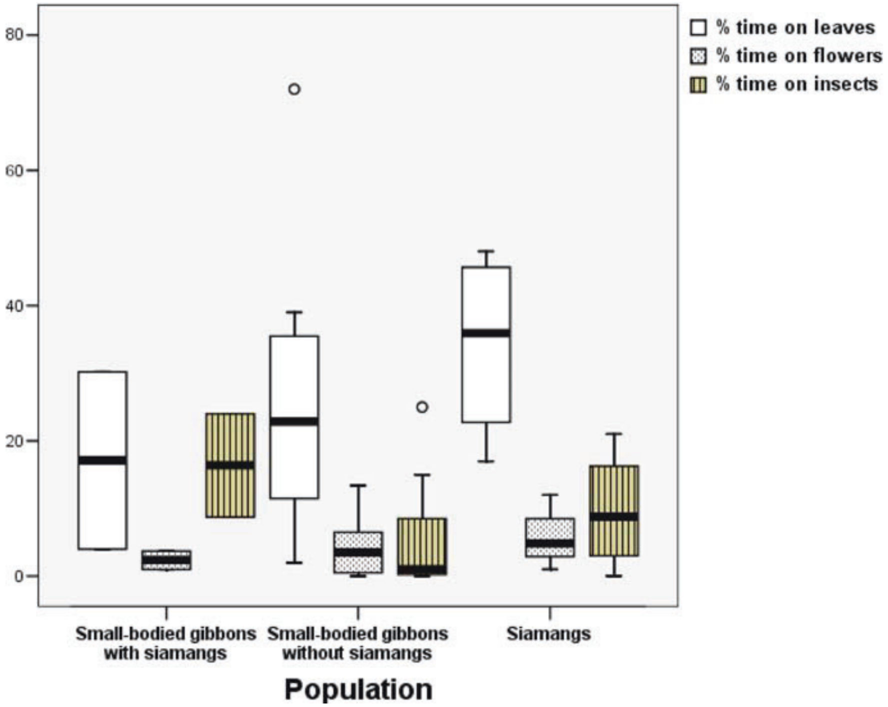


Fig. 8.6 Mean percentage of feeding time spent eating (1) leaves, (2) flowers, and (3) insects for small-bodied gibbons living sympatrically with siamangs, small-bodied gibbons living allopatrically from siamangs and siamangs

Thus, the percentage of feeding time that gibbons spent on figs was not found to significantly relate to body mass, mean annual rainfall, or site latitude.

As no significant relationships were found between the degree of insectivory and the test variables, no further analyses were conducted. Similarly, only a non-significant trend was found between body mass and the percentage of feeding time spent on flowers, while no significant relationships were found between the percentage of time spent eating flowers and either rainfall or latitude. Thus, further analyses were not conducted.

What Is the Impact of Interspecific Competition on Gibbon Diets?

Populations living sympatrically with other hylobatid species were found to adhere to the same dietary profile as those living allopatrically (Fig. 8.9). Sympatric hylobatid populations spent 58% of their feeding time on combined fruit (29% on figs and 31% on nonfig fruits), 26% on leaves, 11% on insects, and 5%

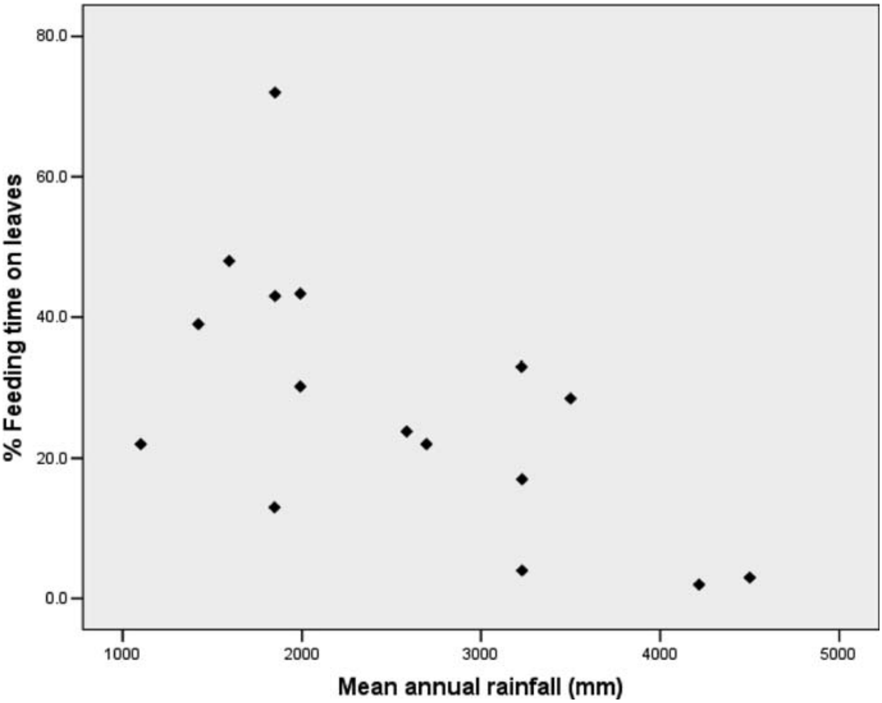


Fig. 8.7 The percentage of feeding time spent eating leaves plotted against mean annual rainfall ($r = -0.61, p < 0.05$)

on flowers. Similarly, allopatric hylobatids spent 62% of their feeding time on combined fruit (23% figs and 41% nonfig fruits), 29% on leaves, 5% on insects, and 4% on flowers. Additionally, sympatric small-bodied gibbons and siamangs did not significantly differ in the percentage of time spent eating combined fig and nonfig fruit (Fig. 8.5; $U = 2.00$, $p = 0.53$), nonfig fruit (Fig. 8.5; $U = 2.00$, $p = 0.80$), figs (Fig. 8.5; $U = 1.00$, $p = 0.40$), leaves (Fig. 8.6; $U = 2.00$, $p = 0.53$), flowers (Fig. 8.6; $U = 1.50$, $p = 0.27$), and insects (Fig. 8.6; $U = 2.00$, $p = 0.53$).

Overall, dietary variables did not significantly discriminate between sympatric and allopatric populations (Wilks' Lambda = 0.53, $X^2_5 = 6.01$, $N = 14$, $p = 0.31$). The correlations of the dietary variables with discriminant function one were 0.43 for nonfig fruit, −0.32 for figs, 0.08 for leaves, −0.15 for flowers, and −0.32 for insects. The means of the two groups on this function were −0.87 for sympatric populations and 0.87 for allopatric populations. Overall, 71.4% of cases were classified correctly, with 28.6% of allopatric cases being misclassified as sympatric and 28.6% of sympatric cases being misclassified as allopatric. Classifications based on levels of frugivory and folivory alone also failed to accurately discriminate between sympatric and allopatric hylobatid populations. For this second analysis only 71.4% of total cases were correctly

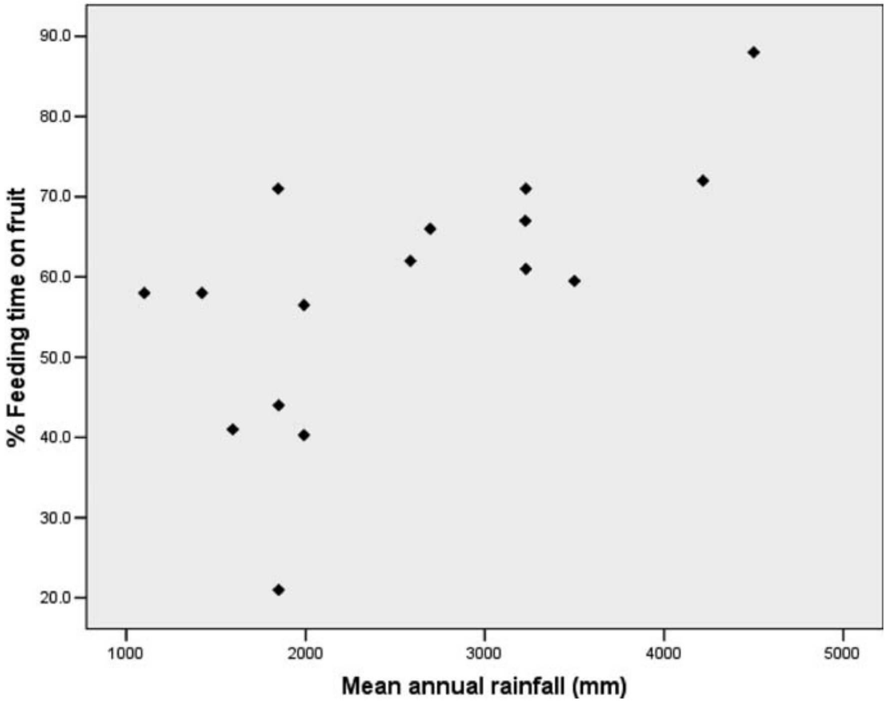


Fig. 8.8 The percentage of feeding time spent eating fruits plotted against mean annual rainfall ($r = 0.65$, $p < 0.01$)

classified, with 85.7% of allopatric cases accurately placed, but only 57.1% of sympatric cases classified correctly.

Discussion

Siamangs Are as Folivorous as Other Hylobatids

Overall, the diet of siamangs does not differ from that of smaller-bodied hylobatids. Results here largely match those found by Palombit (1997): hylobatids, regardless of body size, are frugivorous, spending a large portion of their feeding time on figs. The only qualitative differences found between siamangs and small-bodied gibbons are in the relative time spent eating leaves and nonfig fruits (Fig. 8.1). That is, siamangs are apparently more folivorous than other species (34 vs. 25%), while small-bodied gibbons eat more nonfig fruit (39 vs. 25%). However, no significant difference in folivory is found between these groups. Siamangs and small-bodied gibbons do, on the other hand, significantly differ in their levels of frugivory. Furthermore, results from the discriminant

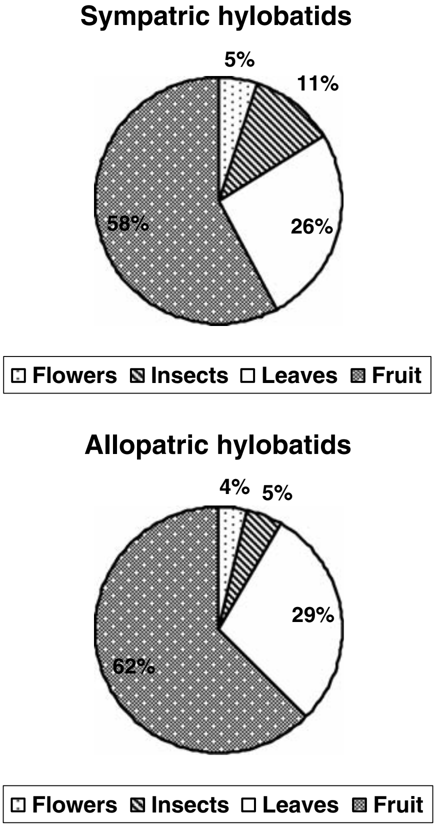


Fig. 8.9 Mean dietary proportions for sympatric and allopatric hylobatids based on the percentage of feeding time

function analyses conducted reveal that siamangs cannot be accurately classified by diet separately from other gibbon taxa. Instead, dietary overlap is large for hylobatids across their distribution. Small-bodied gibbons vary in their level of folivory, and may in fact exceed the levels observed for siamangs. Most notably, the most folivorous gibbon species are actually from the genus *Nomascus* (Lan 1993). However, these gibbons live at extremely high altitudes (up to 3100 m asl) and in a very rugged and seasonal habitat where fig trees are not available as a fallback food and no fruits are available for several months of the year (Haimoff et al. 1986; Bleisch and Chen 1991).

Folivory Is Poorly Linked to Body Mass in Gibbons

The expectation that siamangs are more folivorous than smaller-bodied gibbons is largely based on the assumption that with increased body size, the proportion of foliage in the diet increases. This relationship has been shown to be powerful and significant across primate taxa (Clutton-Brock and Harvey 1977). However, at the time of their analysis, hylobatid data were restricted to siamang and white-handed gibbons in the Malaysian peninsula. A more complete sample of gibbon diets presented here reveals a strikingly different result. For the hylobatid family there is no significant relationship between body mass and folivory (Fig. 8.2). Even when the effects of food availability (i.e., annual rainfall and latitude) are controlled through a multiple regression analysis, body mass does not significantly explain variance in the degree of hylobatid folivory. However, a significant relationship between the mass of smaller-bodied gibbons and their degree of folivory is found to be driven by the larger body mass (~7 kg) of gibbons from the genus *Nomascus*. As discussed previously, the crested gibbons from which data are available are unusual in the high percentage of time (up to 72%) they spend eating leaves and the harsh conditions in which they live. Although body mass may be critical for the digestion of foliage and the subsequent survival of crested gibbons, it is unclear whether body mass is actually related to the high degree of folivory in these populations. No substantial differences in body mass have been reported among *Nomascus* populations and it is not known whether a high level of folivory is typical for the genus *Nomascus* across their range. Thus, there may not be any relationship between the body mass of crested gibbons and their degree of folivory. Alternatively, the larger body mass of *Nomascus* gibbons relative to *Hylobates* and *Hoolock* gibbons may permit them to exploit more foliage, rather than driving them to do so. Until dietary data for crested gibbons throughout their range are available, the relationship between body mass and folivory in this genus cannot be clarified.

Body mass does significantly predict the percentage of time gibbons spend eating combined fig and nonfig fruit (24.3% of variance). The non-significant trend between body mass and flower eating is likely driven by the data from one site in southern Sumatra where siamangs spend unusually large percentages of time eating flowers (12%) compared to the sites in Northern Sumatra and Malaysia (Nurcahyo 2001; Lappan 2005). The range in body mass present in the hylobatid family may, in fact, not be wide enough to differentiate larger and smaller species by diet.

Small-Bodied Gibbons Living Sympatrically vs. Allopatrically with Siamangs Do Not Differ in Diet and Interspecific Competition Does Not Significantly Impact Gibbon Diets

In areas where small-bodied gibbon species share their habitat with siamangs, they are expected to be under strong competitive pressure. However, very little qualitative difference is found between the diets of small-bodied gibbons when living with and without siamangs (Fig. 8.4). In allopatry, gibbons spend 6%

more time eating fruit, 1% more time eating leaves, and 5% less time foraging for insects. These subtle differences may simply reflect the differences in resource availability in Malaysia and Sumatra (where siamangs live) compared to other gibbon habitats. As siamangs represent just one geographically restricted species and small-bodied gibbons come from three genetically (Takacs et al. 2005) and behaviorally distinct genera that have a much wider combined distribution, it is not surprising that small-bodied gibbon diets vary more than those of siamangs. Despite the expected pressure for dietary segregation, sympatric gibbons and siamangs have highly similar diets. No significant differences are found in the diets of small-bodied gibbons in habitats with and without siamangs, nor do sympatric siamangs and small-bodied gibbons significantly differ in any dietary parameter. Additionally, dietary variables do not accurately distinguish all sympatric gibbon populations (including siamangs) from all allopatric gibbon populations. Thus, local ecology may be more critical in driving hylobatid diets than interspecific competition.

There Is a Significant Relationship Between Resource Availability and Hylobatid Diets

I found significant relationships between dietary variables and mean annual rainfall (Table 8.2). As mean annual rainfall increases, gibbons decrease the time spent eating leaves (Fig. 8.7), while increasing the time spent eating fruit (Fig. 8.8). Controlling for body mass and latitude through multiple regression analysis, mean annual rainfall is the best predictor for both the degrees of folivory (37.1% of variance) and frugivory (39.5% of variance) in gibbons. Previously, strong positive correlations have been found between rainfall and tree species diversity and density (Gentry 1988; Kay et al. 1997; but see Gupta and Chivers 1999). Thus, in gibbon habitats with heavier rainfall, resource availability may be higher, allowing these populations to exploit more or larger fruit patches and reduce their reliance on foliage. Thus, there may be a tradeoff between the time spent eating leaves and fruits.

I did not, however, find significant relationships between proxies of resource availability and the percentage of time spent eating figs. Because figs are less dependent on rainfall for their growth compared with large fruit trees, fig availability likely cannot be predicted by the same proxies. Instead, measures of fig species diversity and fig densities are needed for each gibbon habitat to fully examine the relationship between fig abundance and the proportion of feeding time that gibbons spend eating figs.

Morphological Consequences of Large Body Size

In addition to metabolic differences, with increased body size there are increases in gut volume (Chivers and Hladik 1980), mandibular length (Hylander 1985;

Ravosa 1996), and molar area (Pilbeam and Gould 1974; Gingerich et al. 1982). With a longer mandible and larger posterior dentition, siamangs should be able to chew more leaves faster relative to small-bodied gibbons, and observational data confirm this predicted relationship for leaves of one plant species (Raemaekers 1979). Furthermore, among hylobatids, siamangs have the highest molar shearing quotients, which have been linked to folivory (Kay and Simons 1980; Kay 1984). Thus, siamangs are expected to be better equipped to process and digest a higher-fiber, lower-energy diet (i.e., more folivorous) than smaller-bodied hylobatids (Raemaekers 1979; Raemaekers 1984). However, for absolute measures of food intake, real feeding rate data are required across food species for both siamangs and smaller-bodied gibbons.

Conclusions and Future Perspectives

Other Modes of Niche Segregation

In light of the ecological similarity shared by gibbons across their distribution, one must ask how sympatric hylobatid species are able to coexist. Due to the difference in body mass, siamangs are expected to have a competitive advantage over smaller gibbons (Raemaekers 1978a). Large body size should lead to increased resource holding potential, with larger species winning contests and gaining access to resources (Morse 1974; Maynard Smith 1982; Abrams 1983). However, dominant groups cannot occupy all patches at any one time, such that heterospecific groups may maintain overlapping home ranges by dividing the habitat spatiotemporally. Even if siamangs consistently win encounters, small-bodied gibbons may survive by fleeing from direct competition and more rapidly reaching and consuming food patches. In fact, locomotor costs should be higher in siamangs due to their larger mass, but nearly equivalent forelimb lengths, and therefore their proportionately short stride (Raemaekers 1979). Siamangs may have slightly smaller home ranges and shorter daily path lengths (MacKinnon and MacKinnon 1980), and use slower modes of suspensory locomotion (Fleagle 1976; Fleagle 1980) than smaller-bodied gibbons. Thus, sympatric hylobatids may divide niche space through more subtle dynamic interactions and by using different foraging strategies that best fit their species-specific energetic constraints. Siamangs and small-bodied gibbons may also target food patches that differ in size or distribution or both. Furthermore, sympatric species may diverge in foraging strategies only during times of very low resource availability. For example, during El Niño-Southern Oscillation events when rainfall sharply decreases and fruit supplies are limited, siamang dietary flexibility (as aided by longer mandibles, higher chewing rates, and larger, higher-crested molars) may prove beneficial. These differences can only be revealed through detailed, simultaneous observations of resource use within a shared habitat.

Gibbons Within the Larger Southeast Asian Community

Hylobatids make up between 7 and 20% of the primate density and 10–25% of the primate biomass in Southeast Asia (O'Brien et al. 2004). Thus, gibbons have a major impact on the ecology of this region, and understanding how local conditions influence their behavior is critical for a larger understanding of primate communities (Marshall et al. this volume). Hylobatid ecology is likely to be affected by both the presence and the local population densities of primate and nonprimate competitors and the availability of resources in the forest. While rainfall has been found to be positively correlated with forest productivity (tree density and diversity) (Gentry 1988), and in turn productivity with primate species richness and biomass (Reed and Fleagle 1995; Peres and Janson 1999), these relationships do not apply to Southeast Asia (Kay et al. 1997; Gupta and Chivers 1999). Instead, beyond a certain threshold of precipitation (around 2500 mm/year), local primate species richness starts to decrease. The sigmoidal relationship between rainfall and species richness may be explained by a decrease in forest productivity due to soil leaching (Kay et al. 1997).

Contrary to the patterns found in previous studies, this study found that rainfall explains the largest portion of variance in hylobatid diets, and is the best predictor of folivory and frugivory. It follows that in gibbon habitats with high rainfall, there should be higher fruit availability. Most hylobatid habitats receive more than 2500 mm of rain annually (Table 8.2). Because estimates of forest productivity are usually based on gross measures of tree size, the different food products of trees are often not measured separately (i.e., fruits vs. leaves). Additionally, individual plants below a given diameter at breast height are routinely not included in phenological plots. This could affect the estimates of resource availability if the animals in question preferentially eat small-diameter plants such as lianas, as is the case for hylobatids (Palombit 1997). Figs are also a particularly important resource for gibbons as well as other frugivorous mammals and birds (Marshall 2004; Marshall et al. this volume). Figs function as key fallback foods; they provide large crops, fruit asynchronously, and tend to have high species diversity in a given area (Raemaekers 1978b; Raemaekers et al. 1980). Thus, figs are likely available at all times in many forests. Like lianas, estimates of forest productivity and tree density may also exclude strangler figs. Even if only a few large free-standing fig trees are available in each gibbon home range, the sheer output of these superabundant fruits may be enough to sustain hylobatid populations. More precise measures of habitat quality are needed to further evaluate the relationships among rainfall, forest productivity, primate species richness, and primate biomass in Southeast Asia.

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Chapter 9

Competition and Niche Overlap Between Gibbons (*Hylobates albibarbis*) and Other Frugivorous Vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia

Andrew J. Marshall, Charles H. Cannon, and Mark Leighton

Introduction

Interspecific competition is considered to be one of the fundamental forces driving a wide range of evolutionary and ecological processes, but its importance in limiting mammalian populations has been hotly debated (Hairston et al. 1960; Fleming 1979; Schoener 1982; Walter and Paterson 1995). Early ecologists held the view that competition between species was of overriding importance in shaping vertebrate communities (e.g., Grant 1972; MacArthur 1972; Cody 1975; Diamond 1978). Others argued that interspecific competition was sporadic, and that its effects may be relatively unimportant compared to other ecological forces, such as climate or predation (e.g., Connell 1975; Wiens 1977; den Boer 1986; Post and Forschhamer 2002), and non-equilibrial and stochastic factors (e.g. Sæther 1997; Hubbell 2001). Despite continued uncertainty over the precise nature of interspecific competition (Schoener 1982; Eccard and Ylönen 2003; Cooper 2004), few ecologists would deny that competition between species can have powerful effects on animal populations. Field experiments have demonstrated that the ecological effects of interspecific competition are widespread (reviewed in Connell 1983; Schoener 1983). Begon, Harper, and Townsend (1996: 800) concluded that competition "appears frequently to be important in vertebrate communities, particularly those of stable, species rich environments." Most primates live in tropical rainforests, among the most stable and species rich environments on earth, suggesting that interspecific competition may be particularly important for these taxa.

Primate field studies have indirectly inferred the importance of interspecific competition, either with primates or other vertebrate species. For example, density compensation—an increase in the density of one species in response to the decline in abundance of a competing species—has been reported in a wide

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number of primate communities in South America, Africa, and Asia (Struhsaker and Oates 1975; Struhsaker 1978; Lawes and Eeley 2000; Peres and Dolman 2000; González-Solís et al. 2001). In addition, decreases in dietary overlap during lean periods in primate assemblages at Krau Game Reserve, Malaysia, and Manu National Park, Peru, are thought to be caused by feeding competition between primate species (Waser and Case 1981). Strum and Western (1982) reported that feeding competition with ungulates explained the majority of the variance in indices of the reproductive output of female anubis baboons (*Papio anubis*). Finally, Ganzhorn's (1999) comparative analysis of factors that affected a large number of primate assemblages suggested that competition with non-primate taxa has had profound effects on the evolution of primate communities, particularly in Asian forests.

Such patterns are not universal: the overlap in foraging heights and diets of *Cercopithecus* monkeys increased when they were in polyspecific associations (Gautier-Hion et al. 1983) and the overlap in the consumption of resources between two tamarin species (*Saguinus* spp.) in polyspecific associations increased substantially during periods of lowest fruit availability (Peres 1996). These results are the opposite of what would be expected if interspecific competition were important for these species, and suggest that broad generalizations are unlikely to apply to all primate species or communities.

Here we consider how gibbons in a Bornean rainforest are affected by interspecific competition with other vertebrate frugivores. Many excellent field studies have examined competitive interactions among primate species within communities (e.g. Rodman 1973; Raemaekers 1984; Waser 1987; Guillotin et al. 1994; Ungar 1996; Wrangham et al. 1998; Reed 1999; Stevenson et al. 2000; Simmen et al. 2003), but only a limited number permit the examination of interactions with a wider set of frugivorous vertebrates (e.g., Leighton and Leighton 1983; Estrada and Coates-Estrada 1985; Gautier-Hion et al. 1985; Charles-Dominique 1993; Poulson et al. 2002). Consideration of primates within the context of the broader vertebrate community promises to provide a richer understanding of the ecological and evolutionary forces that shaped primate adaptations.

We present an analysis of long-term data on vertebrate feeding ecology gathered over a 6-year period of intensive sampling at Gunung Palung National Park, West Kalimantan, Indonesia. We use these data to address three general sets of questions: First, how specialized are gibbon diets when compared to other vertebrate frugivores? Second, which species are gibbons' major competitors for food? Third, how similar (or different) are the feeding niches of gibbons and their main competitors, and what are the effects of this competition?

How Specialized Are Gibbon Diets?

While primates are broadly considered to be dietary generalists, numerous studies have demonstrated a high degree of feeding selectivity, indicating that all primate species specialize on a relatively small subset of available foods (e.g., Oates et al. 1977; Milton 1979; McKey et al. 1981; Davies et al. 1988; Leighton 1993; McConkey et al. 2002). Here we consider how specialized gibbon diets are relative to the diets of other vertebrate frugivores that inhabit the same forests. We also consider whether the degree of specialization of gibbon diets is related to the abundance of food. Specifically, we test the following hypothesis:

H1: Gibbon diets are more diverse during periods of low fruit availability than during periods of high fruit availability.

Classic foraging models predict that diet breadth increases as the total availability of food decreases, because individuals can restrict feeding to the more preferred food items during periods of high food availability (Charnov 1076; MacArthur and Pianka 1966; Emlen 1968; Levins and MacArthur 1969; Schoener 1971). Although many empirical studies have documented this inverse relationship between food availability and diet breadth (e.g., Schoener 1971; Wrangham et al. 1991; McKnight and Hepp 1998; Rödel et al. 2004; Murray et al. 2006), other field studies have failed to detect this relationship (e.g., Wrangham et al. 1998; Di Fiore 2003), or have shown that in some species more items are included in the diet during periods of high food availability (Renton 2001; Simmen et al. 2003). Thus, some species appear to become more generalized during periods of resource scarcity while others become more specialized. However, some ambiguity may result because the relative abundance of foods of different preference rank was not monitored; *specialization* may occur because a low-ranked food is very abundant.

Here we hypothesize that gibbons adopt the former strategy (i.e., we predict an inverse relationship between food availability and diet breadth). Gibbons focus on a very limited set of high-quality, super-abundant resources during periods of highest resource availability (i.e., mast fruit events), but they must add more and more less-preferred items to their diet as food becomes scarce. We tested this prediction by comparing the total number of fruit taxa in gibbon diets during periods of high, medium, and low resource abundance, controlling for sample size. In order to compare the relationship between fruit availability and dietary diversity in gibbons to that of other vertebrates, we present the results of this simple comparison for several other species.

Which Taxa Are the Major Competitors of Gibbons?

Vertebrate frugivores in Bornean forests experience extreme temporal fluctuations in food availability due to the unusual community-wide phenological patterns characteristic of the island (Leighton and Leighton 1983; Curran and Leighton 2000; Marshall and Leighton 2006). While we assume that both intra- and interspecific feeding competition intensify during periods of fruit scarcity, little quantitative information exists that might allow us to identify which vertebrate taxa compete most intensely (or at all) with gibbons. Although for a variety of reasons there need not be a direct positive correlation between niche overlap and competition (see Discussion), we here follow convention and use dietary overlap as an indicator of potential feeding competition (MacArthur and Levins 1967; Schoener 1982).

The methods used to calculate dietary overlap can strongly affect the results obtained (Poulson et al. 2002). Several pioneering studies of feeding competition among vertebrate frugivores assessed resource overlap by simply calculating the number of items that two species consumed in common (Fleming 1979; Gautier-Hion et al. 1985). However, these simple indices tend to inflate the true extent of dietary overlap as they do not account for the relative abundance of items in the diet. More recent studies of resource competition in primates have used more sophisticated measures that incorporate both the dietary composition and the relative proportion of individual food items (e.g., Stevenson et al. 2000; Poulson et al. 2002). In this chapter we use a measure of dietary overlap that incorporates both factors to identify gibbons' major potential competitors at Gunung Palung. As the absolute and relative densities of vertebrates vary substantially between peat and non-peat forests (e.g., Janzen 1974, Leighton, unpubl. data), and since phenological patterns (Marshall 2004; Wich et al. unpubl. data) and floristic composition (Cannon and Leighton 2004) of peat forests differ substantially from other forest types, we conducted additional analyses to determine whether the ranking or degree of dietary overlap of gibbons' major vertebrate competitors differed between these two forest types.

How Similar Are the Feeding Niches of Gibbons and Their Major Competitors?

Ecological theory states that no two species can occupy exactly the same niche (Hutchinson 1957). Therefore, in order to coexist with other sympatric vertebrate frugivores, gibbons must occupy a unique part of multidimensional niche space. As diet is one of the major components defining gibbon fundamental niches, we test three hypotheses that address the mechanisms gibbons might employ to reduce feeding competition with other vertebrates.

H2A: Gibbon diets diverge more from their competitors during periods of low resource availability than during periods of high food availability.

Models of niche partitioning predict that resource overlap between competitors decreases when resources are limited (Schluter 1981; Schoener 1982). When preferred resources are available, sympatric species may pursue generalist feeding strategies, leading to considerable overlap in resource utilization. In contrast, during periods of food scarcity competition intensifies, causing feeding niches to diverge (Schoener 1982; Schluter 1994). Such a pattern has been reported from several primate communities. Waser (1987) compared the dietary overlap of 23 pairs of primates during seasons of high and low fruit availability and found that diets diverged during lean times in over 90% of the pairs examined. Similarly, Guillotin et al. (1994) reported that the lowest periods of dietary overlap between three frugivorous primate species in French Guiana occurred when fruit production was lowest. Finally, Wrangham, Conklin-Brittain, and Hunt (1998) found that when fruit availability was low, the diets of cercopithecines and chimpanzees in the Kibale forest diverged. Although niche divergence during lean periods is not universal (e.g., Peres 1996), it is the most common response in primate communities, particularly in species that do not engage in poly-specific associations. Therefore, we predicted that the diets of gibbons and their major potential competitors would be more divergent during periods of low food availability than during periods of higher food availability.

H2B: Gibbons feed in smaller patches than their major competitors.

Another mechanism by which gibbons may reduce direct competition with species that consume similar diets is by utilizing small patches that are ignored by other vertebrate frugivores (Raemaekers and Chivers 1980). Some major vertebrate frugivores in Bornean rainforests are known to preferentially feed in large patches (e.g., orangutans: Leighton 1993; orangutans and long-tailed macaques: Wich et al. 2002), presumably because the total number of patches that can be visited in 1 day are tightly constrained by high travel costs (Wheatley 1982; Rodman 1984; Leighton 1993). Gibbon brachiation is an unusually rapid and efficient locomotor adaptation, allowing them to cross larger gaps and follow more direct travel routes between food patches than other primates (Cannon and Leighton 1994, 1996). This suggests that gibbons may be able to overcome the costs of travel that tightly limit the number of patches that can be visited by species with larger body size or less efficient locomotor adaptations, permitting them to visit more, smaller patches in a single day than is possible for other frugivores. Therefore, we hypothesize that gibbon fruit patches are significantly smaller than those of their major competitors. We use fruit tree diameter at breast height (dbh) as a measure of patch size, as it is highly correlated with tree fruit crop size (i.e., pulp weight/patch: $r = 0.72$, Leighton 1993).

H2C: Gibbons occupy different forest types than their major competitors.

Habitat selection can act to substantially reduce or eliminate interspecific competition between species that utilize very similar sets of resources (Schoener 1974; Pianka 1976; Pyke et al. 1977). For example, Rodman (1979; 1991) showed that despite high degrees of dietary overlap, populations of *Macaca nemestrina* and *Macaca fascicularis* coexist by using different habitats in Kutai National Park. Gibbons may reduce feeding competition by occupying different habitats than vertebrates with whom their diets overlap substantially, or by preferentially occupying habitats where the densities of potential competitors are low. Following Rodman (1973) as a preliminary test of this hypothesis, we predict that gibbon population densities are significantly negatively correlated with the densities of their major competitors.

Methods

Study Site and Subjects

We gathered data at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park, West Kalimantan, Indonesia (1°13′ S, 110°7′ E). The study site contains seven distinct forest types that differ due to variations in soil type, drainage, altitude, and underlying rock type. Detailed descriptions of these forest types and the research site can be found in Cannon and Leighton (2004), Webb and Peart (2000), and Marshall (2004). When the data presented here were collected, little hunting or timber extraction had occurred within the immediate study area since the establishment of the national park in 1937, with the exception of hand extraction of *gaharu* (*Aquilaria malaccensis*) and *belian* (*Eusideroxylon zwageri*) (Webb 1997; Paoli et al. 2001). The vertebrate and plant communities at the site are therefore diverse and presumably at the densities characteristic of the area over recent ecological history. Species lists from the site have been published for birds (Laman et al. 1996) and mammals (Blundell 1996).

The populations of Bornean white-bearded gibbons (*Hylobates albibarbis*) found at CPRS have been the subjects of focused study intermittently since 1984 (Mitani 1987, 1990; Cannon and Leighton 1994, 1996; Marshall 2004; Marshall and Leighton 2006; Marshall in press). Their diet comprised mainly the pulp of ripe non-fig fruits (65% of the diet on average), augmented by figs (23%), flowers (6%), leaves (3%), and seeds (3%). The relative importance of different plant parts in gibbon diets at CPRS varies substantially across seasons: flowers comprise from 0 to 28% of the feeding observations, fruit pulp and seeds from 25 to 95%, figs from 0 to 75%, and leaves from 0 to 25% (Fig. 9.1). During times when preferred foods are unavailable, figs become an increasingly important portion of the diet (i.e., they are a fallback food; Marshall and Leighton 2006; Marshall and Wrangham 2007).

Vertebrate Feeding Observations

We used a long-term data set of 4090 independent vertebrate fruit feeding records collected between March 1985 and March 1992. Feeding observations were gathered while walking standardized vertebrate census routes across all forest types ($n = 1909$ observations, 47% of the total) and from opportunistic observations made while conducting other fieldwork ($n = 2181$, 53%). Data collected on fruit tree watches or in other contexts that would bias estimates of vertebrate dietary intake were excluded, as were observations of vertebrates feeding on non-fruit items (e.g., leaves, insects, pith). Thus, all comparisons of dietary overlap between species incorporate only the fruit portion of the diets of each species.

Our data set includes the observations of feeding by a wide range of mammalian and avian taxa. There are roughly twice as many observations of

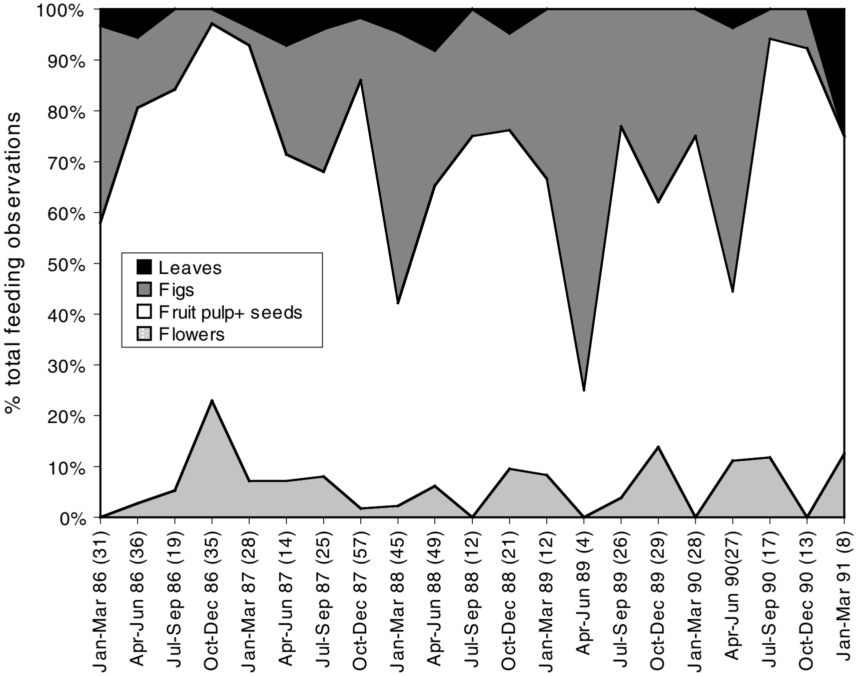

Fig. 9.1 Gibbon dietary composition over time by plant part. Figure is based on 536 independent feeding observations recorded between January 1986 and March 1991. Data are lumped into 3-month periods to reduce the effects of sampling error associated with small sample sizes. Parentheses indicate the number of independent feeding observations during each period. See Marshall (2004) for details of the analysis

mammal feeding (*n* = 2828 observations, 69% of the total) as there are for birds (*n* = 1262, 31%). The most commonly represented mammalian orders in the data set are Primates (*n* = 1711, 42%) and Rodentia (*n* = 784, 19%), with additional observations of Artiodactyla, Carnivora, and Chiroptera, (5, 1.6, and 1.5%, respectively). The most commonly represented avian orders are Bucerotiformes (*n* = 553, 14%), Passeriformes (*n* = 282, 7 %), and Piciformes (*n* = 251, 6%); with additional observations of Columbiformes, Galliformes, Psittaciformes, and Trogoniformes (1.9, 1.4, 0.6, and 0.2%, respectively). The following families each contribute >2.0 % of total observations: Sciuridae (squirrels: *n* = 782, 19%), Cercopithecidae (macaques and leaf monkeys: *n* = 756, 19%), Bucerotidae (hornbills: *n* = 553, 14%), Pongidae (orangutans: *n* = 515 obs, 13%), Hylobatidae (gibbons: *n* = 440 , 11%), Megalaimidae (barbets, *n* = 251, 6%), Suidae (pigs: 181, 4%), and Pynotidae (bulbuls: 99, 2%); the remaining observations are divided among 16 other avian and mammalian genera. Mammalian taxonomy follows Payne and Francis (1985); avian taxonomy follows Inskipp, Lindsey, and Duckworth (1996).

We gathered the observations of vertebrates eating the fruits from trees, lianas, and hemiepiphytes from 115 plant families and 167 genera. In order to boost sample sizes and reveal general patterns, we used genera as the taxonomic unit for our analyses (see Marshall and Leighton 2006, for further discussion). The following families comprised more than 2% of feeding observations: Moraceae (n = 1414, 35%), Annonaceae (n = 214, 5%), Fagaceae (n = 199, 5%), Burseraceae (n = 159, 4%), Dipterocarpaceae (n = 152, 4%), Euphorbiaceae (n = 132, 3%), Myrtaceae (n = 127, 3%), Myristicaceae (n = 126, 3%), Meliaceae (n = 125, 3%), and Apocynaceae (n = 123, 3%). The most commonly eaten plant genus was *Ficus* (n = 1348 obs, 31%). After figs, the most commonly eaten fruit genera were *Lithocarpus* (n = 164, 4%), *Shorea* (n = 142, 3%), and *Willughbeia* (n = 124, 3%). The following genera each comprised more than 2% of the total feeding observations: *Syzygium* (n = 107), *Diospyros* (n = 93), *Hydnocarpus* (n = 91), *Alangium* (n = 88), and *Canarium* (n = 88). Thirty six other plant genera were represented by at least 20 independent observations.

Fruit Phenology

We used data from 126 phenological plots that were monitored monthly between January 1986 and September 1991 (n = 69 months) to assess temporal variation in fruit availability for gibbons at CPRS. Phenology plots were 0.10 ha in size and were placed using a stratified random design across all seven habitat types (Cannon and Leighton 2004; Cannon et al. 2007a, b). In these plots all trees larger than 14.5 cm dbh, all lianas larger than 3.5 cm dbh, and all hemi epiphitic figs whose roots reached the ground were identified, measured, and tagged. The phenological phase of each tagged stem in these phenology plots was recorded each month (or two out of every 3 months during some periods). Based on the objective, the operational criteria that incorporated the density of trees with ripe fruit available (# stems per ha per month), and the diversity of gibbon food trees in fruit (# of distinct food taxa per month), each month was assigned to one of three classes (in order of decreasing food availability): mast, high fruit periods (HFP), and low fruit periods (LFP). Since the phenological patterns of the peat swamp forest differ significantly from the other habitats, analyses that incorporated food availability were done separately for peat and non-peat forest types (see Marshall 2004; Marshall and Leighton 2006, for details on all analyses). We consider peat swamp forests to be non-masting habitats (Marshall 2004; Cannon et al. 2007a; Wich et al. unpubl. data).

Primate Density Transects

AJM established a pair of replicate 2–4 km-long census routes in each of the seven forest types found at CPRS (total n = 14 routes), and systematically recorded all observations of primate species using a standardized protocol between September 2000 and June 2002 (n = 409 censuses; 1,374 km). Details of transect methodology are provided in Marshall (2004). As a complete treatment of the habitat-specific densities of all major frugivorous vertebrates at Gunung Palung is beyond the scope of this chapter, we use the number of independent observations per census as a simple index of the density of the four most common primate species at Gunung Palung in each habitat.

Analyses

We conducted analyses using Mathematica 5.1, SPSS 11.0.4, and JMP 5.0.1. To accommodate different sample sizes for different species, we used a randomization approach to test most of our hypotheses (Manly 1997). We performed all randomizations 1000 times and set significance at $\alpha = 0.05$. As a measure of specialization and feeding selectivity, we calculated use ratios for all fruits in the gibbon diet by dividing the number of times a plant genus was observed to be eaten by the number of times it was included in a random sample of the same size that was drawn from the entire set of vertebrate feeding records. Plant genera observed to be eaten more or less than expected by chance were classified as sought or avoided foods.

In order to compare diets we used an index of dietary identity that incorporated both diet composition and frequency of consumption. The index was calculated by compiling complete lists of all feeding observations for each consumer (i.e., items eaten multiple times were listed multiple times) and examining the overlap between the lists of two consumers in comparison to the food items eaten by each consumer. The index can be used from either consumer's perspective; from the perspective of consumer A:

$$A \cap B_N / A_N$$

or from the perspective of consumer B:

$$A \cap B_N / B_N$$

where $A \cap B_N$ is the number of food items shared by the two consumers and A_N, B_N are the number of food items in each respective consumer's diet. The index can vary from 0 to 1, where 0 indicates no overlap in diets and 1 indicates complete overlap of the competitor's diet with the focal consumer's. We generated a null model for this index by comparing random diets across a range of feeding observations up to the maximum number obtained for any species. These random diets were drawn from all feeding observations, pooled together, without regard to the taxonomic identity of the feeding organism. This null distribution represents the amount of dietary identity expected, given purely stochastic processes. The mean dietary identity of the observed diet for each species to the random diets was then compared to the null model, given the number of observations for each species, to determine significance. The same analysis was performed at the family level to increase the sample size for vertebrates with small samples for individual species.

We used the same procedure to compare the observed dietary identity between gibbons and each of the major vertebrate species with the expected dietary identity, given random feeding behavior. First, we drew 1000 random diets out of the pooled feeding observations, given the number of observations for the non-gibbon species in each comparison. The dietary identity of the observed gibbon diet to each random diet then represented the null distribution of identities. The dietary identity of the observed gibbon diet with the observed diet of the non-gibbon species was then compared to the null distribution and its significance determined. We conducted this comparison for the full data set, and also conducted separate analyses that assessed dietary overlap in different seasons and habitats.

For our analysis of diet breadth we sub-sampled seasons with more feeding observations so that sample sizes were equal across seasons. This eliminated biases that would have been introduced by the fact that observed diet diversity is related to sample size in a positive but non-linear way.

We compared the distribution of feeding tree sizes among vertebrate species with a one-way ANOVA, and used post-hoc Tukey-Kramer honestly significant difference (HSD) tests to identify pairs of species that differed significantly. Finally, we used Spearman's rho to assess the strength and direction of correlations between the habitat-specific densities of the four most common primate species at CPRS.

Results

How Specialized Are Gibbon Diets?

Our analysis of gibbon use ratios identified 21 fruit genera that were sought by gibbons and 14 that were avoided at CPRS (Table 9.1). The most strongly sought fruits were *Artabotrys*, *Aglaia* (including only species with primate dispersed fruits), *Garcinia*, and *Diospyros*; the most strongly avoided were *Lithocarpus*, *Dysoxylum*, *Strychnos*, and *Shorea*. Interestingly, few plant families contained both sought and avoided taxa; genera in the common families Fagaceae, Lauraceae, Myristicaceae, and Burseraceae were avoided by gibbons.

Gibbon dietary identity is significantly below the null model (Fig. 9.2), confirming that, as indicated by the use ratio analysis, gibbons do not forage randomly for fruits. However, our data suggest that gibbons are relatively unspecialized compared to most other vertebrates in our sample. With the exception of Prevost's Squirrel, the frugivorous portion of gibbon diets are less specialized than those of all vertebrates for which we have more than 100 feeding observations (two hornbill species, pigs, giant squirrels, macaques, leaf monkeys, and orangutans; Fig. 9.2). Of the other species in our sample, tufted ground squirrels, dog-faced bats, and long-tailed parakeets appear to be particularly specialized in their frugivory. The analysis of dietary specialization by

Table 9.1 Family, genus, growth form (T = Tree, L = liana, H = hemiepiphyte), and use ratio of plant genera observed to be consumed by gibbons at Gunung Palung between 1985 and 1992

Family	*Genus*	Form	Use ratio[a]
Annon	*Artabotrys*	L	+ 3.86*
Melia	*Aglaia*[b]	T	+ 3.75*
Clusi	*Garcinia*	T	+ 3.50*
Ebena	*Diospyros*	T	+ 3.43*
Rubia	*Unknown*	T	+ 2.50*
Tilia	*Microcos*	T	+ 2.33*
Sapot	*Chrysophyllum*	T	+ 2.00*
Annon	*Friesodielsia*	L	+ 2.00*
Rubia	*Psychotria*	T	+ 2.00*
Eupho	*Baccauria*	T	+ 1.83*
Flaco	*Hydnocarpus*	T	+ 1.80*
Fabac	*Dialium*	T	+ 1.67*
Sapot	*Palaquium*	T	+ 1.67*
Polyg	*Xanthophyllum*	T	+ 1.67*
Sapin	*Nephelium*	T	+ 1.67
Elaeo	*Elaeocarpus*	T	+ 1.60*
Melas	*Pternandra*	T	+ 1.50
Morac	*Artocarpus*	T	+ 1.44*
Chyrs	*Parinari*	T	+ 1.33*
Anaca	*Gluta*	T	+ 1.33
Myrta	*Syzygium*	T	+ 1.20
Apocy	*Willughbeia*	L	+ 1.14
Rubia	*Anthocephalus*	T	+ 1.00*
Eupho	*Antidesma*	T	+ 1.01*
Areca	*Calamus*	L	+ 1.02*
Sapin	*Unknown*	T	+ 1.04*
Fagac	*Lithocarpus*	T	–9.00*
Melia	*Dysoxylum*	T	–5.00*
Logan	*Strychnos*	L	–4.00*
Dipte	*Shorea*	T	–3.5*
Burse	*Canarium*	T	–3.00*
Laura	*Cryptocarya*	T	–3.01*
Burse	*Dacryodes*	T	–3.02*
Irvin	*Irvingia*	T	–3.03*
Myris	*Myristica*	T	–3.04*
Laura	*Nothapheobe*	T	–3.05*
Fagac	*Quercus*	T	–3.06*
Annon	*Polyalthia*	T	–2.67*
Burse	*Santiria*	T	–2.50*
Laura	*Litsea*	T	–2.00*
Tetra	*Tetramerista*	T	–1.66

Table 9.1 (continued)

Family	*Genus*	Form	Use ratio[a]
Myris	*Horsfieldia*	T	−1.50
Annon	*Mezzettia*	T	−1.50
Morac	*Ficus*	H	−1.09

[a] Only plant taxa with use ratios with an absolute value greater than 1.0 are listed. Positive numbers indicate foods sought by gibbons; negative numbers indicate plant genera that were avoided. See text for details.

[b] Only trees of the genus *Aglaia* that produce primate-dispersed fruits (i.e., those with seeds surrounded by a watery, sugary pulp) are included.

* $p < 0.05$.

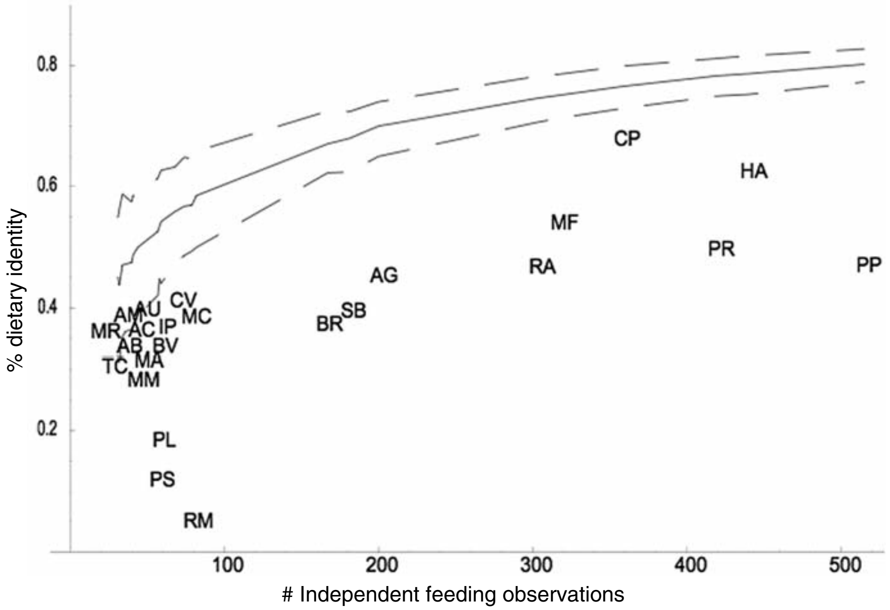

Fig. 9.2 Dietary specialization of vertebrate frugivores by species. The x-axis represents the number of independent feeding observations, the y-axis represents the percent dietary identity (a measure that integrates diet composition and frequency of specific items in the diet). The solid line shows the expected dietary identity between two randomly selected diets of a given sample size, the dashed line gives the $\alpha = 0.05$ significance limits based on 1000 iterations (see Methods). The further a species is below the line, the less their diet resembles a randomly sampled diet of the same sample size. Therefore, species further from the line can be considered to be more specialized than those close to the line. Abbreviations indicate: bushy-crested hornbill (*Anorhinus galeritus*, AG), Binturong (*Arctictis binturong*, AB), black hornbill (*Anthracoceros malayanus*, AM), bearded pig (*Sus barbatus*, SB), Prevost's squirrel (*Callosciurus prevostii*, CP), dog-faced bat (*Pteropus* spp., PS), fairy bluebird (*Irena puella*, IP), long-tailed macaques (*Macaca fascicularis*, MF), green broadbill (*Calyptomena viridis*, CV), Bornean white-bearded gibbon (*Hylobates albibarbis*, HA), helmeted hornbill (*Buceros vigil*, BV), red leaf monkey (*Presbytis rubicunda rubida*, PR), little barbet (*Megalaima australis*, MA), gold-whiskered barbet (*Megalaima chrysopogon*, MC), gaudy barbet (*Megalaima mystacophanes*, MM), red-crowned barbet (*Megalaima rafflesii*, MR), Western Bornean orangutan (*Pongo pygmaeus wurmbii*, PP), long-tailed parakeet (*Psittacula longicauda*, PL), giant squirrel (*Ratufa affinis*, RA), rhinoceros hornbill (*Buceros rhinoceros*, BR), Little green pigeon (*Treron capellei*, TC), tufted ground squirrel (*Rheithrosciurus macrotis*, TG), wreathed hornbill (*Aceros undulatus*, AU), and wrinkled hornbill (*Aceros corrugatus*, AC)

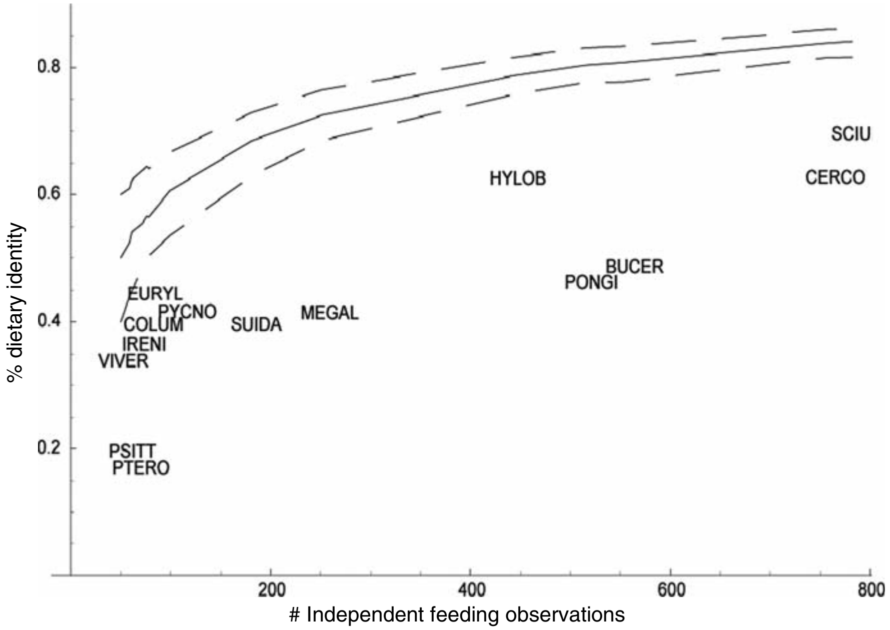

Fig. 9.3 Dietary specialization of vertebrate frugivores by family. Axes and lines are the same as in Fig. 9.2. Abbreviations indicate Bucerotidae (BUCER), Cercopithecideae (CERCO), Columbidae (COLUM), Eurylaimidae (EURYL), Hylobatidae (HYLOB), Irenidae (IRENI), Megalaimidae (MEGAL), Pongidae (PONGI), Psittacidae (PSITT), Pteropodidae (PTERO), Pynotidae (PYCNO), Sciuridae (SCIUR), Suidae (SUIDA), and Viveridae (VIVER)

family shows a similar pattern: the hylobatids are less specialized than hornbills (Bucerotidae), monkeys (Cercopithecidae), and barbets (Megalaimidae), and about as specialized as squirrels (Sciuridae; Fig. 9.3).

Gibbon diets are slightly less diverse during HFP than LFP in peat forests, and during masts gibbon diets include 25% fewer items than during other seasons (Fig. 9.4). This provides modest support for H1, although the pattern is not strong. Patterns in other taxa vary considerably, both within a taxon in different forest types (e.g., orangutans increase dietary diversity in peat swamp forests during lean periods, but show the opposite trend in non-peat forests; Fig. 9.4) and between taxa (e.g., barbets show a pattern that is consistently opposite to that exhibited by squirrels; Fig. 9.4).

Which Taxa Are the Major Competitors of Gibbons?

The species with the highest degree of dietary overlap with gibbons was Prevost's squirrel, (*Callosciurus prevostii:* 51% overlap), followed by the three most common diurnal primates at CPRS: orangutans (*Pongo pygmaeus wurmbii*: 49%*)*, long-tailed macaques (*Macaca fascicularis*: 48%), and red leaf monkeys

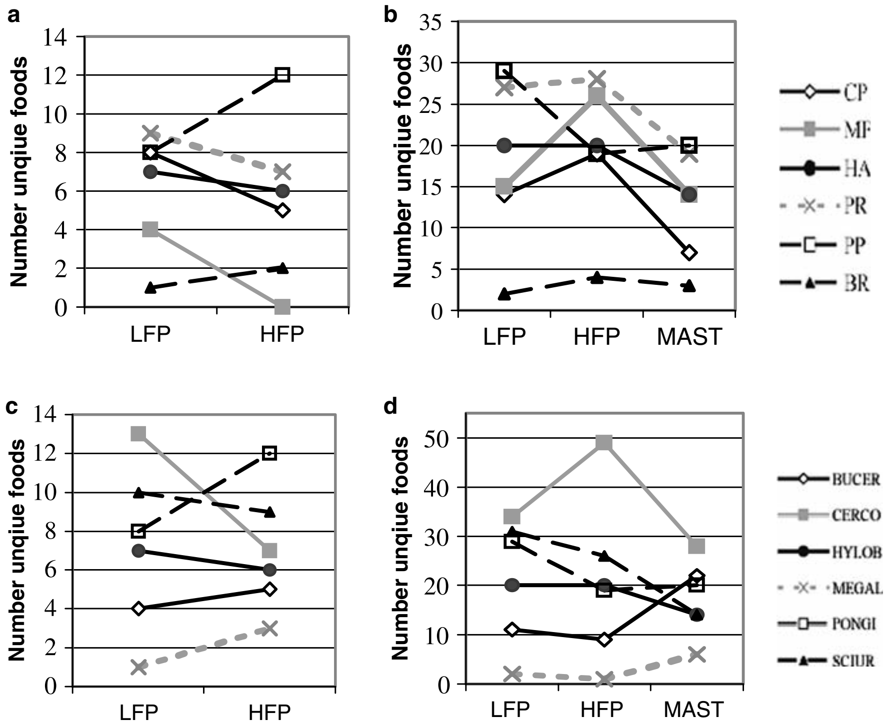

Fig. 9.4 The number of unique food items included in the diets of gibbons and their major vertebrate competitors. Graphs show the number of distinct plant taxa fed on by vertebrate species during (**a**) peat forests and (**b**) non-peat forests, and those fed on by vertebrate families in (**c**) peat forests and (**d**) non-peat forests during high fruit period (HFP), low fruit periods (LFP), and masts. The analysis controls for differences in sample sizes between periods. See legends to Figs. 9.2 and 9.3 for abbreviations

(*Presbytis rubicunda rubida*: 41%, Table 9.2). Given various types of sampling error, overlap with at least the first three species should be considered co-equal and not significantly different. Other taxa with substantial dietary overlap (>5%) with gibbons included bearded pigs (*Sus barbatus*), binturong (*Arctictis binturong*), and several species of hornbill (Bucerotiformes), barbets (Megalaimidae), bulbuls (Pynotidae), and squirrels (Sciuridae).

We also examined whether forest type affected the intensity of feeding competition (as indexed by dietary overlap) between gibbons and other taxa. We limited this analysis to taxa for which the percent dietary overlap with gibbons exceeded 30% (Table 9.2), and examined the patterns on both the species and the family level. Although absolute measures suggest that the fruit component of the diets of most species overlapped with gibbon diets substantially less in peat forests than non-peat forests, these results are due to

Table 9.2 The ten vertebrate frugivores with the highest degree of dietary overlap with gibbons at Gunung Palung

Order	Family[a]	Latin name	Common name	Dietary overlap[b] (%)
RODEN	SCIUR	*Callosciurus prevostii*	Prevost's squirrel	50.5
PRIMA	PONGI	*Pongo pygmaeus wurmbii*	Orangutan	48.6
PRIMA	CERCO	*Macaca fascicularis*	Long-tailed macaque	48.2
PRIMA	CERCO	*Presbytis rubicunda rubida*	Red leaf monkey	41.4
BUCER	BUCER	*Buceros rhinoceros*	Rhinoceros hornbill	30.7
RODEN	SCIUR	*Ratufa affinus*	Giant squirrel	27.5
BUCER	BUCER	*Anorhinus galeritus*	Bushy-crested hornbill	17.3
PICIF	MEGAL	*Megalaima chrysopogon*	Gold-whiskered barbet	16.8
ARTIO	SUIDA	*Sus barbatus*	Bearded big	15.5
BUCER	BUCER	*Buceros vigil*	Helmeted hornbill	13.4

[a] Family abbreviations are the same as used in Fig. 9.3.

[b] Analysis combines all fruit-feeding records from all habitat types.

differences in sample sizes between peat and non-peat forests – actually all species showed the same patterns of overlap in peat and non-peat forests (Fig. 9.5). The family analysis revealed some differences between the two habitat types. Cercopithecine monkey diets showed significantly lower dietary

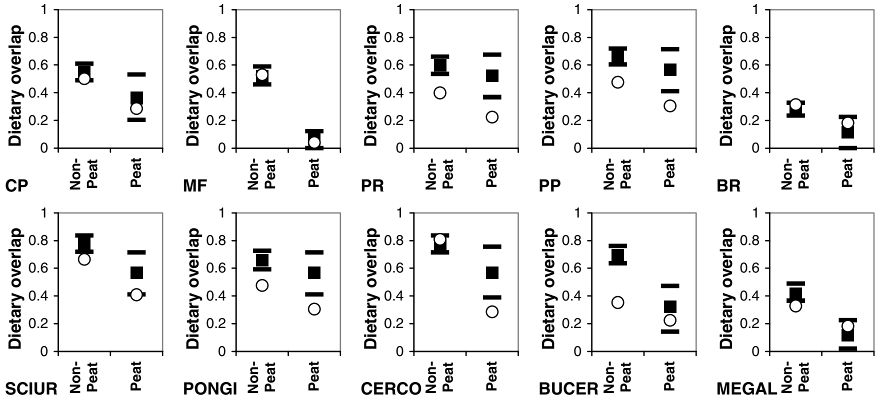

Fig. 9.5 Overall diet overlap between gibbons and other important vertebrate frugivores in peat and non-peat forests. The *y*-axis lists the proportion of overlap with gibbon diets (a measure incorporating both dietary composition and the frequency of items in the diet). Black boxes and lines indicate, respectively, the mean and upper and lower 95% limits of expected overlap with gibbons based on 1000 randomly drawn diets. Open circles indicate observed dietary overlap with gibbons. The top row of graphs shows data for vertebrate species (abbreviations follow Fig. 9.2); the bottom row shows data for vertebrate families (abbreviations follow Fig. 9.3)

overlap with gibbons in peat forests (Fig. 9.5). Hornbill diets overlapped gibbon diets significantly less in non-peat forests, a trend that was also apparent in squirrels and barbets (Fig. 9.5).

How Similar Are the Niches of Gibbons and Their Major Competitors?

Our hypothesis that gibbon diets diverge more from their competitors during periods of low resource availability than during periods of higher food availability (H2A) received mixed support. For most species the results were very similar between peat and non-peat forests; on the family level, most patterns were broadly similar between forest types, but we note some differences. As predicted, the diets of both orangutans and leaf monkeys diverged significantly from gibbon diets during periods of food scarcity and showed greater overlap during periods of resource abundance in both peat and non-peat forests (Figs. 9.6 and 9.7). But, contrary to our prediction, in both peat and non-peat forests food availability had no effect on the degree to which the diets of Prevost's squirrels, long-tailed macaques, and rhinoceros hornbills overlapped with gibbon diets (Figs. 9.6 and 9.7).

Our analysis of the effects of food availability on dietary overlap among vertebrate families showed that the Sciuridae tended to exhibit high dietary overlap with gibbons during periods of high food availability and reduced levels of overlap when resources were relatively scarce in both forest types. A similar pattern was observable for Bucerotidae in non-peat forests and Cercopithecidae

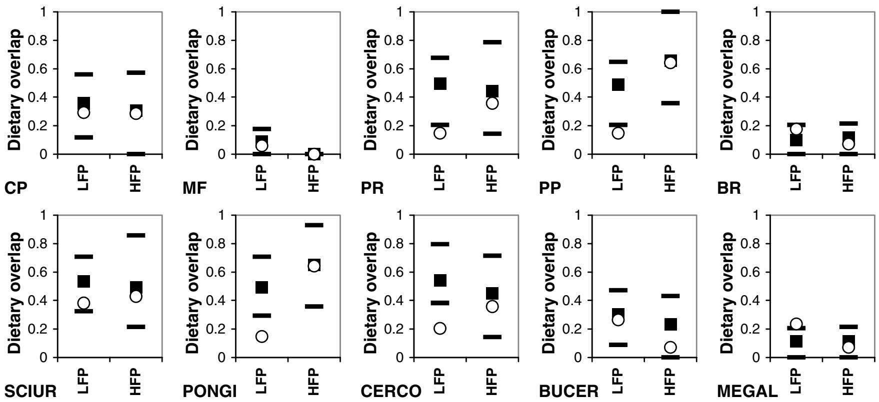

Fig. 9.6 Diet overlap between gibbons and other important vertebrate frugivores during low fruit periods (LFP) and high fruit periods (HFP) in peat forests. Explanation and abbreviations as in Fig. 9.5

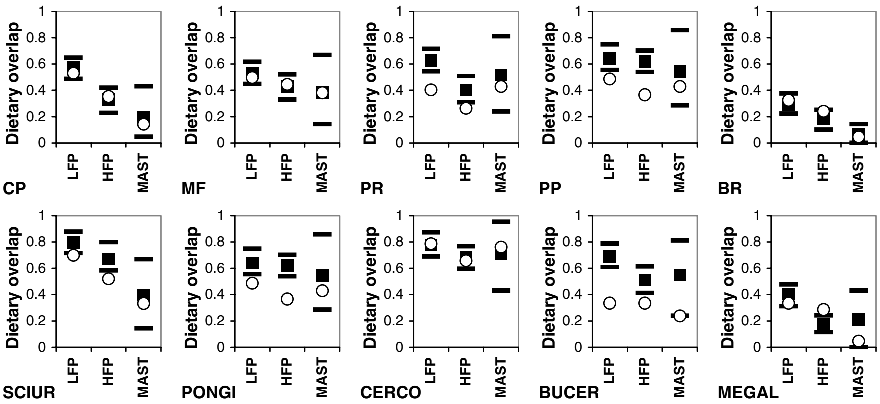

Fig. 9.7 Diet overlap between gibbons and other important vertebrate frugivores during low fruit periods (LFP), high fruit periods (HFP), and masts in non-peat forests. Explanation and abbreviations as in Figs. 9.5 and 9.6

in peat forest, but not for hornbills in peat forests or cercopithecine monkeys in the non-peat forests. These patterns demonstrate that ecological interactions between vertebrate taxa can vary in different habitat types. Finally, the overlap between barbets (Megalaimidae) and gibbons was unrelated to food availability (Figs. 9.6 and 9.7).

We tested the hypothesis that gibbons fed in smaller patches than their competitors (H2B) by conducting a one-way ANOVA that compared the average size (dbh) of gibbon feeding trees with those fed on by their five most important competitors: Prevost's Squirrels, orangutans, long-tailed macaques, red leaf monkeys, and rhinoceros hornbills. These species differed significantly in the mean size of feeding trees (*F* ratio = 21.3, df = 5, $p < 0.0001$). Post-hoc tests revealed that gibbons fed in smaller trees than red leaf monkeys and orangutans (Tukey-Kramer HSD $q > 2.82, p < 0.05$), but that the size of feeding trees did not differ between gibbons and Prevost's squirrels, long-tailed macaques, or hornbills (Fig. 9.8).

Finally, we tested the prediction that gibbons utilize different habitats than their major competitors (H2C) by examining the correlations between indices of gibbon density and the densities of orangutans, leaf monkeys, and macaques. Significant negative correlations would suggest that gibbons preferentially inhabit forest types in which other primates are scarce. Gibbon densities were uncorrelated with the densities of any of these three species. All Spearman's rho values were positive (>0.35), allowing us to reject the hypothesis that gibbons reduce competition with other species by dispersing themselves across space differently. These results are consistent with those from a larger set of censuses conducted by ML and colleagues between May 1985 and January 1992 (n = 4,588; 12,889 km, unpublished data).

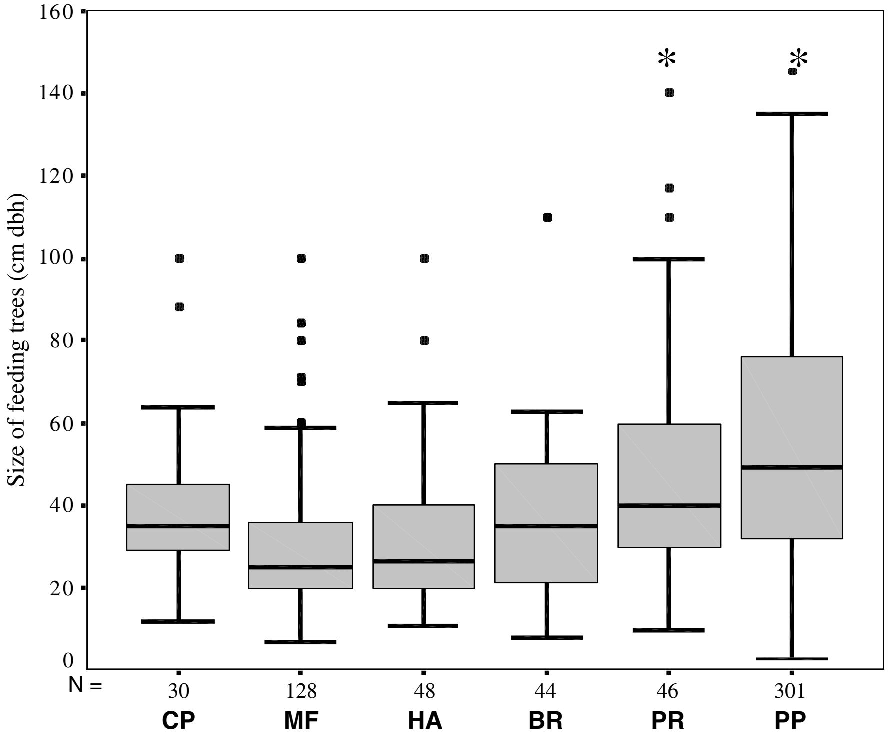

Fig. 9.8 Diameter of feeding trees of gibbons and their major competitors. The boxplots depict the diameter of feeding trees for each vertebrate taxon, showing the median (*black horizontal lines*), interquartile range (*gray boxes*), extent of points within 1.5 of the quartile range (*upper and lower range lines*), and outliers (*points*). Red leaf monkeys (PR) and orangutans (PP) fed in significantly larger trees than did all other taxa (* Tukey-Kramer HSD $q >$ 2.82, $p < 0.05$); the size of trees fed in by gibbons (HA) did not differ significantly from Prevost's squirrel (CP), long-tailed macaques (MF), or rhinoceros hornbills (BR). Sample sizes for each taxon are given above initials

Discussion

In this chapter we have considered the composition of gibbon diets at CPRS in relation to sympatric frugivorous vertebrates found at the site using a broad, long-term data set. This data set provides an unusual opportunity to study gibbon ecology in the context of the broader vertebrate community, and promises to provide a fuller understanding of the ecological and evolutionary forces that shaped primate adaptations. Our data were collected during vertebrate censuses and other instances where observations were random and independent. Therefore, we avoided pseudoreplication and many of the biases that can plague studies of vertebrate, particularly primate, feeding ecology.

Despite these strengths, several limitations of the data set and our analyses warrant discussion. First, as our data were collected during daylight hours, the importance of nocturnal competitors (e.g., bats, civets) cannot be quantitatively assessed. Second, we based all our randomizations on iterative samples from the database of independent feeding observations. This method carries the assumption that our observations of feeding reflect general patterns of food availability and consumption in the forest (i.e., they are unbiased samples of the full set of feeding occurrences that occurred in the forest at the time they were collected). Although we cannot explicitly test this assertion, the fact that we confined our analysis to independent, random samples allows us to feel confident that this assumption was not violated. Third, all of our analyses were based on only the frugivorous portion of the diets of the vertebrates we studied. Since non-fruit items comprise a proportion of the diets of most of the vertebrate taxa included in this analysis, this may have inflated estimates of overlap in some cases. Finally, as only items that were observed to be eaten at least once were considered in the analysis (because we used the database of vertebrate feeding records), we underestimated degrees of specialization, selectivity, and avoidance relative to the full set of potential foods in the forest.

While we acknowledge these limitations, our results provide new information about gibbon feeding ecology at CPRS and the importance of competition with other vertebrate frugivores. Below we discuss each of the three sets of questions that we have addressed in this chapter.

How Specialized Are Gibbon Diets?

Our analysis of the use ratios of gibbon foods are a fairly course-grained method of detecting dietary selectivity, as they do not incorporate spatial (e.g., habitat-specific plant stem density) or temporal variation in food availability. Nevertheless, the results generally confirm the results from more detailed analyses of gibbon food preference at CPRS (Marshall 2004) and other sites (McConkey et al. 2002; McConkey et al. 2003; McConkey this volume). They confirm that gibbons prefer pulpy, sugar-rich fruits with generally low levels of tannins and toxins, and avoid toxic plant species and those with extremely hard seeds (McConkey et al. 2002).

Despite this evidence for strong selectivity, in our comparison of the frugivorous portion of diets, gibbons appear to eat a relatively unspecialized diet when compared with most other vertebrate frugivores at CPRS. Few studies provide quantitative estimates of the degree of dietary specialization in gibbons relative to all sympatric frugivorous vertebrates, but MacKinnon and MacKinnon (1980) compared the degree of specialization among sympatric primates at Krau Game Reserve, Peninsular Malaysia. In contrast to our results, their intensive study concluded that hylobatids were the most specialized primates in the community (MacKinnon and MacKinnon 1980). It is possible that this discrepancy is a result of differences in analysis or sampling strategy, but MacKinnon and MacKinnon (1980) provide insufficient details to enable us to address this possibility. The most likely reason for the differences is, however, the fact that the MacKinnons' study was limited to 6 or 7 months. As our analyses demonstrate, the relative degree of specialization between species varies between seasons (e.g., compare red leaf monkeys and orangutans in Fig. 9.4). Therefore, conclusions based on comparisons over such short durations may be misleading, particularly in forests in which plant productivity is so temporally variable. Our longer-term data set includes only independent observations drawn over the full range of variation in resource availability, and therefore is likely to provide a more accurate picture of the comparative feeding ecology of these species.

Assuming that our results accurately assess the degree of specialization of gibbons compared to other vertebrate frugivores, why are gibbons so relatively unspecialized? One possibility is that gibbons lack a highly specialized gut morphology that would enable (or constrain) them to become highly specialized on a limited set of food items (cf. colobines). Another (and probably complementary) possibility is that gibbons' fast locomotion releases them from the requirement of focusing solely on large fruit patches, and enables them to visit a wider variety of fruit trees and lianas per day than could smaller (e.g., squirrels), larger (e.g., orangutans), or slower (e.g., macaques) species (see below). When compared to their major avian competitors, the most likely reason that gibbons eat a wider range of fruits is that their manual dexterity enables them to open indehiscent fruits that are largely unavailable to the birds. Thus gibbons are released from the factors forcing most sympatric vertebrates to specialize, and are therefore able to reap the benefits of eating a more generalized diet – the greatest of which are likely to be a greater total amount of food available and less temporal variation in food availability.

A third possibility depends on our definition and analysis of specialization and the relative abundance of fruits of different types. Gibbons are generalists in that they consume fruits from many genera, but these genera represent convergence among many families toward a primate-fruit type of similar chemistry and morphology (Leighton and Leighton 1983; McConkey this volume). If this type is rich in genera and relatively common in the forest compared to other types, gibbons may be quite specialized on this type, but generalized in our comparative analysis. We expect to address this possibility in future analyses.

Finally, our analysis suggests that gibbons become more generalized feeders during periods of resource scarcity. This conformed to our prediction (H1) and was the most common pattern in the other primates at CPRS. However, we consider the test presented here to be preliminary. A full examination of this question will require explicit incorporation of a more fine-grained measure of fruit availability, such as the number of food patches per hectare, as well as inclusion of non-fruit items in the diets of all species.

Which Taxa Are the Major Competitors of Gibbons?

In this chapter we use dietary overlap as a simple proxy for feeding competition. We recognize that dietary overlap does not necessarily indicate competition: species utilizing highly overlapping diets may not compete if they occupy different habitats or if factors other than resources (e.g., predation) limit carrying capacity (Colwell and Futuyma 1971; Pianka 1974, 1976; Yamagiwa and Basabose 2003). In this community, however, we would argue that dietary overlap is a good proxy for feeding competition because our study subjects are generally large-bodied, food-limited, canopy-foraging, mainly frugivorous, diurnal species that occupy the same forest habitats. This competition need not be symmetrical; that is, dietary overlap may not have equivalent effects on the fitness of competing species (Connell 1983). For example, pigs that feed on fruits at the base of trees experience reduced food availability due to competition with arboreal frugivores, but arboreal species are not similarly affected by pigs.

Our analysis indicated that the most important competitor for gibbons at CPRS was not another primate species but a squirrel instead. This unexpected result reminds us that competition with non-primate species can have major ecological impacts on primate species. While some primatologists have realized this for some time (Strum and Western 1982; Estrada and Coates-Estrada 1985; Ganzhorn 1999), the role of non-primate competitors, as members of the same ecological community, is rarely considered. Also, two of gibbons' major competitors, Prevost's squirrels and red leaf monkeys, tend to eat immature fruits and seeds before they ripen sufficiently for gibbons to eat them. This pattern results in asymmetrical competition, whereby Prevost's squirrels and red leaf monkeys reduce food availability for gibbons but experience few negative effects from the gibbons' feeding behavior.

How Similar Are the Niches of Gibbons and Their Major Competitors?

We predicted that gibbon diets would diverge more from their competitors during periods of low resource availability than during periods of higher food availability (H2A). This hypothesis was supported for two important primate competitors: red leaf monkeys and orangutans. During fruit-poor times red leaf monkeys utilize toxic seeds and tannic leaves that gibbons are unable to digest (Marshall 2004), and orangutans utilize low-quality pith, cambium, and leaves that would be insufficient to support gibbons during lean times (Leighton 1993; Knott 1999). These species specialize on foods that are unavailable to gibbons and therefore reduce feeding competition with gibbons during fruit poor times. However, there was no relationship between food availability and gibbon dietary overlap with squirrels, macaques, or hornbills. Gibbons, as relative generalists, cannot fall back on a food type that other species ignore. Instead, they rely heavily on figs as their fallback food (Marshall and Leighton 2006), a pattern characteristic of many Southeast Asian rainforest vertebrates, including macaques and hornbills (Leighton and Leighton 1983; O'Brien et al. 1998). Thus, some species shift their diets away from gibbons during periods of low fruit availability (e.g., orangutans, leaf monkeys), but gibbons appear largely unable to shift their own diets to rely on a fallback food not utilized by other species.

In support of hypothesis H2B, our results indicated that gibbons may reduce competition with two of their major competitors, orangutans and leaf monkeys, by exploiting smaller trees than these species. There are at least two interpretations of this result. First, orangutans and leaf monkeys may displace gibbons from larger feeding sites, relegating gibbons to smaller, less favorable sites. This may occasionally occur with orangutans, although interactions between orangutans and gibbons at feeding trees are very rare and are not always won by orangutans. This explanation seems even less plausible for leaf monkeys, who are generally deferential to gibbons on the rare cases that they interact with them (pers. obs.). Moreover, direct competition over common food resources between gibbons and leaf monkeys is rare, because leaf monkeys eat these items at earlier maturity stages than gibbons. We favor a second interpretation: that gibbons' more efficient locomotor adaptations allow them to profitably visit and feed on a far larger number of food patches in a day than can either orangutans or leaf monkeys (Raemaekers and Chivers 1980). This hypothesis is supported by the observation that gibbon day ranges (mean 1200 m, Leighton 1987) are 1.5 times longer than leaf monkey day ranges (mean 850 m, Bennett and Davies 1994), and 2.5 times larger than orangutan day ranges (<500 m, Rodman 1984). Gibbons did not utilize smaller trees than hornbills, macaques, or squirrels, but may compensate for this by visiting more patches per day than these species (Cannon and Leighton 1996).

Gibbons and their major competitors inhabit all of the forest types found at CPRS, and there was no relationship between gibbon population density and the density of any of their important primate competitors. We therefore rejected our final hypothesis (H2C), which postulated that habitat selection helps to ameliorate competition between gibbons and other primates. Data were unavailable to test this hypothesis for the non-primate competitors, but our observations suggest that high-quality lowland forests have high densities of most non-primate vertebrates as well, and that spatial partitioning of forest types is not an important mechanism that gibbons use to reduce feeding competition.

In this chapter we have used a unique, long-term data set to examine gibbon diets in relation to sympatric frugivorous vertebrates. This analysis provided us with a view of gibbon feeding ecology within the broader community of vertebrate frugivores that is rarely possible. It has demonstrated that gibbons, while clearly highly selective foragers, are nonetheless relative generalists compared with most vertebrates that occupy the same forests. It has allowed us to identify gibbons' major vertebrate competitors, and has indicated the importance of non-primate frugivores as competitors with gibbons. Finally, it has allowed us to test hypotheses about some of the mechanisms that might reduce feeding competition between gibbons and their competitors. We expect that more refined analyses of these data that incorporate explicit consideration of temporal and spatial variation in patterns of food availability and consumption by vertebrates will expand our understanding of gibbon ecology and their role in the larger community of frugivorous vertebrates.

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Chapter 10
The Seed Dispersal Niche of Gibbons in Bornean Dipterocarp Forests

Kim R. McConkey

Introduction

Most tropical rain forest plants are adapted to have their seeds dispersed by animals (Richards 1996). A profusion of birds, mammals, insects, and occasionally reptiles and amphibians consume fruits, but they differ in their ranging behavior, ability to manipulate seeds, and, hence, their seed dispersal effectiveness (van der Pijl 1982; Corlett 1998). It was assumed for many years that effective seed dispersers had close coevolutionary relationships with their selected fruit species (McKey 1980), but more recent research indicates that coevolution has generally been on a diffuse scale – between suites of dispersers and fruits (Herrera 1985). The development of close relationships are hindered by the diversity of frugivores that feed on most plant species [only rarely is a plant species dispersed by a single species (e.g., Cochrane 2003)] and by inconsistencies in frugivore foraging over time or space (Chapman and Chapman 2002), or even within a single fruiting season of a plant species [e.g., small sources may attract a different array of frugivores than large sources (Russo 2003)]. Furthermore, very few dispersed seeds produce a reproductive, adult plant with subsequent life stages overriding any subtle advantages of one dispersal mode over another (Howe and Mitiri 2004). For a frugivorous species to develop a more direct coevolutionary relationship with favored plant species, it must have a clearly defined niche in the frugivore community, providing a consistent and unique dispersal service that can have a lasting positive impact on the survival and establishment of dispersed seeds.

Effective seed dispersers should disperse many seeds (quantitative component), from multiple sources, and in a manner that maximizes the survival and subsequent germination of the seeds (qualitative component) (Schupp 1993). One of the most important aspects of seed dispersal is the removal of seeds away from the canopy of the parent plant, where there are often higher rates of seed

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predation and seedling competition (Barot et al. 1999; Connell 1971; Howe and Mitiri 2004; Janzen 1970; Nathan and Muller-Landau 2000). Seed dispersal also enhances gene flow (Hamilton 1999; Nathan and Muller-Landau 2000), influences plant distribution (Levin et al. 2003; Howe and Mitiri 2004), may help colonize new sites (such as tree fall gaps) (Dalling et al. 2002; Levine and Murrell 2003), and in some cases ensures seeds reach targeted sites, which are crucial for germination (Wenny 2001).

Gibbons (Hylobatidae) are good seed dispersers in Asian rain forests. Studies throughout their distribution indicate that gibbons are consistently frugivorous (Chivers 1984; Elder this volume), swallow most seeds whole, few seeds are dropped or destroyed, and the seeds are subsequently scattered via their scats throughout their home range (Ahsan 1994; McConkey 2000; McConkey and Chivers 2007; Whitington and Treesucon 1991). Two gibbon species inhabit the forests on the island of Borneo [*Hylobates muelleri* and *H. agilis albibarbis* or *H. albibarbis*; the species status of this taxon is controversial (Chatterjee this volume)], and these apes share the forest with many other animals that consume fruit. Despite the apparent efficiency of gibbons as seed dispersers, other animals may adequately disperse the same plant taxa, thereby hindering the development of coevolutionary relationships between gibbons and the plants whose seeds they disperse.

The aim in this chapter is to evaluate the role of gibbons in seed dispersal in Bornean dipterocarp forests with respect to how this role is distinct from other frugivorous animals. First, I describe what type of fruit gibbons favor, since favored fruit species have the most potential to develop coevolutionary relationships. Second, I evaluate the likelihood of gibbons dispersing seeds from multiple individuals of a single plant species and across all fruit patch sizes. Third, the pattern of seed dispersal produced by gibbons and other animals are compared to determine whether the gibbons have a unique dispersal mode and whether this may facilitate the establishment of new individuals of favored species.

Methods

I studied seed dispersal by gibbons (*Hylobates muelleri x agilis/albibarbis*, viable hybrids of two species present in Borneo) in the dipterocarp forests at the Barito Ulu research area, Central Kalimantan, Indonesia between October 1996 and September 1997 (McConkey 1999). I use this research as a basis for evaluating the role of gibbons, while the effectiveness of other frugivores is described from the work of other authors and from observations during the above study.

Study Area and Gibbon Groups

The Barito Ulu research area occurs virtually at the geographic center of the island of Borneo (0°12'N and 114°6'E), in the watershed of the upper Barito

River. The area has a rugged, hilly to mountainous terrain, with altitude ranging from 100 to 350 m asl. Various forest types are present (including heath forest and various stages of secondary forest), but the most expansive is lowland dipterocarp forest (Mirmanto et al. 1999; Brearly et al. 2004). The mean annual rainfall from 1990 to 1997 was 3738 mm. Temperature was very equitable, with a mean maximum of 34°C and a nighttime low of 22°C.

I collected data for two gibbon groups (four individuals each) with adjacent home ranges (46 and 43 ha in size, respectively). My assistants and I followed each gibbon group from their waking site to their sleeping tree, for 5 days in every month for 12 months (a total of 10 days each month). I compiled gibbon diet by direct observations of the feeding gibbons and collection of food items [see McConkey et al. 2002 for more details]. I also collected scats during the follows, from which seeds were identified, counted, and then returned to the defecation location. I checked scats after 1 week and then monitored monthly until the end of the study period (4–12 months after returning scats) (see McConkey 2000, 2005a for details). Seeds that had been destroyed by insects, vertebrates, or had disappeared or germinated were recorded. I noted the removed seeds as vertebrate predation for the analysis, although some of these may have been hoarded by rodents and subsequently germinated (McConkey 2005a). There was no evidence that topography and rainfall (which was very low during the study) were responsible for the disappearance of some seeds. I determined the selection of fruit taxa by gibbons by comparing feeding data with information on the availability of plant taxa. Full methods are given by McConkey et al. (2002), and a summarized version of the resulting selection list is given in the Appendix. Although 17% of fruit feeding observations were of figs (McConkey et al. 2002), figs are not included in the analysis and subsequent discussion since they represent a specially favored food item for many animal species.

I collected phenology data for 1000 trees [selected using the point-center-quarter method (Mueller-Dombois and Ellenberg 1974)] monthly during the study period. The presence of fruit (unripe, ripe), flower, and young leaf in the trees, and lianas within them, was noted (McConkey et al. 2002). I collected and examined the available fruit (general description, fruit and seed measurements) from all phenology trees and the lianas within them, and also opportunistically from other locations.

Bornean Frugivores

Many animals consume the fruits or the seeds of plants, or both, but it is reasonable to assume that animals that are primarily seed predators [e.g., langurs, rodents, some squirrel species, pigs (Corlett 1998)] are unlikely to disperse similar quantities of seeds as gibbons, even if some of the same species are dispersed. Hence, details on these animals were not collected. Similarly, gibbons feed almost exclusively in the upper strata of the forest, and arboreal and volant animals that rarely, or never, use these strata are also excluded. Some terrestrial animals consume fallen fruit (e.g., deer, pheasants and partridges), but these animals are also excluded. Deer (mouse deer, muntjac, and sambar) can disperse small or very hard seeds, while most other seeds are destroyed (Corlett 1998). Though almost nothing is known about frugivory by terrestrial birds (Corlett 1998), their role (if one of seed dispersal rather than seed predation) is likely to have some similarities to other frugivorous birds in terms of fruit selection and handling.

In this chapter I evaluate the roles of 16 animal taxa (Table 10.1), with respect to their diet and dispersal overlap with gibbons. Some species are grouped in higher taxonomic divisions, because either the role is likely to be similar amongst species (i.e., macaques, most bird taxa) or there is inadequate knowledge to treat species separately (i.e., civets, fruit bats).

Table 10.1 Main seed dispersal agents in Bornean dipterocarp forests

Frugivore	Taxa (number of species in each group)	Seed dispersal references
Bornean orangutan	*Pongo pygmaeus*	1, 2
Gibbon	*Hylobates* (2 spp.)	3, 4
Macaque	*Macaca* (2 spp.)	2, 5
Prevost's squirrel	*Callosciurus prevostii*	6, 7, 8
Sun bear	*Helarctos malayanus*	9, 10, 11
Civets	Viverridae (approx. 4 spp.)[1]	8, 12, 13
Fruit bats	Pteropodidae (11 genera)[1]	14
Hornbills	Bucerotidae (8 spp.)	15
Barbets	Capitonidae (8 spp.)	15, 16
Pigeons	*Ducula* and *Ptilinopus*[2]	15, 17
Black magpie	*Platysmurus leucopterus*[3]	15
Green broadbill	*Calyptomena viridis*	15
Asian fairy bluebird	*Irena puella*	15
Bulbul	Pycnonotidae (approx. 16 spp.)[1]	15, 18
Leafbird	Chloropseidae (3 spp.)	15
Flowerpecker	Dicaediae (approx. 4 spp.)[1]	15

[1] Habits of taxa are not fully understood, and the exact number of frugivorous species feeding in the canopy is not known. [2]Other pigeon genera tend to be seed predators. [3]Other Corvidae may also disperse seeds, but data were only available for this species.

References: 1 – Leighton (1993); 2 – Ungar (1995); 3 – McConkey (2000); 4 – McConkey et al. (2002); 5 – Lucas and Corlett (1998); 6 – Payne (1979); 7 – Becker et al. (1985); 8 – McConkey (1999); 9 – McConkey and Galetti (1999); 10 – Wong and Servheen (2002); 11 – Fredriksson et al. (2006); 12 – Bartels (1964); 13 – Colón (1999); 14 – Hodgkison et al. (2003); 15 – Leighton (1982); 16 – Fogden (1970); 17 – McConkey et al. (2004), 18 –Weir Also see (Payne et al. 1985; MacKinnon and Phillipps 1993; Corlett 1998).

Quantity: Selection of Food Plants

Many frugivores include a diverse array of fruit and plant types in their diet, but the bulk of their feeding time is usually spent on a more limited selection of species. Selection of food plants is an important component of a frugivore's seed dispersal niche; it determines the quantity of seeds that a frugivore is likely to disperse for a particular species when it is available and the number of sources from which they feed. Since only a very small proportion of dispersed seeds survive to adulthood (Howe and Mitiri 2004), animals that disperse many seeds of a particular species (away from the parent canopy) are more likely to disperse a seed that produces a reproductive adult than an animal that feeds sporadically on that species. Dispersal of seeds from multiple individual plants is essential for the development of coevolutionary relationships between frugivores and plants (since the animal should exert selection pressure across the plant's population) and also helps to maintain gene flow.

General Fruit Types

Broad categories in fruit types are frequently used for distinguishing frugivore preferences (van der Pijl 1982). These categories are based on the observed preferences of, mainly, birds, primates, and bats for certain fruit colors and pulp types and also on their ability to process certain fruit morphologies. Most birds, for example, are unable to remove a thick rind (Fogden 1970), so are limited to consuming fruit that is dehiscent or with a thin edible skin. Birds also tend to prefer pulp that is rich in lipids, which are usually avoided by primates (and other mammals) (Corlett 1998). Consistent differences in the colors of different fruit types are probably related to the visual capabilities of the respective animals, rather than an active preference for color [e.g., fruits favored by night-foraging bats tend to not change color on ripening (Hodgkison et al. 2003)].

A simplified version of fruit types is given below. These divisions describe the "average" fruit eaten by most Asian birds and primates (Kitamura et al. 2002; Leighton 1982; Leighton 1993; McConkey 1999; McConkey et al. 2002; Ungar 1995), reflecting the preferences of primarily pulp-eating (and seed dispersing) animals, rather than those species that consume seeds and exhibit different choices [e.g., langurs (Ungar 1995)]. Alternative fruit types are consumed by birds and primates to varying degrees (Chapman and Russo 2007), but frugivores are likely to visit more sources and disperse more seeds of favored species. A bat fruit type is not defined, since the only distinguishing feature of such fruits appears to be color (Hodgkison et al. 2003). Fruit that appear to be bat-dispersed at Barito Ulu are included in the "other" category. This category includes a variety of fruit-types, which are not typically, bird, primate, or generalist.

Bird fruit: Lipid-rich aril, dehiscent capsule, or berry or drupe with a thin skin, often red, blue, or black in color (e.g., *Myristica* spp.). A second type of bird fruit is also frequently described: small, sugary fruit with a thin skin and small seed(s) (e.g., *Hydnocarpus anomala, Macaranga* spp.).

Primate fruit: Sweet or sour, with juicy pulp and a thick rind, often orange-yellow in color; frequently, with a single large seed (e.g., *Willughbeia* spp., *Nephelium rambutan-ake, Zizyphus sulvensis*).

Generalist fruit: Sweet juicy pulp, with a thin skin and medium-sized seed(s), usually orange-yellow in color. These are frequently grouped with primate fruit, but the absence of a rind makes them accessible to a wider variety of frugivores (e.g., *Prunus javanica, Rourea minor*).

Gibbons are unspecialized frugivores, consuming fruits from a wide range of taxa (Marshall et al. this volume), but at Barito Ulu the favored taxa [over-selected: amount of time spent feeding on species is greater than expected by the species' abundance in the forest (McConkey et al. 2002)] almost always displayed fruit traits associated with primate fruit (Fig. 10.1). Generalist fruit had a weaker tendency to be over-selected, while bird fruit were eaten rarely and were usually under-selected or not eaten by gibbons. Lianas may be particularly important for gibbons. Almost all consumed liana fruit were over-selected and most lianas included in their diet had primate fruit (70% of liana species). The gibbons were more likely to forage at multiple individuals of plant species with primate fruit each month, than for species with generalist or bird fruit (Kruskal-Wallis, $H = 17.05$, $P = 0.0002$; Fig. 10.2).

At Barito Ulu I observed 19 fruiting tree and liana species (Appendix) eaten by gibbons and displaying one of the three types of fruit. Only plant sources actually visited by gibbons were watched and the number of hours spent watching each species was low (7–26 h each; watches were mainly in the mornings); however, some general patterns can be seen in the foraging behavior of different animals when the plant species are grouped into fruit types (primate fruit, $n = 112$ h; generalist fruit, n = 82 h; bird fruit, $n = 90$ h). Primate fruits were consumed almost exclusively by gibbons, while bird fruits (small sweet berries rather than the lipid-rich drupes, which were virtually ignored by the gibbons

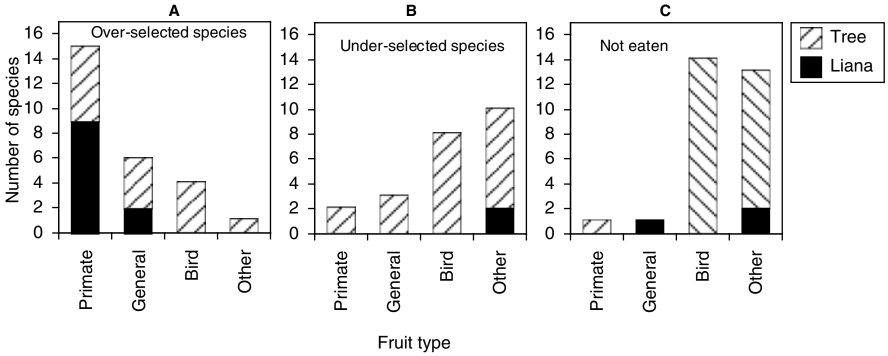

Fig. 10.1 Number of species (**a**) over-selected, (**b**) under-selected, and (**c**) not eaten by gibbons at Barito Ulu according to fruit and plant types ($n = 79$ species). Species listed as "not eaten", exclude those with fruits lacking an edible pulp

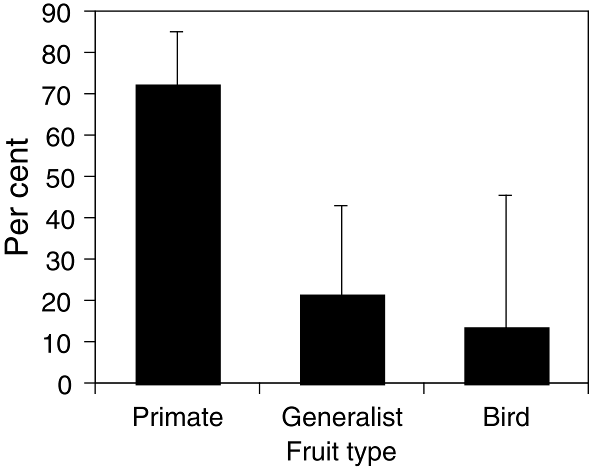

Fig. 10.2 Mean percentage (+ 1 sd) of plant species consumed by Barito Ulu gibbons each month for which gibbons use multiple sources. Species are divided according to fruit-type

during the study period) were consumed mainly by small birds (bulbuls, Asian fairy bluebirds, flowerpeckers) (Fig.10.3). Gibbons provided an inconsistent dispersal service for these species as they fed on few available sources (Fig. 10.2).

In West Kalimantan, gibbons exhibited the highest diet overlap with Prevost's squirrel, orangutans, and macaques (Marshall et al. this volume). Prevost's squirrels have an unspecialized diet (Marshall et al. this volume) and were observed feeding at 10 of the 13 plant species exhibiting primate fruits that were watched in the present study. This high diet overlap with gibbons, however, does not reflect a high dispersal overlap since Prevost's squirrels removed few fruits (Fig. 10.3) and were also noted to feed in some species when unripe or they actually consumed the seeds rather than the pulp (Marshall et al. this volume).

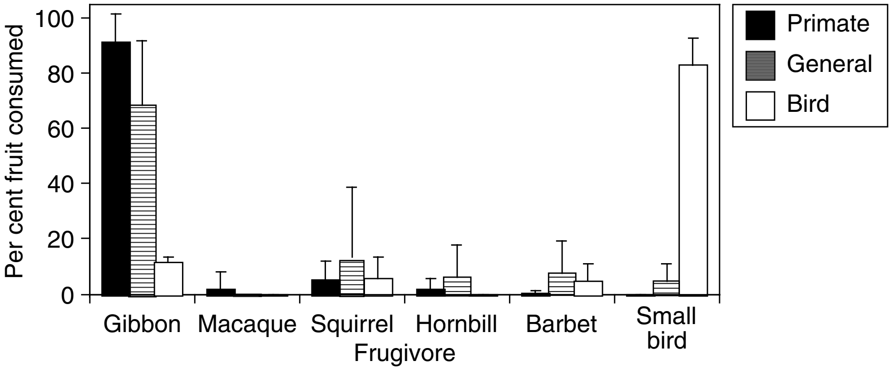

Fig. 10.3 Estimated mean percent fruit (+ 1 sd) consumed by different frugivores from plants displaying three fruit-types and watched at Barito Ulu

Long-tailed macaques were at low density at Barito Ulu and orangutans and pig-tailed macaques were very rare (McConkey and Chivers 2004). Hence, their virtual absence during the plant observations will reflect these low densities rather than fruit choice. Differences in fruit preferences between these primates have been noted in Sumatra (Ungar 1995); orangutans consistently preferred larger fruit to the other two primate species and were more likely to consume fruits that had a hard husk, dry pericarps or were unripe. In contrast, macaques preferred small fruit and were more likely to consume dry fruit than gibbons. Lastly, gibbons showed less preference for fruit size, but had a strong preference for ripe fruits with a fleshy pericarp and low pH value. Despite these differences, all three primate taxa consume many of the same favored plant species (primate fruit) and dispersal overlap may be substantial.

Hornbills and barbets were noted to have significant diet overlap with gibbons in West Kalimantan (Marshall et al. this volume), and they also visited some of the 19 plant taxa watched in the present study (Fig. 10.3). Of the taxa with primate fruit, however, only four species ($n = 13$ species watched) were visited by hornbills and one species by barbets, suggesting these species primarily target fruits with a different morphology to that favored by gibbons (Leighton 1982). Similarly, the seasonally frugivorous sun bears consume many fruit species also eaten by gibbons (Fredriksson et al. 2006; McConkey and Galetti 1999; Wong and Servheen 2002). However, many of the favored taxa [e.g., *Syzigium, Santiria, Dacryodes, Durio* (Fredriksson et al. 2006)] are either inaccessible to gibbons (because of a hard husk or very large seed) or exhibit traits that make them unattractive to gibbons; hence, while significant diet overlap may occur, the favored species are likely to differ. This means that the plant species for which overlap exists may not be sought over multiple seasons and multiple individuals by hornbills, barbets, and sun bears.

Relatively less is known about the fruit choices of bats and civets, although they are good seed dispersers for some plant species. Civets feed on primate fruit, but may use other fruit types as well including the species not known to be eaten by gibbons (Bartels 1964; Colón 1999; McConkey 1999; Rabinowitz 1991). Many species are noted to be opportunistic frugivores, consuming fruit seasonally (Rabinowitz 1991). Some bat species select a distinct type of fruit (Hodgkison et al. 2003), but are more likely to include primate fruit in their diet than bird fruit, indicating some overlap will exist (Banack 1998; Hodgkison et al. 2003; Meehan et al. 2005). Although this overlap has not been documented in Borneo, the main fruits targeted by bats appear not to be favored by gibbons (Hodgkison et al. 2003).

Seed size is another fruit characteristic that limits fruit consumption by some species. Progressively larger seeds limit dispersers due to the inability of small frugivores to manipulate large seeds, while it is often inefficient for large frugivores to forage on small fruits (Corlett 1998; Kitamura et al. 2006). The fruit types frequently have some trends in seed size (i.e., primate fruit tend to be larger-seeded than sugary bird fruit), but often a range of seed sizes is present (Corlett 1998; Kitamura et al. 2006). Gibbons are able to swallow seeds up to

21 mm wide (McConkey 2000) and 44% of diet species had seeds 10–20 mm wide (McConkey 1999). The smaller birds, macaques, and bats are unable to disperse seeds of this size by endozoochory (although macaques and bats spit larger seeds) (Fig. 10.4). Orangutans, civets, sun bears, and several bird taxa can disperse seeds of this size and greater; but, if we combine fruit choice and seed size, only orangutans are potentially regular endozoochoric dispersers of the species favored by gibbons.

Patch Size

Although gibbons feed on plants of all sizes within the forest overstorey (median dbh [diameter at breast height] of food trees at Barito Ulu was 18 cm; range 7–60 cm), they are often noted to be well adapted for foraging among plants with small fruit crops (Chivers 1984) and may be important seed dispersers of small fruiting plants that produce primate fruit. Orangutans were noted previously to be the only regular endozoochoric dispersers of species favored by gibbons, but orangutans in Borneo showed strong preferences for fruit available in large patches (Leighton 1993; Marshall et al. this volume), and appeared to actually avoid small patches (<22 cm dbh) despite the availability of primate fruit that appeared suitable for orangutan consumption (Leighton 1993). An important aspect of this tendency is that smaller fruit patches are frequently lianas. Leighton (1993) found that lianas produced fruit patches less than half the size of average tree species. Sun bears also appeared to

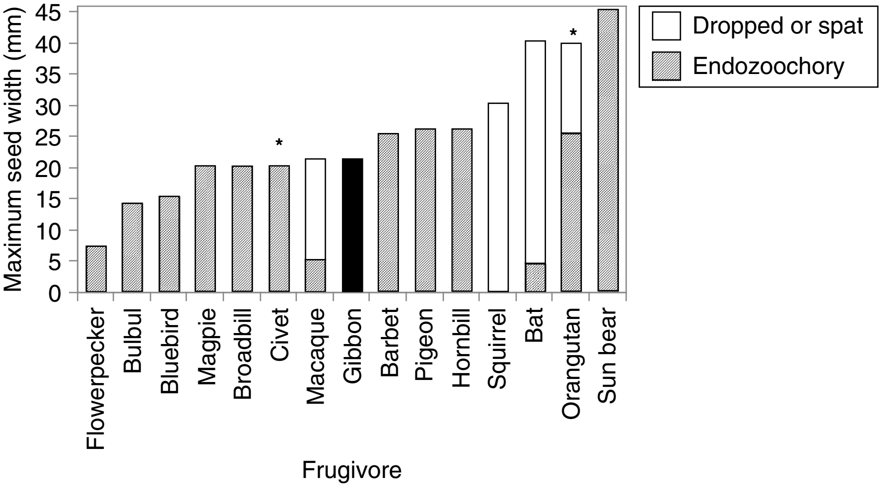

Fig. 10.4 Maximum width of seeds dispersed by Bornean frugivores (up to a maximum width of 40 mm). Bars indicated by *may be an underestimate as there was little published information on dispersed seeds or gape width available for the species. References are given in Table 10.1

preferentially feed in large fruit patches in East Kalimantan and only rarely consumed liana fruit (Fredriksson et al. 2006). All other frugivores addressed in the present study appear to forage frequently in small patches (Fogden 1970, Hodgkison et al. 2003; Leighton 1982; McConkey 1999; Payne 1979; Marshall et al. this volume).

The ability of gibbons to subsist on smaller fruit patches than orangutans (whose seed dispersal niche has a high overlap) has important consequences for seed dispersal. If gibbons are specifically targeting certain plant species that are always small, then they may be the only frugivorous primates offering a regular endozoochoric seed dispersal service for that species. Some plant species may offer both large and small fruit patches; while the large fruit patches may be visited regularly by both primate species, the small fruit patches may only regularly attract gibbons (but field studies have yet to be done to test this). Because the gibbons may be the only effective dispersers of a subset of individuals of these species, they would be important for ensuring the genetic variation of the species is maintained.

Quality: Primary Seed Shadow and Post-Dispersal Processes

Once a seed has been swallowed by a gibbon and deposited in the forest within their scats, it faces several obstacles before it can germinate and establish as a seedling. At Barito Ulu, 1470 gibbon-dispersed seeds (>4 mm wide) were monitored over 1 year and only 11% of seeds germinated (McConkey 2005a). Seed predation [including seeds that disappeared (McConkey 2005a)] was the most significant cause of seed death, killing 88% of seeds (<1% seeds did not germinate). Seed predation has been recognized as a major cause of seed death in tropical forests (Hulme 1998) and the primary granivores in Asia are rodents, pigs, deer, and various insect species (Blate et al. 1998; Curran and Webb 2000; Ickes et al. 2001; Kitamura et al. 2006; McConkey 2005b). Although the primary seed shadow (pattern of seed fall) formed by frugivores often has little lasting impact on the chance of a seed germinating (Jordano and Herrera 1995; Rey and Alcántara 2000), there are some ways in which frugivores may influence the survival probability of seeds.

How Seeds Are Deposited

There are two main ways in which frugivores deposit seeds on the forest floor (Table 10.2). Seeds may be swallowed and later regurgitated or defecated (endozoochory), or they may be spat or dropped after the pulp is consumed. Endozoochory is usually the most efficient form of dispersal, as seeds have a better chance of being deposited away from the parent canopy (Corlett 1998) and germination is frequently enhanced (Traveset and Verdú 2002). Dispersed

Table 10.2 Main dispersal modes by different frugivore taxa (for seeds greater than 4 mm wide)

		Clumped-dispersal	
Seed treatment	Scatter-dispersal	Multiple species	Single species
Spat or dropped	Fruit bats[1]		Fruit bats[1] Macaques[2] Squirrels[2]
Endozoochory	Birds	Gibbons (small clumps) Orangutans (large clumps)	Civets (small clumps) Sun bear (large clumps)

[1] Fruit bats drop many seeds under fruiting crowns, or at feeding roosts, but a significant number are also scatter-dispersed.

[2] Most seeds are spat or dropped under parent trees

seeds also vary according to whether they are scattered singly or deposited in clumps, and seed clumps may be small or large, mono- or multispecific. The respective benefits of these dispersal modes are not clearly understood, but seeds dispersed singly or in small fecal clumps are usually more efficient dispersal modes than seeds dispersed in large fecal clumps or spat or dropped singly around the fruiting tree, since the latter frequently suffer high rates of seed predation or seedling competition (Willson and Whelan 1990; Pizo and Simao 2001). Limited evidence also suggests different plant species show physical and chemical adaptations to different broad forms of dispersal [i.e., scatter (single seeds) and clumped (many seeds) dispersal (Howe 1989; Blate et al. 1998)], and it is possible that the seeds of a particular fruit type may have higher survival, due to intrinsic qualities, if dispersed in the mode of the frugivore that favors them.

At Barito Ulu, gibbons dispersed by endozoochory the seeds of 81% of consumed fruit species (McConkey 2000). The remaining species were eaten while unripe, destroyed, or dropped under the parent crown. The seeds of consumed liana species were more likely to be dispersed (90% of liana species in the gibbons' diet had their seeds dispersed, $n = 40$) than the seeds of consumed tree species (72% of tree species, $n = 94$; Chi-square = 5.6, $p < 0.05$). These seeds were deposited in multispecific, small clumps containing between 1 and 51 seeds (seeds greater than 3 mm in length only; mean = 7 seeds) and up to 6 species (mean = 2 species) (McConkey 2000). Seed clumping was reduced by the scattering of scats as they fell through the canopy and seeds were occasionally buried by dung beetles [1% of defecated seeds 4–9 mm wide (McConkey 1999)].

In Borneo, eight other frugivorous taxa can disperse seeds up to 20 mm wide by endozoochory (Fig. 10.4), but only some arboreal mammals dispersed seeds in clumps (Table 10.2). Seed depositions of orangutans are most similar to gibbons since they also produce multispecific clumps, but orangutans destroy more seeds than gibbons and they spit rather than swallow some seeds [of any species (Rijksen 1978)]. Clump size is also much larger in orangutans [median of

111 seeds (Galdikas 1982)], with potential negative effects on seedling survival. Hence, gibbons produce a unique seed shadow in terms of seed deposition.

No evidence is available to assess whether the unique dispersal mode of gibbons is specifically beneficial to those plant species that they favor (compared to dispersal modes of other frugivores); however, through their behavior, gibbons positively influenced seed survival of over-selected species in their diet (McConkey unpubl. data). Since gibbons fed more in over-selected species, the scats subsequently produced contained fewer seed species. At Barito Ulu, this led to a significantly lower chance of vertebrate seed predation and a higher chance of germination for over-selected species [21% seed survival for over-selected species, compared to 5% for under-selected (McConkey 2005a)]. Hence, gibbons can have a direct influence on the post-dispersal fate of selected species.

Where Seeds Are Deposited

Effective seed dispersers remove seeds from the parent canopy and deposit them some distance (often cited as at least 5–10 m) away in sites that are suitable for germination (Howe and Smallwood 1982; Howe and Mitiri 2004). Long-distance seed dispersers (dispersal distances >100 m) are often of particular importance since they help to maintain higher levels of gene flow and are likely to disperse seeds across a wider variety of sites (Cain et al. 2000; Nathan and Muller-Landau 2000).

The gibbons at Barito Ulu dispersed > 90% of seeds more than 100 m from parent plants and <1% were dispersed under parent plants (McConkey and Chivers 2007). Mean dispersal distances exceeded 300 m for both studied groups with a maximum distance of >1000 m; hence, they are effective, regular, long-distance seed dispersers. Due to their behavior of visiting many fruiting trees in a day, 27% of scats were deposited under a fruiting tree of any species and 3.6% under conspecific plants (McConkey 2000); but these actually conveyed an advantage to seeds as seed predation (on defecated seeds) was lower in this region, probably due to the abundance of alternative foods (McConkey 2005a). There were no other obvious patterns in where gibbons deposited seeds.

Endozoochory frequently results in seeds being deposited away from parent plants and, consequently, many other Bornean frugivores are also capable of dispersing seeds to considerable distances. Regular long-distance dispersers include hornbills (Whitney et al. 1998; Holbrook and Smith 2000) and probably orangutans, sun bears, and large fruit bats (*Pteropus* spp.). No dispersal distances are currently available for orangutans, but they are probably on average greater than those for gibbons. Although day ranges of the two primates are similar (if not smaller for orangutans), home ranges of orangutans are usually much larger (McConkey 2005c), and the tendency of gibbons to encircle their home range within a single day reduces potential seed dispersal distances (McConkey and Chivers 2007). Sun bears have large home ranges (approximately 14 km^2), with day ranges exceeding 1 km (Wong 1997). Assuming long gut retention times, they can potentially disperse seeds long distances; however, when favored plants are fruiting, they may confine their movements to that area for several days (Wong 1997) forming a very clumped seed shadow (McConkey and Galetti 1999). Dispersal distances for Asian *Pteropus* fruit bats are also unavailable, but on Pacific archipelagoes they are capable of carrying large fruit for distances exceeding 1 km (Banack 1996).

Several other frugivores are likely to disperse seeds beyond 100 m occasionally, but most seeds will be deposited closer to fruiting trees. *Ducula* pigeons deposited most seeds away from parent plants, but usually within 50 m, in a Pacific archipelago (McConkey et al. 2004). Bulbuls in Hong Kong regularly dispersed seeds within 100 m of fruiting trees, with maximum dispersal distances of over 1000 m (Weir and Corlett 2007). Macaques spit large seeds and the vast majority are deposited under fruiting trees (Lucas and Corlett 1998). The extra handling time macaques require for primate fruit results in more seeds being spat under tree crowns (90% of handled seeds) compared to 60% for one generalist species (McConkey et al. unpubl. data). Nevertheless, some seeds are deposited at least 40 m from fruiting trees, with the potential for greater distances (McConkey et al. unpubl. data). Little is known about the seed shadow produced by most other Bornean mammals. Some civet species have large home ranges compared to gibbons (Colón 2002; Grassman Jr. et al. 2005; Joshi et al. 1995; Rabinowitz 1991), and civets regularly deposit seeds away from fruiting trees (Bartels 1964; McConkey 1999); however, the use of “latrines” by some species causes seed clumping (Corlett 1998) and home ranges are often reduced when food is abundant (Rabinowitz 1991; Joshi et al. 1995). Many smaller bird species (including barbets and broadbills) feed for prolonged periods in fruiting trees (Lambert 1989), and with their short retention times probably disperse most seeds under the tree (Pratt and Stiles 1983). Squirrels appear to be very poor distance dispersers, with seeds deposited no more than 10 m from fruiting crowns (Becker et al. 1985; McConkey et al. unpubl. data).

What Is the Seed Dispersal Niche of Gibbons?

Gibbons may be the main seed dispersers for primate fruit found in small patches (Fig. 10.5) and may be particularly important for the dispersal of lianas bearing primate fruit. Seeds of all plant types are dispersed in a unique manner – small, multispecific scats – and are almost always dispersed away from parent trees, frequently at long distances. It is not clear whether this unique seed shadow conveys a strong advantage to gibbon-dispersed seeds over other dispersal modes, but, in terms of fruit choice, only macaques appear to favor the types of fruit and plants for which gibbons are most suited and macaques are inefficient seed dispersers (Fig. 10.5). The larger mammals (orangutans and sun bears) tend to avoid small sources, while the smaller mammals and birds show no specialization for primate fruit. This means that (1) other animals probably

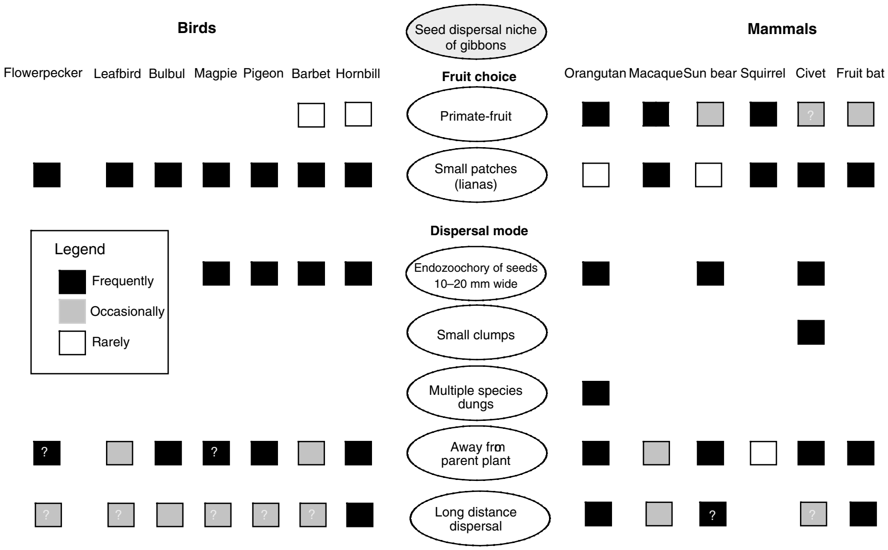

Fig. 10.5 Summary of the seed dispersal niche of gibbons and its overlap with the fruit choice and dispersal modes of other frugivores in Borneo

consume and disperse much smaller quantities of seeds than gibbons, (2) it is unlikely that any other animals would seek multiple sources of such plants, and, therefore, do not exert selection pressure across the plants' population, and (3) other animals may not feed consistently on the species across multiple fruiting seasons.

Gibbons regularly feed on, and disperse the seeds of, many other plant species that are not primate fruits. Since the seeds of these plants appear intact in the gibbons' feces, it may be assumed that they are also effective dispersers of these plants. It is unlikely coevolutionary relationships can develop though, since they feed inconsistently on these species – during years when more favored species are available, it is possible they ignore these species completely and they are less likely to consume fruit from multiple sources. Moreover, seeds from nonfavored species had much higher predation rates in the gibbons' feces than those from favored species, indicating gibbons may be less suited for their dispersal.

Gibbons satisfy several requirements necessary for the development of coevolutionary relationships with their food plants. Fruit is the favored food item of all gibbon species [although some populations rely more heavily on leaves (Elder this volume)] and the seeds of most diet species are dispersed effectively by endozoochory. There is almost no variation in their treatment of seeds within species (few seeds are dropped while foraging, and there have been no records of significant seed damage on swallowed seeds). They also appear to be best suited for specific fruit/plant types, of which they feed on selectively when available, use multiple sources, and which have very few other effective dispersers. Finally, gibbons produce a unique seed shadow, although the importance of this is not yet understood.

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Appendix

Selection of plant taxa consumed by gibbons at Barito Ulu. Only plant taxa that are dispersed by gibbons are shown. Taxa are arranged in approximate order of preference[1]. Plants that were watched at Barito Ulu are indicated by an asterix.

Taxa	Family	Source	Fruit type
Over-selected			
Liana sp. 16*	Unidentified	Liana	Primate
Gnetum spp.*	Gnetaceae	Liana	Primate
Garcinia spp.*	Clusiaceae	Tree	Primate
Artabotrys lanuginosa	Annonaceae	Liana	Primate
*Diospyros puncticuolsa**	Ebenaceae	Tree	Primate
*Tetrastigma trifoliolatum**	Vitaceae	Liana	Primate
*Zizyphus sulvensis**	Rhamnaceae	Liana	Primate
*Strychnos colubrine**	Loganiaceae	Liana	Primate
*Erycibe maingayi**	Convolvulaceae	Liana	Primate
Nephelium rambutan-ake	Sapindaceae	Tree	Primate
Zizyphus horsfieldii	Rhamnaceae	Liana	General
Calamus spp.*	Arecaceae	Liana	Primate
Willughbeia sp.*	Apocynaceae	Liana	Primate
Polyalthia glauca	Annonaceae	Tree	General
Prunus javanica	Rosaceae	Tree	General
Parkia javanica	Fabaceae	Tree	Other
*Cryptocarya crassinervis**	Lauraceae	Tree	Primate
Xanthophyllum flavescens	Polygalaceae	Tree	Other
Artocarpus spp.*	Moraceae	Tree	General
Eugenia spp.	Myrtaceae	Tree	Other
Dillenia borneensis	Dilleniaceae	Tree	Other
Blumeodendron elateriospernum	Euphorbiaceae	Tree	Primate
*Litsea ferruginea**	Lauraceae	Tree	General

(continued)

Taxa	Family	Source	Fruit type
Macaranga sp. 1	Euphorbiaceae	Tree	Bird
*Rourea minor**	Connaraceae	Liana	General
*Aglaia ganggo**	Meliaceae	Tree	Primate
Neutral or under-selected			
Beilschmiedia dictyoneura	Lauraceae	Tree	Other
Xanthophyllum amoenum	Polygalaceae	Tree	Other
Adinandra dumosa	Theaceae	Tree	Other
Mangifera sp. 1	Anacardiaceae	Tree	Other
Embelia coriaceae	Myrsinaceae	Tree	Bird
*Hydnocarpus anomala**	Flacourtiaceae	Tree	Bird
Litsea angulata	Lauraceae	Tree	Other
Baccaurea spp.	Euphorbiaceae	Tree	Bird
Xerospernum norohanum	Sapindaceae	Tree	Primate
Vitis imperialis	Vitaceae	Liana	Other
*Pternandra rostrata**	Melastomataceae	Tree	Bird
Artobotrys rosea	Annonaceae	Tree	Primate
Prunus arborea	Rosaceae	Tree	General
Zizyphus angustfolius	Rhamnaceae	Tree	General
Diospyros dictioneura	Ebenaceae	Tree	General
Xanthophyllum sp. 2	Polygalaceae	Tree	Other
Ashtonia excelsa	Euphorbiaceae	Tree	Bird
Polyalthia lateriflora	Annonaceae	Tree	Bird
Erycibe impressa	Convolvulaceae	Liana	Other
Xanthophyllum stipitatum	Polygalaceae	Tree	Other
Palaquium sp.	Sapotaceae	Tree	Other
Polyalthia sumatrana	Annonaceae	Tree	Bird
Myristica spp.	Myristicaceae	Tree	Bird

[1] Actual selection ratios were calculated for three time periods differing in fruit abundance (high, medium, low). Hence, order is determined by calculated ratios as well as consistency in selection (McConkey et al. 2002).

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Part IV
The Relationship Between Ecology and Social Organization

Chapter 11
Ecology and the Social System of Gibbons

Warren Y. Brockelman

Introduction

How does the social system of gibbons relate to the way in which they exploit their environment? For several decades, the major focus of vertebrate ecologists has been on how the environment influences or constrains social systems. To a certain extent, phylogenetic inertia or current morphology constrains ecological and social evolution, but this partly begs the question because these may already have been shaped by natural selection by the environment. Gibbons, for example, have hands and limbs highly adapted for terminal branch feeding and not ground foraging, and these are part of the complex of characters we are trying to explain. As Clutton-Brock and Harvey (1977: 574) put it, "The end products of natural selection are clusters of functionally interrelated traits." They considered, however, that adaptations to the feeding niche were usually the most basic adaptations and probably constrained the evolution of most other functional characters.

The gibbons' highly specialized morphological characters for life in the forest canopy and for terminal branch feeding (Tuttle 1972; Fleagle 1980; Raemaekers 1984) indeed define the family Hylobatidae, and probably have heavily influenced all other behavioral aspects. The locomotion and feeding adaptations of gibbons thus may help to explain the lack of variability in the foraging methods seen in gibbons, in general, despite considerable variation in diet, and their relative uniformity of social structure. For reasons that are still incompletely understood, the study of gibbons is in many respects a study in adaptive constraints rather than of adaptive radiation.

Have the gibbons' marvelous adaptations to terminal branch feeding and frugivory (Grand 1984; Kay 1984; Preuschoft and Demes 1984), possibly

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stimulated by competition with cercopithecids, placed them in a specialized adaptive zone from which there is no evolutionary escape? The lack of sympatry between species of gibbons (with the exception of the larger and slightly more folivorous siamang), suggests that this may be the case. The antiquity of the divisions between the four hylobatid genera (Roos and Geissmann 2001), which predate the chimpanzee–human split, supports the idea that the evolution of the lesser apes has been surprisingly conservative in comparison with that of the hominids.

In this chapter I will review and comment on current ideas about the relation between the ecology and social structure of gibbons. The socio-ecology of gibbons comprises an interrelated set of general traits including small group size, territorial behavior, monogamy with long-term pairing, and a preponderance of frugivory (Chivers 1977; Raemaekers and Chivers 1980; Leighton 1987). Some exceptions to monogamy have been reported (Srikosamatara and Brockelman 1987; Palombit 1994; Jiang et al. 1999; Fuentes 2000; Sommer and Reichard 2000; Reichard 2003; Lappan 2007, this volume; Malone and Fuentes this volume; Reichard this volume), but these may be expected given the rather flexible nature of pair formation and dissolution reported from more recent, long-term studies (Palombit 1994; Brockelman et al. 1998). Many apparent exceptions consist of groups with extra males that are either late-dispersing subadults or older, nonbreeding males, but this is not always the case (Lappan this volume; Reichard this volume). It is now necessary to distinguish between "social monogamy," "mating (or sexual) monogamy," and "genetic monogamy" (Gowaty 1996; Reichard 2003). Clearly, however, these must be correlated, and in this discussion I use "monogamy" in a general sense, which implies a high prevalence of all three indications of monogamy in a population.

In attempting to explain the general features of gibbon social systems, I do not wish to imply that the Hylobatidae are uniform in their ecology and behavior. It should be borne in mind that a substantial part of our detailed knowledge of gibbon behavior has come from a single species (*Hylobates lar*) at about four study sites. More variations will surely be found in gibbons, especially when the species of *Nomascus* have been more thoroughly studied. The relatively recent findings of intraspecific flexibility alluded to above will likely be found to apply to all species eventually. Put another way, however, no gibbon has so far been found to be nonterritorial, predominantly polygamous, or living in large groups.

It is not an easy exercise to explain which of the traits characterizing gibbons was the prime mover or the first to appear in the gibbon lineage; this information is buried unrevealed in evolutionary history some 15–20 million years ago. Instead of exploring the origin of monogamy, I will attempt to rationalize the selective forces that currently maintain the social system of gibbons. The ecological conditions and even the biology of the animals, when monogamy first appeared, may well have been different from those today (Brotherton and Komers 2003; van Schaik and Kappeler 2003).

Grades of Explanation

The development of our understanding of primate socioecology and social evolution can be divided into phases as new insights and theoretical developments have become incorporated into the field (Terborgh and Janson 1986). Below I divide the attempts to understand gibbon social structure and evolution into four phases or groups of explanations. The phases represent differing approaches to the evolution of social behavior and the role of ecology, but they are not mutually exclusive. In the future they must become integrated into a more comprehensive—and more complex—explanation. At present, there is a tendency for mate competition and sexual selection theory to dominate the explanations of primate social systems. This is partly a reaction to attempts in earlier literature to search for ecological correlates of social systems without considering Darwinian selection on individual males and females (cf. van Schaik 1996).

Ecological Explanations

Ecological explanations are based on the considerations of such things as habitat type, foraging methods and diet, forest homogeneity, seasonal variation, food resource patch size, and effects of intra- and interspecific competition. Ecological factors help explain why gibbons live in small territorial groups, but by themselves say little about the mating system. Unfortunately, our inability to quantify such variables as dietary requirements, food availability, and foraging costs in the tropical forest has hampered our ability to test hypotheses.

Caring for Young: Parental Investment Theory

An important explanation of monogamy is the investment by males in feeding or caring for the young of a single female, defending resources for them, or both (Trivers 1972). The main reason for investing in a single female is believed to be the inability of a male to monopolize enough resources to support the offspring of more than one female (Emlen and Oring 1977). Why this should be the case in gibbons is much debated (see Reichard 2003 and Bartlett this volume for recent discussions). The success of a long-term relationship with one female also depends on the male's ability to maintain paternity over her offspring, which leads to the issue of whether the territorial male is actually defending resources or guarding his mate (e.g., Clutton-Brock 1991). I will address this critical issue below.

Mate Competition Theories and the Trivers–Wrangham Model

The theory of sexual selection and mate competition (Darwin 1871), especially as elucidated by Williams (1966) and Trivers (1972), has been successfully used to explain many features of vertebrate social organization (e.g., Emlen and Oring 1977). Wrangham (1979) formulated a highly influential model of primate social organization based on the parental investment theory of Trivers (1972). It has been most successfully used to explain the social structure of polygynous species (Wrangham 1980), but has also been applied to monogamous species, including gibbons (Wrangham 1987). Rutberg (1983) and van Schaik and Dunbar (1990) have used elements of parental investment and mate-competition theories to explain monogamy, but they differ with respect to what type of male parental investment is considered most important.

Trivers' model explains why the sex that initially makes the larger investment per offspring (females) becomes the limiting sex in competition for mating opportunities. Females in turn are limited in reproduction not by access to mates but by their ability to channel available resources into offspring. Hence, females increase their fitness mainly by obtaining more resources while males increase their fitness mainly by obtaining more opportunities for mating. From this perspective, females are said to be a limiting "resource" for males.

Wrangham (1979) has extended this theory into a model, which states that females are selected to compete more for resources whereas males compete for females. In the "gibbon model" (Wrangham 1987), the females spread themselves out over the relatively homogeneous habitat and defend territories, and the males attach themselves to females and defend their access to mating opportunities. Monogamy results when each male can defend access to only a single female, or when aggression between females prevents more than one from occupying the same range. While most people accept that the distribution of resources and mutual repulsion among females are critical in preventing or reducing the chance of polygyny (e.g., Tenaza 1975; Wittenberger and Tilson 1980; Leighton 1987; Dunbar 1988; van Schaik and Dunbar 1990; Sommer and Reichard 2000; Brotherton and Komers 2003), there is still wide disagreement over the role of paternal reproductive investment. The major merit of the model for gibbons is that it purports to explain why gibbons are monogamous despite the apparent lack of indispensable male care of the female and young.

Guarding Mates and Young

Two additional hypotheses about the male's reproductive investment have been made that help to explain the male's commitment to one female: (1) that the male maintains a bond with a single female to prevent infanticide (van Schaik and Dunbar 1990; van Schaik and Kappeler 2003), or (2) that he seeks to maintain future mating opportunities (Palombit 2000). These hypotheses are argued to be sufficient to maintain monogamy without any male parental investment. The assertion is based on the assumption that territorial defense is actually a mate-guarding activity (or at least evolved primarily as such) and is not primarily resource defense.

Gibbon Ecology and Foraging

One of the first modern explanations of primate social structure was the seminal paper by Crook and Gartlan (1966), which classified primate societies into five "grades" based on group size and composition. The main underlying causal factors were identified as habitat, resource type and predictability, and predation pressure. Sexual selection was seen as important to the evolution of mating behavior and sexual dimorphism, but its full implications for the evolution of the social systems was not foreseen. Gibbons were in Grade II, which consisted of forest frugivores with small group size and territorial behavior. Crook and Gartlan (1966) interpreted the territorial behavior of forest groups as "ensuring an adequate provisioning area for the individuals comprising them."

Eisenberg et al. (1972) presented another classification of primate social systems based primarily on breeding structure, but selective forces from the environment were not emphasized. A paper by Goss-Custard et al. (1972) expanded on many of the themes of Crook and Gartlan (1966), including the effect of food dispersion on ranging behavior, territorial defense of resources, sexual selection, and competition among males for mating opportunities. Goss-Custard et al. (1972) had a distinctly Darwinian approach to primate social organization, possibly reflecting the influence of Williams (1966). It was not long before new field studies of primates began to make it clear that a small number of habitat types or grades of breeding structure could not accommodate the complexity and variability of primate social organization (Jolly 1972; Clutton-Brock 1974). Considerable variability in diet and group size can be found within genera and even within species. Gibbons share the forest canopy with primates that overlap in diet and have completely different social structure. Somewhere in their past, gibbons evolved radically different ways of moving about, finding foods, and communicating from macaques and leaf monkeys that had implications for social structure which we still cannot quite unravel.

Small group size has been linked to territorial behavior, because of the difficulty of males being able to move easily enough to defend the boundaries of a large area (Mitani and Rodman 1979; Raemaekers and Chivers 1980). A large group also contains less-closely related individuals, and therefore selection for territorial behavior through kin selection is weaker (Brockelman and Srikosamatara 1984; see similar arguments by Rodman 1984).

Foraging and Food Patch Size

A further selective force on group size is resource patch size, which may limit feeding group size in primates (Wrangham 1979; Rutberg 1983; Terborgh 1983, 1986; Terborgh and Janson 1986) and in gibbons in particular (Raemaekers and Chivers 1980; MacKinnon and MacKinnon 1984). Resource patch size, however, is not a rigid constraint because either small or large groups can exploit large patches (Terborgh and Janson 1986), and large groups can exploit small patches by using a fission-fusion strategy (e.g., Ghiglieri 1984; Rodman 1984; McFarland 1986; Norconk and Kinzey 1994; Phillips 1995) or by simply utilizing more patches.

A study of gibbons' food patch utilization by Grether et al. (1992) revealed the interesting result that gibbon patch use times did not conform to the marginal value model (Charnov 1976), which predicts that, for foragers using patches of food, individuals should leave the patch when its quality (marginal gain rate) is equal to the average of that for all patches. The reason for this seems to be that the predictions assume that foragers have no detailed knowledge of the availability of food sources outside the immediate patch they are in. Observers of foraging gibbons, however, quickly get the impression that gibbon groups often move toward food sources they are familiar with beyond their vision.

Knowledge of the Territory

Some researchers have suggested that foraging efficiency is enhanced by detailed knowledge of food sources (Crook and Gartlan 1966; Gittins and Raemaekers 1980; Milton 1980; Raemaekers and Chivers 1980; Terborgh 1983; MacKinnon and MacKinnon 1984; Oates 1987; Janson 2000). This knowledge may give gibbons an advantage over monkeys such as pig-tail macaques (*Macaca nemestrina*) in locating and defending ripe fruit sources (Whitington 1992). By having small, highly mobile groups, gibbons can exploit their knowledge of the forest to the maximum. This factor, rather than food patch size distribution, may provide the primary advantage of living in small groups in relatively small, defended territories.

The value of knowledge of the territory depends on the relative difficulty of finding high-quality foods using only random search. This depends on the area that can be covered by a group per day, which in turn is contingent on the daily ranging path length, the visibility of the forest from the foraging path, and also how much the path crosses itself. I present here some simple calculations which show that the advantage of directed foraging (using knowledge of food locations) confers a critical advantage over random search.

The daily path of the smaller gibbons varies from about 800 to 1500 m (Leighton 1987). For Khao Yai white-handed gibbons (*Hylobates lar*), average daily range has been estimated at from 850 to about 1200 m, depending on the group and season, by Nettelbeck (2003) and Reichard (1991), and from 672 m (November) to 1791 m (April) by Bartlett (this volume). Bartlett's yearly average was 1245 m for two groups (A and C).

Estimating the width of the search path is more problematic. As I could not test the gibbons' eyesight in the forest, I decided to test my own, on the Mo Singto forest dynamics plot in Khao Yai Park. From four different tree platforms that had been placed at various heights in the main canopy where gibbons travel, I measured the visibility in each of eight compass directions. Using an optical Ranging Rangefinder (Forestry Suppliers, Jackson, MS), I measured the distance to the farthest branch on which I might be able to detect fruit through the foliage in each direction. The results (Fig. 11.1) indicate an average visibility for me of about 21 m. Although the assumption that I can see as well as a gibbon in the canopy may seem dubious, I do not believe that I have seriously

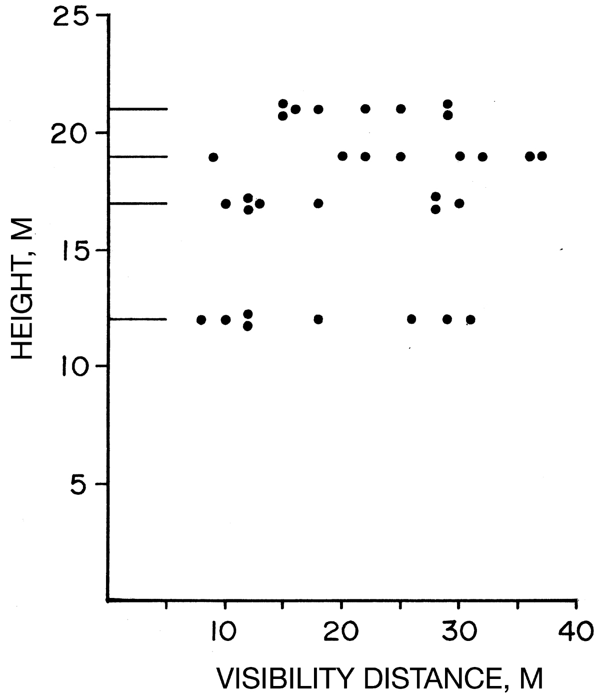
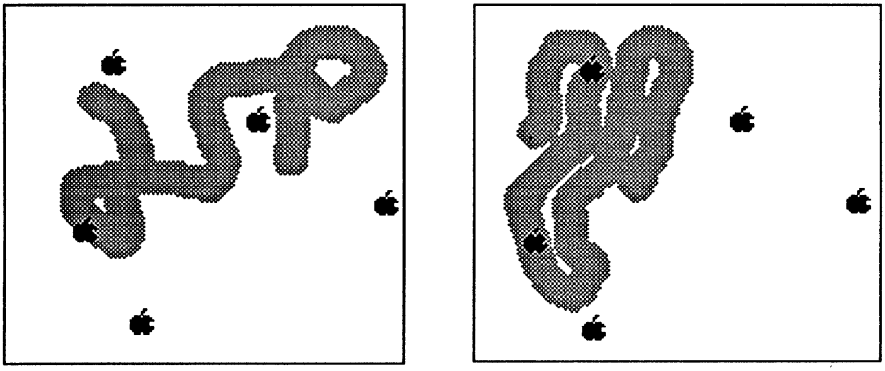


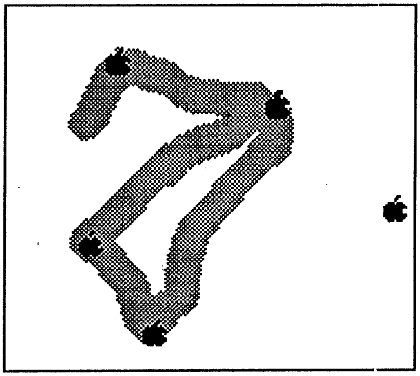
Fig. 11.1 Visibility distances in the forest canopy in Khao Yai National Park from four platforms at various heights

underestimated visibility, which in fact may be greater from the platforms near the centers of large trees than from where the gibbons normally travel. In any event, if we assume that a gibbon group travels 1200 m/day and has a search path 42 m wide, it can search an area of 5 ha/day if the path does not cross itself. This represents 20% of an average gibbon home range in Khao Yai Park of about 25 ha. Search area would be effectively increased if gibbons used information from other species in finding food sources, which they probably do for small-seeded foods such as figs that are shared by numerous species of birds and mammals.

The total area searched per day is illustrated in Fig. 11.2 for two methods of searching: random and systematic. In systematic search, it would require 5 days for the group to cover all parts of its range, and half of the range could be



RANDOM SEARCH SYSTEMATIC SEARCH



DIRECTED TRAVEL

Fig. 11.2 Schematic diagram illustrating three types of foraging pathways through a rectangular gibbon territory. The width of the pathways (42 m) is drawn to scale with the size of the rectangular territory covered in 2.5 days. Using random search, coverage of the range is appreciably slower. It can easily be estimated from the Poisson distribution: at a coverage rate of 5 ha/day, or 20% of the range, the area searched after t days is calculated from $A = 25(1 - e^{-0.20t})$. With a search rate of 0.20 per day, half of the area will be searched after 3.4 days, and three-quarters after 6.9 days. If the food supply of the gibbons is limiting, it is difficult to see how they could utilize their territory efficiently through either random or systematic search. This partly depends on the optimal harvest interval; for individual food sources this interval should be considerably less than 3 days. Rapidly renewing resources require rigid feeding schedules that depend on detailed knowledge (e.g., Schülke 2003).

These conclusions are supported by experimental findings about food detection in capuchin monkeys by Janson and Di Bitetti (1997), in which detection distances were in the same range as those reported here. The probability of detecting a food platform varied with platform size and the speed of travel, which suggests that the value of knowledge in exploiting small and rare food sources is greater than that for large sources.

Examination of the foraging paths published for some species of primates suggests that some search systematically while others wander about seemingly at random. In those illustrated in MacKinnon and MacKinnon (1980), for example, the path of *Macaca fascicularis* appears to wind about at random, whereas that of *Presbytis melalophos* appears to loop back and forth in a systematic way. The paths of *P. melalophos* in the Krau Reserve published by Curtin (1980) also give the impression of systematic search of the home range. To the contrary, gibbon ranging patterns, and probably those of other species in defended ranges, give quite a different impression. They show the group ranging widely but using the same pathways repeatedly (e.g., Gittins and Raemaekers 1980; MacKinnon and MacKinnon 1980; Bartlett 1999; Brockelman unpubl. data). In the forest, they usually appear to be moving over the easiest route through the branches single file with one of the adults (more often the female) leading. Thus, movement to major fruit sources appears to be goal-directed travel (Fig. 11.2). There are exceptions, such as when the gibbons are foraging on leaves, shoots, or insects (unpubl. data). The problem is how to demonstrate that gibbons know where their favored food sources are.

Knowing where food sources are as soon as they are ripe must provide a decisive advantage in foraging over competitors that do not have such knowledge. Sympatric species or intruders of the same or different species will lose foraging opportunities if the resident gibbons get there even 1 hour before and skim off the ripe fruit of the day. It would seem, therefore, that random search cannot compete against prior knowledge and directed travel, by which a gibbon group can cross its territory to reach a fruiting tree or vine in a few minutes (cf. Janson 2000).

Gibbon species in tropical forests generally have diets that include many ripe fruits, which overlap with the diets of other sympatric primates (MacKinnon and MacKinnon 1980; Ungar 1995), as well as other mammals and birds (Marshall et al. this volume). The benefit of a defended territory is enhanced if critical fruits are used exclusively by gibbons and not shared with interspecific competitors (Brockelman and Srikosamatara 1984). Gibbons in most forests have relatively few interspecific competitors for some of the succulent fruit species that they eat (unpublished data). Fruits most favored by gibbons are often relatively large-seeded drupes or berries that are covered with a tough rind that birds such as hornbills cannot remove, and that smaller mammals such as squirrels have difficulty removing (Leighton and Leighton 1983; McConkey et al. 2002, this volume; Kanwatanakid and Brockelman unpubl. data; but see Marshall et al. this volume).

Several hypotheses about food and foraging relationships in gibbons are suggested by the above considerations, some of which are supported by available evidence. First, food sources should be visited repeatedly, and not just opportunistically, especially those that ripen over a period of days or weeks. Second, territorial primates such as gibbons that rely heavily on knowledge should be more efficient seed dispersal agents for uncommon or rare fruiting species than are nonterritorial primates. Such fruiting plant–disperser relations should promote tighter coevolution because gibbons should be nearly exclusive dispersal agents of these plant species.

A third prediction is that more efficient food-finding ability should permit gibbons to subsist on resources in a smaller range (or at a greater biomass density) than would primates with a similar diet, but without such detailed knowledge of food sources. If this is true, use of a smaller territory will promote easier memory of food sources and even more efficient foraging, as well as easier defense. Thus, small group size, territorial defense, relatively small feeding range, and increased foraging efficiency are mutually reinforcing and should form an associated character complex. Testing these hypotheses will demand community-wide knowledge of plant–animal relations, which will require more work on long-term, intensively studied field sites.

These ecological explanations help explain why gibbons live in small territorial groups, but they say little about why they should necessarily be monogamous.

Parental Investment Theory

Types of Investment

Parental investment has been defined by Trivers (1972) as any form of parental care of individual offspring that reduces the parents' ability to invest in other offspring, including the parents' ability to survive, grow, and mate again (Clutton-Brock 1991). Parental investment in offspring is a form of reproductive effort (Williams 1966), which also includes mating effort. In mammals, mating effort nearly always consumes more time and energy in males than in females, which generally invest much more energy in offspring production and care (Trivers 1972).

The necessity for male parental care is regarded as a major determinant of the evolution of monogamy (Emlen and Oring 1977; Kleiman 1977; Wittenberger 1979). If the male must give his undivided attention to investing in the brood or young of one female, he will not be able to invest in the brood of a second female. The male's ability to invest in another female's offspring will often depend on whether he can monopolize sufficient resources, which will depend on how the resources are distributed in space and time (Emlen and Oring 1977).

One of the most unsettled issues of the socioecology of gibbons is whether paternal investment in young is sufficient to account for monogamy. Views vary widely, with some commentators claiming that paternal care is completely absent in gibbons (Woodroffe and Vincent 1994). The following categories of paternal care arguably exist in gibbons.

Territorial Resource Defense

Most early field researchers (e.g., Carpenter 1940; Ellefson 1968; Chivers 1974; Gittins 1980; Raemaekers and Chivers 1980; Whitten 1982) have unhesitatingly assumed territorial defense to be primarily resource defense, rather than mate defense. Strong territorial defense by males would seem to support the importance of paternal investment, because the female and offspring feed almost entirely inside the area defended by the male. The areas of range overlap that do occur between white-handed gibbon groups, usually 20–30% of the group range, are mostly due to neighboring territorial male incursions. The overlap of the actual feeding ranges of neighboring groups has yet to be determined. Bartlett (1999, 2009) found that in white-handed gibbons at Khao Yai, 47% of intergroup agonistic encounters at range borders involved disputes over food trees, supporting the idea that territorial defense ultimately concerns the competition for food.

Territorial resource defense is sometimes considered to be a form of "indirect" parental investment, perhaps to be devalued in comparison with direct care such as feeding and infant carrying (Kleiman 1977). Wittenberger (1979) and Wittenberger and Tilson (1980) exclude territorial defense from "parental care," in claiming that gibbons have no male parental care, but include it as a "benefit" of pairing with a particular male. It is important to know whether a form of parental investment is "shareable" (Wittenberger 1979; Wittenberger and Tilson 1980), meaning that it can be shared by additional females and their offspring without diminishing its quantity or quality, or "nonshareable," such as food provisions, which cannot be shared without being diminished. "Nondepreciable" and "depreciable" are somewhat clearer terms (Altmann et al. 1977; Clutton-Brock 1991).

Territorial defense may also be considered to be a form of investment, which can in a sense be "shared" amongst females, but the food resources being defended are nonshareable. Territorial resource defense in gibbons may be a strong predisposing factor for monogamy, especially when combined with aggression or repulsion among females. It is sometimes argued, however, that males should be able to defend enough territory for two or more females and their offspring living in separate ranges (Dunbar 1988; van Schaik and Dunbar 1990; Reichard 2003). Such a claim has been rejected by some observers of gibbons (e.g., Ellefson 1968; Raemaekers and Chivers 1980; Brockelman and Srikosamatara 1984), although there is no proof one way or the other. The quality of territorial defense would likely be diminished with a territory twice as large as normal, and the male might be at a disadvantage in foraging within the larger area. Reichard (2003) argues that it is probably in the male's interest to have only a single female because the increased costs due to overlap of ovarian cycles of neighboring females, increased male–male competition over mating opportunities, and increased costs of territorial defense make the net benefits of large-range or multiple-territory polygyny too low in relation to monogamy. In addition, he argues that opportunities for extrapair copulation, as well as for other types of paternal investment including more effective resource defense, may tip the balance in favor of monogamy.

Another problem with the male resource-defense theory of monogamy is that territory defense should not be sex-specific, but should be directed against both sexes (Brotherton and Komers 2003; van Schaik and Kappeler 2003). Such a simple prediction, however, cannot be made when all the needs of the male and the female are considered, and several arguments can be made against it. In the first place, the data on sex-specificity of male defense in gibbons are sparse and ambiguous. Brockelman and Srikosamatara (1984) reported three instances of males evicting adult female intruders from their territories during observations of pileated gibbon (*H. pileatus)* groups. A "bigamy threshold" model was presented, which showed under what resource conditions a territorial male might have higher reproductive fitness with one female than with two, especially if territorial space is limiting (Brockelman and Srikosamatara 1984).

Females usually hang back during intergroup encounters and do not often become involved in chasing (Carpenter 1940; Ellefson 1974; Leighton 1987). Playback experiments using male and female solos demonstrate strongly sex-specific responses to songs played in the center of the territory [*Hylobates agilis* and *H. muelleri* (Mitani 1990a); *H. lar* (Raemaekers and Raemaekers 1985)]. Playbacks of strange pair duets from their territory elicited duets in response, and sometimes approaches by the male and sometimes by the female, depending on the species. Such responses demonstrate the role of vocalizations in both mate competition and territorial defense. As argued below, females are likely to have higher risks in fighting over resources than males, and hence usually avoid it. Since their partners actively defend against opposing adult and subadult males, there is little need for them to do so.

Nevertheless, females sometimes do become involved in territorial encounters. Bartlett (2003) observed that in 17 out of 87 intergroup encounters involving three groups of white-handed gibbons in Khao Yai Park, Thailand, the adult male of one group approached the adult female of the other. In three encounters, the male charged or chased the female. In five others, the male touched or contacted the female, and the female squealed and chased the male in one of these encounters. Observations of the same population by Reichard (2003) also are ambiguous; in 162 intergroup encounters observed, males attacked other males more than females, but attacks involving contact aggression were not significantly sex-specific. These observations suggest that the male's relationship to neighboring females is ambivalent. Neighboring females are potential sexual partners in addition to resource competitors, and it is the former role that has the most immediate effects on the male's reproductive fitness.

A further point made by Brotherton and Komers (2003) is relevant to gibbons and requires comment. They assert (p. 46) that "If defense by males is sex-specific, monogamous females would have no more resources available to them than solitary females." This would hold true only if such defense represents real mate competition and not the routine territorial defense that occurs in most species of gibbons every few days (e.g., Carpenter 1940; Chivers 1974; Ellefson 1974; Bartlett 2009). Routine defense at the territorial border involves conflicts with neighboring groups in which the mated males usually play the dominant role, but has never been observed to result in mate replacement. It helps to maintain the size of the exclusive feeding territory; failure to maintain the territorial border results in food resources there being encroached and shared, or taken over, by neighboring groups. The effect of relative group strength in maintaining the territorial boundary, and relative territory size, has been discussed by Brockelman et al. (1998) and Savini et al. (2008).

Guarding Against Predators

It has been noted that male gibbons are vigilant against potential predators (Uhde and Sommer 2002). Male gibbons are very active in mobbing and harassing pythons in trees, and are most often the first group members to discover human observers below them, to which they respond with low-intensity "hu hu hu hu . . ." sounds (unpubl. data). Van Schaik and Dunbar (1990) rated male vigilance against predators as only a minor or supplementary benefit of monogamy, and not a deciding factor, in its evolution.

Grooming

The adult male usually grooms the adult female, but often males spend relatively large amounts of time grooming subadults or older juveniles. The adults groom each other for an average of about 4–6% of the activity period, and female gibbons groom with young for up to an hour or more every day while resting (unpubl. data). The male grooms the young less, but sometimes extensively grooms subadults (Suwanvecho 1997; Nettelbeck 2003; Brockelman unpubl. data). Grooming does seem to condition and oil the fur (important when gibbons sit out rain storms) and possibly remove ectoparasites, and may be an important form of direct care of the female and sometimes the offspring (Reichard and Sommer 1994; but see Dunbar and Sharman 1984 for grooming as a low-cost behavior).

Palombit (2000) has noted that since it is the male that more often grooms the female, it is the male that is investing more in the pair bond and therefore likely benefits more from the relationship. However, this conclusion is complicated by the fact that in newly established pairs, it is the female that grooms the male more, and for longer periods, than in more established pairs (unpubl. data).

Grooming between adults may be seen either as a bond-reinforcing activity that offers some fitness benefit, or as an indirect investment in the offspring by the male through the female. This is probably why, in established pairs, the male grooms the female more than the reverse. The relative contribution to the fitness of the groomee will determine the optimal direction and amount of grooming by each partner; these may have little relation to the overall benefit of the monogamous relationship to either. In gibbons, there is considerable variation between individuals of the same age and sex class in grooming behavior, which makes it difficult to generalize from a small number of groups.

Play

In white-handed gibbons, the adult male occasionally engages in play with the young, but this constitutes a very low percentage of activity on average in this species (Suwanvecho 1997; also for siamang: Lappan this volume). Treesucon (1984), however, noted that the adult male of his study group engaged in increased amounts of play with a young juvenile after the subadult male left the group and the youngster had no other play partners.

Infant Carrying

In the siamang, males may carry infants from the age of 12–15 months until they become independent in the third year of life (Chivers 1972; Lappan 2008, this volume). Such male care reduces the work load of the female and tends to reduce the interbirth interval (Chivers 1972; Lappan 2008, this volume). Male infant-carrying behavior has not been observed in any other gibbon species.

Protection Against Infanticide

Van Schaik and Dunbar (1990) advanced arguments for the idea that protection against infanticide is the major factor that selects for monogamy. They tested the idea against predictions from three other competing hypotheses: males cannot protect two or more dispersed females; males are needed to reduce predation risk; and males are needed to defend exclusive resources. They found that the evidence most strongly supported the infanticide protection hypothesis. The major evidence mounted in favor of the hypothesis is the presence of duetting and close proximity of the male and female, male vigilance, the tendency of widowed females with infants not to sing (of *H. klossii*: Tilson 1981), and the reluctance of females to show interest in strange males. The last evidence was said to militate against the resource-defense hypothesis, but it seems logical that females should also be reluctant to risk the replacement of their mates if their mates have already invested in defense of resources for their own growing young.

Van Schaik and Kappeler (1997, 2003) have more recently promoted the infanticide theory for the maintenance of monogamy and have outlined reasons why infanticide is to be expected in gibbons. Infanticide will tend to be selected if the new male has a low probability of being the infant's sire, the female returns to estrus more quickly after infanticide, and the new male has a high probability of siring the next infant. Gibbons are good candidates because of the relatively long period of lactation and infant-carrying in relation to the gestation period (Reichard 2003), which will select for male guarding behavior. While infanticide protection may indeed be important in gibbons with their long-term pair-bonds, the argument that it is a sufficient condition for the evolution (or at least maintenance) of monogamy is not compelling. It is difficult to see why remaining with one female to protect her infants would have been a strategy superior to roving and searching for new females or to being polygynous in pre-monogamous ancestors of gibbons (Brotherton and Komers 2003). In any event, in the present context I am most concerned with the argument that infanticide protection precludes the existence of resource defense, or that territory defense represents an infanticide-prevention strategy (an idea I have already rejected on the basis of observations).

The fact that infanticide and infanticide prevention behavior exist in many non-monogamous species would seem to refute this theory, but its proponents require us to assume that monogamy and pair territoriality originally evolved for entirely different reasons, which are no longer operative, but are now maintained by the need for preventing infanticide. This scenario, although possible, seems improbable and requires further explanation of why the selective forces for monogamy in gibbons have changed since its origin.

Is Territorial Defense Mate- or Infant-Guarding?

The issue of whether territorial defense by the male represents resource defense or mate defense has been discussed by Clutton-Brock (1991) and van Schaik et al. (1992). Analyses by Dunbar (1988) and Reichard (2003) assume that territoriality is a mate-guarding strategy and then conclude, on the basis of Mitani and Rodman's (1979) model of defendability, that it should be possible for one male to defend the ranges of more than one female. Simple random search models (van Schaik and Dunbar 1990; Reichard 2003) suggest that a male should be able to find his females frequently enough to allow him to mate with each of them while they are receptive. However, male gibbons should not need to search randomly for willing females; they can locate them easily from the sounds of branch movements or vocalizations. The ability of a male to protect his paternity and his infant offspring against other males will not depend on his random searching ability, but on how much time he spends with each female, and on their reproductive synchrony (Reichard 2003). Gibbon reproduction may be seasonal (e.g., Savini et al. 2008) but it is not synchronous. Thus, it probably does not matter if a male gibbon could defend enough territory for two or more females—he could not afford to divide his time between them.

My observations strongly indicate that defending a territory and protecting a mate are two different types of activity. Mate defense occurs relatively infrequently and hence it has never been described as such. Palombit (1993) evidently witnessed it and referred to it as territorial aggression, and it represents territorial defense in the sense that if the resident male loses, he loses his territory as well as his mate. In the long-term study of white-handed gibbons in Khao Yai Park in Thailand, at least 10 male replacements and three involving females have occurred (Brockelman et al. 1998, unpubl. data). In only about four cases was the actual aggression witnessed. In most cases the resident male disappeared or was found to have been evicted and replaced afterward. In no cases did a neighboring mated territorial male replace the resident or usurp his entire territory (but see Palombit 1994 for cases involving mate desertion). Resident adult replacement may occur in a short time if the resident gives up quickly, but sometimes it involves protracted bouts of chasing and conflict lasting weeks or even many months. Such conflicts are characterized by penetration of a single outside male deep into the resident's territory, lethal fights in some cases, low volume "hoo" vocalizations or none at all, and involvement of only the two males. Territorial conflicts, on the other hand, involve whole groups at the territorial border and are normally accompanied by loud screaming and hooting by most or all group members.

Some researchers on birds have reached the same conclusion; in a study of the great tit (*Parus major*), Slagsvold et al. (1994: 115) conclude: "We suggest that mate guarding and territorial defense are demanding and often mutually exclusive activities." The same seems to be true with gibbons; a male often has to leave his mate unprotected and out of sight to defend the territorial border. During such times extrapair copulations have been observed (Reichard 1995; Brockelman unpubl. data). The best mate protection strategy is to accompany the mate while she moves about the territory, which is what males do most of the time. Extra-pair copulations could be a serious threat to a male's paternity; the group A female in the Khao Yai Park study area has been seen copulating with at least four different neighboring adult and subadult males over the past 15 years (Reichard 2003, this volume; Brockelman unpubl. data). These extrapair copulations all occurred while the group A resident male was not accompanying her.

The problem of defending a territory and defending a mate at the same time is illustrated by the following observations in Khao Yai Park. The adult female and male of Group A were Andromeda and Fearless, respectively.

> A [dark] gibbon from Group C came and sat very close to Andromeda (~1 ft.). She didn't chase him. After 5 mins, Fearless came back from chasing Group C and chased him away. (Sept. 24, 2000)

The strange dark male was most likely the subadult from neighboring Group C who within a couple of months invaded Group A's territory and took over the adult female, displacing fearless.

One weakness of the territoriality-as-mate-guarding hypothesis is that it does not explain why a territory is as large as it is. Mate defense does not require defending a fixed area—only the proximity of the female. Proponents of this theory would argue that it is the female that defends, or at least defines, the territory by her movements. But to argue that females are defending resources while males only defend the females, as in the Trivers–Wrangham model, both contradicts field observations and is illogical, as I will discuss below.

An empirical test of the resource-defense *versus* mate-defense explanations of monogamy should be possible. The territoriality-as-resource-defense theory predicts that males should reduce territorial defense efforts and increase proximity when their females are receptive (because territory defense and mate protection represent tradeoffs), while the mate-defense theory of territoriality predicts just the opposite.

Evidence for Resource Territoriality

Stronger evidence needs to be sought that food resources are at least sometimes limiting, and that they are increased by territorial defense. The fact that territorial border defense involves a trade-off with mate defense would seem to be prima facie evidence. That many territorial border clashes are over food trees is also supporting evidence. The resource theory also predicts that territory size should correlate with group size within particular study sites. This has been found in Khao Yai Park, where Groups A and C have traded territorial space, with the larger group with extra subadult males expanding at the expense of the other (Brockelman et al. 1998). Savini et al. (2008) have shown that gibbon groups in the Mo Singto study area in Khao Yai Park with larger and richer ranges tend to be larger, and hence more productive. Researchers have observed that small, newly formed groups with only two adults often have the smallest territories, although new groups are too infrequently seen and studied to provide convincing quantitative evidence. Better evidence would be provided by long-term observations of interbirth intervals or dispersal events in relation to group size (e.g., Schülke 2003 for the fork-marked lemur).

The argument that gibbon males should have the ability, based on their ranging path length, to defend a much larger territory (Mitani and Rodman

1979) has been countered by Bartlett on empirical grounds (this volume). He has shown that food availability and daily range have considerable seasonal variation in the seasonally wet forest of Khao Yai Park, central Thailand. Succulent fruit is in short supply in the early dry season and gibbons must rely more heavily in less energy-rich foods, and as a consequence travel much less per day. We should not assume, moreover, that the costs of territory defense are similar across primate taxa. In theory, the costs of defending larger territories in gibbons must also include trade-offs in the form of increased risks of losing paternity and reduced foraging efficiency (Leighton 1987) in addition to increased travel time. Because of the increased cost of knowledge and foraging travel costs, food availability will not increase in proportion to territory size. For these reasons, the "optimal" territory size will likely be one small enough to incur some costs of food limitation in lean years, which is what we are finding with white-handed gibbons in the seasonal evergreen forest in Khao Yai Park (Bartlett 2009; Brockelman pers. obs.). These costs will be offset by relatively higher defensibility, foraging efficiency, and easier mate defense. Thus, the determination of the optimal territory size will not simply involve measuring food supply alone, but will require the consideration of all needs of both males and females that are affected by range size.

Mate Competition Theory

In this section, I will concentrate on the role of intrasexual competition for mates and resources in shaping the social system of gibbons. I will also be concerned with how competition for resources may differ between males and females, and how this has affected the evolution of monogamy.

Asymmetry of Parental Investment and Mate Competition

According to Trivers (1972), the female sex invests more energy per sex cell, and in mammals, much more per offspring than does the male; consequently, females are more limited by how much energy they can channel into reproduction, whereas males, whose sex cells are cheap to produce and are abundant, tend to be limited by how many mating opportunities they can obtain. Trivers (1972: 140) states that "the sex whose typical parental investment is greater than that of the opposite sex will become a *limiting resource* for that sex" (italics added). Later, Trivers (1972: 153) makes an analogy that is not entirely appropriate:

> One can, in effect, treat the sexes as if they were different species, the opposite sex being a resource relevant to producing maximum surviving offspring. Put this way, female "species" usually differ from male species in that females compete among themselves for such resources as food but not for members of the opposite sex, whereas males

> ultimately compete only for members of the opposite sex, all other forms of competition being important only insofar as they affect this ultimate competition.

These statements contain the seeds of misunderstanding about two aspects of competition: that energy is important to females and not to males, and that mates and food are somehow alternatives as resources. These misunderstandings have found their way into the Trivers–Wrangham model of primate social structure and have especially caused confusion in our understanding of gibbon socioecology.

Parental investment (PI) or effort is a part of "reproductive effort" (RE), which also includes mating effort. The basic difference between males and females is that females increase RE mostly by increasing parental investment, because mates (except for their quality) are not limiting to female reproduction. Males, on the other hand, increase RE mostly by increasing mating effort. Trivers pointed out that competition among males for females could select for higher RE in males than in females, and even higher mortality, as long as decreases in future reproductive success (RS) were offset by increases in current RS. Hence, the demands for food energy could be higher in males than in females, and Trivers makes it clear that male RS is very sensitive to changes in mating success. We should therefore expect more severe competition for resources in males than in females. Trivers also emphasized that monogamy may result when opportunities for male care and protection of the young lead to reduction of the differences in investment between male and female.

Models of mate competition and infanticide protection described above assume the absence of competition among males for resources. Trivers never assumed that competition for resources would be absent in males—only that the "ultimate" measure of success in competition was success in mating and raising offspring.

The disparity of sex cell size and PI implies differing allocation of energy among different types of RE, but implies nothing about energy limitation overall for males or females. The fact that mates are limiting for one sex implies nothing about whether food resources are limiting for either sex.

Are Female Mates "Resources"?

It is only with tongue in cheek that we can refer to females as "resources" for males, and we should avoid it because of the potential confusion that results. Competition for mates and for resources must be carefully distinguished because competition for resources in both sexes can affect the competition for mates. Females are partners in reproduction—they are not resources.

Competition for mates and competition for resources are conceptually different types of competition that should not be confused. Competition for mates implies nothing about whether there is competition for resources of the environment. Resource competition is dependent on the overall density of the population, whereas mate competition depends only on the relative frequency of the two sexes. If resources are limiting reproduction in one sex, they must also be limiting it in the other unless the sexes utilize different types of resources or have very different foraging methods. The truth of this statement is independent of the frequency or the relative sizes of males and females. As stated above, however, the sensitivity of mating success to resource availability will likely be different in males and females. In both sexes there must be a saturation level in which more resources will not further increase reproductive success; below these levels, resources may be said to be limiting. An interesting question is whether these saturation levels may be different in males and females; in my opinion, they are not likely to be because of overall similarities in physiology and basal metabolic demands in mammals in general. Such demands will adapt to the prevailing availability of resources in the environment and to population density.

Territoriality and Resource Competition in Males and Females

The Trivers–Wrangham model has been applied by numerous authors who have also accepted that it is primarily or only females that need to compete for real resources (e.g., Andelman 1986; Rubenstein and Wrangham 1986; van Schaik and Dunbar 1990; van Schaik 1996; Sommer and Reichard 2000). In polygynous species, it is reasonable that males will devote much energy to mate competition and reduce the allocation to resource defense. However, a major theme developed by Emlen and Oring (1977) is that the ability of males to compete for and sequester resources determines their success in mate competition. This is certainly the case in gibbons, in which territorial defense competes for time and energy with mate guarding and other types of paternal investment.

The model has been specifically applied to gibbons by Wrangham (1987: 291), who identifies very clearly the problems posed by the gibbon social system:

> The gibbon model of monogamy suggests that the distribution of males depends on the distribution of females that are already territorial. Males presumably benefit from accompanying females by guarding their mates from rivals, ensuring future mating opportunities, and protecting their offspring. Females gain male assistance in the defense of resources and protection from infanticide or other dangers . . .
>
> It appears ironic that a system of female-female competition for resources should lead to females sharing their territories with a male and therefore losing precious resources to him. However, although males must impose feeding costs on females, they defer to their mates in ways that reduce feeding competition . . .

This model has considerable heuristic value, but is not fully in accord with observations. There are probably no reported cases of females setting up territories prior to mating. If the male mate dies, the female may occupy and sing in the territory for a while, but cannot prevent other groups from encroaching (Brockelman and Srikosamatara 1984; Brockelman et al. 1998). Such females typically continue to give great-calls on the territory, but the timing of the calls and the lack of male responses make it clear that they are widowed. Female gibbons are probably important in defining the size of the territory by their ranging behavior, and occasionally have to defend it against females, but successful territorial defense is always a joint activity, as suggested by Wrangham (1987) in the first passage quoted above (cf. Terborgh and Janson 1986). The territory size should be automatically adjusted to accommodate feeding by all group members, including the male. However, as argued above, the fact that most of the territory is protected against competitors increases foraging efficiency and makes it likely that the group can thrive on the food resources of a smaller area than they could occupy without active defense.

One further argument may help explain why females of most species engage in less active defense of the territory than males (Leighton 1987). If the risks to females are higher than those to males, maintaining territories through simple avoidance will be more beneficial than encroaching on other females' ranges and fighting, provided the energy yields of exclusive territories are higher than those from shared ranges (Pereira et al. 2003). Females simply "agree" not to fight but to establish boundaries to foraging areas. Of course, where these boundaries are established will depend also on the male's behavior and on the food demands of the group relative to those of the neighboring group.

Can Mate-Guarding by Males Promote Monogamy?

The idea that guarding a mate in order to insure future mating opportunities is sufficient to account for monogamy has been suggested by Brotherton and Komers (2003) and Palombit (2000), who also discount the importance of males in defending resources and paternal care. With a birth interval of wild gibbons of three or more years (Mitani 1990b; Brockelman et al. 1998; unpubl. data), however, male gibbons should have little reason to stay in the territory of a single female; they will sacrifice many other chances of mating except for furtive extrapair copulations. Both the mate guarding and infanticide prevention theories of monogamy assume that finding and protecting a new mate would be difficult and risky (Brotherton and Komers 2003). This would of course be true if all females were already guarded by committed males, but this assumes the social system we are trying to explain. In the absence of males defending mates, a long birth interval and lack of synchrony in births may create a high male-biased operational sex ratio (many males per receptive female), which will also make finding new mating opportunities difficult. Such conditions characterize the other great apes, however, which have neither pair territories nor monogamy. All types of male investment in females and young, including the time spent defending them, must depend on the guarantee of a high probability of paternity, which would collapse if males gave up maintaining long-term pair bonds and defending joint territories with females. How high the guarantee of paternity must be is not clear at present.

Thus, while mate-guarding and infanticide prevention are probably essential correlates or consequences of monogamy, it is doubtful if they are sufficient forces to maintain monogamy in gibbons without further male investment in the form of direct paternal care or indirect care through resource defense.

Unanswered Questions

What Is Territorial Behavior?

Territorial behavior is the active defense of space (Burt 1943). In most female gibbons, however, which engage in little or no active defense, territorial behavior may simply involve the occupation of exclusive ranges. We need to understand better what each sex contributes to territorial defense and how effective it is in increasing the availability of resources. We can begin by tracking the ranges of each sex separately. Male ranges may be larger than female ranges because of their territorial and mate competition behavior. The feeding territory needs to be separately documented, with the intensity of use quantified. Overlap in food resources is likely to be less than overlap in the total ranges of males, but quantitative data are not available.

Is Food Limiting?

One of the most difficult and enduring problems in population ecology is determining what limits populations. It is seldom possible to do experiments with primates by manipulating population density or food supply as with smaller animals, so that a variety of observational and comparative techniques have to be employed to determine if food resources are limiting. Territorial defense implies that food is at least sometimes limiting, and this should be reflected in the diet, activity budget, ranging pattern, and intergroup relations at particular times of the year. The presence of climate variability and supra-annual fruiting cycles in many tropical forest trees adds another layer of complexity that needs study. The food plants and their phenology will have to be precisely known in order to correlate them with gibbon behavior. We must establish the relationships between group size, ranging path, patch use, diet, and food consumption, as well as competitive relations with other species (Waser 1987). Ultimately, our goal will be to correlate changes in food availability and behavioral responses with demographic changes in the population.

Does Territoriality Increase Feeding Efficiency?

The food supply consumed depends on at least three factors: the plants available and their phenology, diet or the accepted range of foods, and the methods of foraging or locating food sources. All of these need to be carefully analyzed. The fraction of the available food crop consumed by gibbons, and by competitors of gibbons, needs to be measured. The types of foods consumed mostly or exclusively by gibbons will be the measure of the value of territorial defense. How this fraction might change in the absence of territorial defense will be difficult to determine; perhaps comparing the overlap zones with core areas of territories will provide an indication. The study of possible mutualisms between gibbons and some of the fruiting species whose seeds they disperse will add insight into the gibbons' feeding niche and their competitive relations with other frugivores. We also need to investigate the role of spatial and phenological knowledge of food resources to gibbons, and how their foraging pathways reflect this knowledge and maximize resource use.

Conclusions

1. I analyze the social system of the gibbons with regard to several levels of explanation: ecological, parental investment, and mate competition theories. All three levels of explanation are needed to make sense of the socioecology and mating system of gibbons, although our empirical evidence is still incomplete. Single-factor explanations and tests of gibbon socioecology or monogamy will not be successful because of the interactions among factors and because the various explanations being tested are not mutually exclusive.
2. The major ecological factors thought to affect the evolution of gibbon group size and territoriality are the relatively high diversity of foods available, use of relatively small food patches, and high foraging efficiency that depends on detailed knowledge of food sources, especially of rare species. Evidence is presented that the last factor is of critical importance in giving gibbons a competitive advantage, and in allowing them to more fully utilize their resources and subsist in smaller ranges than they would otherwise require. Living in smaller ranges in turn makes possible more detailed knowledge and increased foraging efficiency.
3. Possible types of parental investment by male gibbons include territorial resource defense, vigilance against predators, grooming, play, infant carrying (in the siamang), and protection against infanticide. Male territorial defense of resources (sometimes excluded from "parental care") is argued to be an essential male investment in all gibbons, but most or all other forms of care probably also contribute to what may amount to a fairly substantial package of male parental investment, which will select for monogamy.

4. Territorial defense by males is not primarily a form of mate guarding, because the need for defending the border, especially near feeding trees, compromises the need to remain near and guard the mate. Both activities, however, are important in male gibbons, so that neither can be achieved without a tradeoff of effort. The resource defense theory predicts that males should reduce territorial defense of resources while the female is receptive and maintain increased proximity.
5. The parental investment theory of Trivers (1972) predicts that the availability of females, with their higher parental investment, will limit male reproduction and promote more intense competition for mates in males than in females. Female reproduction, especially in polygynous societies, will ordinarily be limited more by food shortage than by a shortage of breeding partners. The model should not be taken to imply that females are more resource limited than are males, or that competition for females is equivalent to competition for resources.
6. Although they are probably both important, neither male mate-guarding to protect breeding opportunities nor guarding to protect against infanticide alone is sufficient to maintain monogamy in gibbons, without the presence of male parental investment primarily in the form of territorial resource defense.

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Chapter 12

The Ecology and Evolution of Hylobatid Communities: Causal and Contextual Factors Underlying Inter- and Intraspecific Variation

Nicholas Malone and Agustin Fuentes

Introduction

The following quotations are indicative of two different philosophical positions that are held among primatologists regarding the observed behavioral variation in the Hylobatidae:

> Some exceptions to a strictly monogamous pattern have been observed, but typically in extreme circumstances (Chivers 2005: p. 211);
>
> Given our current data set, it is apparent that the hylobatids are not 'monogamous' primates, although monogamy is a mating pattern that may characterize a number of individuals in a population at any given time (Fuentes 2000: p. 56);
>
> The labels typically employed to designate hylobatid societies – 'monogamous' and 'territorial' – may provide a useful context for analyzing social behavior, but they underestimate social variation (Palombit 1996, p. 350);
>
> The long term studies indicate that group composition and pair formation methods are more flexible than previously thought, but that long-term monogamous pairing is the predominant, if not the sole, social pattern (Brockelman and Suwanvecho 2002: p. 266).

It is clear that there is disagreement not only in the interpretation of existing data sets but also about the value and importance of variation (behavioral and ecological) in the modeling of hylobatid social organization. We acknowledge these debates here as a precursor to our treatment of variability within and among the four genera and ~12 species that comprise the Family Hylobatidae (following the taxonomy of Roos and Geissmann 2001; Geissmann 2002; Brandon-Jones et al. 2004; Mootnick and Groves 2005; Table 12.1). For a thorough discussion of hylobatid taxonomy, see Chatterjee (this volume).

The diverse opinions expressed in the opening quotations may derive, in part, from alternative methods of scientific discovery: an inductive process, on one hand, and a deductive, hypothesis-driven approach, on the other hand

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Table 12.1 Basic taxonomy of the family Hylobatidae

Genus (with diploid number)	Species	Common name
Hoolock (38)	*hoolock*	Hoolock or white-browed gibbon
Hylobates (44)	*agilis*[a]	Dark-handed or agile gibbon
	klossii	Kloss's gibbon
	lar	White-handed or lar gibbon
	moloch	Silvery or Javan gibbon
	muelleri	Mueller's or Bornean gibbon
	pileatus	Pileated or capped gibbon
Symphalangus (50)	*syndactylus*	Siamang
Nomascus (52)	*concolor*	Western black-crested gibbon
	gabriellae	Yellow-cheeked crested gibbon
	cf. nasutus	Eastern black-crested gibbon
	leucogenys	White-cheeked crested gibbon

[a] Some researchers recognize the white-bearded agile gibbon of Borneo as a distinct species (*Hylobates albibarbis*).

(Fuentes 2007; Sussman 2007). In the analysis of gibbon sociality, deductive approaches have centered on the hypotheses derived from sexual selection theory. It is possible that, couched in a paradigm that seeks to develop explicitly adaptationist models to "explain" the characteristic features of hylobatid social organization, we have uprooted our models from the ecology and behavior of our study subjects. For example, under this rubric we may be more inclined to model fitness maximization schema responsive to intersexual parental investment than to consider the group size and ranging limitations of ecological parameters and patterns of intergroup behavior (Bartlett 2007; but see Robbins, Chapman and Wrangham 1991). When researchers initiate a study using a basal set of assumptions about the systems being studied, interpretations of collected data have the potential to be alienated from the actual ecological and behavioral processes involved (Longo and Malone 2006). That is, social classifications that are *created* by the system are said to be the *basis* of the system (Levins and Lewontin 1985). In the case of gibbons, their classification as "monogamous" primates resulted in a specific suite of accompanying assumptions about their ecological and behavioral adaptations that have potentially inhibited broader investigation into behavioral variation and the evolution of their patterns of social organization and social structure.

The strength and nature of the pair bond is at the center of many, if not all, explanations of hylobatid social organization (van Schaik and Dunbar 1990; van Schaik and Kappeler 1997; Palombit 1999). Three key hypotheses are routinely advanced for the evolution of pair bonding in gibbons: (1) ecological constraints on group size and subsequent limitations on female gregariousness (Emlen and Oring 1977; Leighton 1987; van Schaik and Dunbar 1990); (2) protective alliances between females and males as a form of infanticide defense (van Schaik and Dunbar 1990; Riechard and Sommer 1997; van Schaik and Kappeler 1997; Sommer and Reichard 2000); and (3) mate-guarding by males (Palombit 1996; 1999). A fourth category includes population-level

Table 12.2 Hypotheses and predictions for the evolution of Hylobatid social organization

Hypothesis	Example predictions	References
1. Ecological constraints on group size and female gregariousness	A. Female range exclusivity. B. Intra- and intergroup behavioral differences are predicted to be significant in two-adult vs. greater-than-two-adult groups due to increased competitive pressures.	Leighton 1987, Emlen and Oring 1977 and van Schaik and Dunbar 1990
2. Protective alliances between females and males as a form of infanticide defense	A. Female responsibility for the maintenance of close proximity. B. The avoidance of unmated or neighboring males (those posing the greatest risk to their infants) by females.	Reichard and Sommer 1997, Sommer and Reichard 2000, van Schaik and Dunbar 1990 and van Schaik and Kappeler 1997
3. Mate guarding by males	A. Male responsibility for the maintenance of close proximity. B. Active avoidance of intergroup encounters by males, thus reducing the opportunities for extrapair copulations.	Palombit 1999 and Wittenberger and Tilson 1980
4. Population-level models including the variable community hypothesis	A. Gibbons exhibit individual and temporal variation in composition, cohesion, and relationships between and within groups. B. This variation arises from historical, ecological, demographic, and behavioral processes.	Bartlett 2003, Fuentes 2000 and Reichard 2003

models developed to encompass the emerging aspects of variation in hylobatid social systems (Fuentes 2000; Bartlett 2003; Reichard 2003). All of these hypotheses generate predictions that are relevant to the following review (Table 12.2).

Female mammals, investing more energy per offspring than males, are limited by, and therefore compete for, resources (Williams 1966). Reichard (2003) posits that any additional benefits gained through the formation of multifemale groups (e.g., reduced predation or increased resource holding potential or both) are outweighed by increased intragroup feeding competition, which may explain the common pattern of female range exclusivity in the hylobatids. Males, facing limited access to reproductive females, seek to maximize their own fitness by balancing the costs and benefits of roving versus defending the range of a single female, and additionally attempting to ensure paternity and *potentially* providing indirect benefits to offspring. Pair living, in this scenario, appears to be the optimal (but not necessarily the equilibrium) grouping pattern. The reporting and observation of greater-than-two-adult gibbon groups provides an opportunity to examine the costs and benefits of specific age/sex group compositions.

In this chapter we will argue strongly for a transition from categorization, or typological thinking about the social organization of hylobatids, to a more dynamic process involving the formation of predictions and tests of hypotheses. It is our opinion that preconceptions about gibbon sociality have, in some cases, biased the research questions of previous investigators and influenced the interpretation of the existing data sets. Rather than always assuming optimal solutions, we view the energetic and material exchanges between organism and environment historically. Population-level processes are inherently complex as they encompass a host of factors including environmental conditions, historical changes, density dependent effects, and stochastic processes, and do not necessarily result in optimal adaptive trajectories (Oyama et al. 2001; Longo and Malone 2006).

This chapter is an attempt to synthesize published data on hylobatid ecology and social behavior to elucidate the commonalities and differences among hylobatid populations. Goals of the chapter include outlining observed patterns of variation and examining the ecological underpinnings of these patterns. We will also consider the evolutionary implications of the expression of individual variation and behavioral plasticity for the emergent relationships among individuals and groups in hylobatid communities. Finally, we conclude with a discussion of the role that past and ongoing anthropogenic disturbance plays in our efforts to understand and conserve hylobatid diversity.

Ecological Bases for Variation and Flexibility

Ecological considerations are critical to discussions surrounding the evolution of social structure in primates (Wrangham 1980; Brockelman and Srikosamatara 1984). The distribution (both temporal and spatial), quantity, and quality of food resources within an ecosystem fluctuate over time (Lambert 1999, 2007). Primates should therefore be expected to show seasonal variation in diet to a degree relative to the extent of seasonal shifts in resource availability. Further, individuals from closely related species may show differences in diet and feeding behavior, and these differences will have implications for the social interactions and organization of individuals and groups (Kappeler and van Schaik 2002). Indeed, Palombit (1996, p. 350) noted: “given that *Hylobates* [hylobatids] is [are] distributed over a diverse array of southeast Asian habitats, and that even subtle ecological differences may promote variation in social relationships, wider social variation within the genus [family] would not be entirely unexpected.”

Distribution and Habitat Characteristics

The biogeographic region occupied by the four gibbon genera spans approximately 4000 km (in a north-south direction) and includes both tropical and subtropical (>23.5° N. latitude) areas of South and Southeast Asia. Specifically, gibbons may be found in several of the remaining forested areas from northeastern India to southern China, throughout Bangladesh, Myanmar, Cambodia, Laos, Vietnam, Thailand, the Malay Peninsula, the islands of Java, Borneo, Sumatra, and the Mentawai Islands. The floral community in hylobatid habitats is typically comprised of between 24 and 50 tree families, with approximately 400 trees per hectare (Whitmore 1984; Ahsan 1994; Chivers 2005). Abundant families include Dipterocarpaceae (1–43%; mean of 16%), Leguminosae (13–14%), Moraceae, and Euphorbiaceae (Mather 1992; Ahsan 1994; Chivers 2005). Site-specific variation in the composition and productivity of vegetation is strongly related to the abiotic parameters of soil development, rainfall, and the effects of latitude and altitude (Pianka 1995). While acknowledging a limited dataset for many gibbon populations, and an apparent preference for less seasonal, lowland forests, it certainly can be concluded that, based on a myriad of ecological and climatic variables, hylobatid habitats vary both within and between species.

Patterns of Resource Use

All gibbon species are primarily characterized as frugivores, with fruit comprising ~60% of the annual diet, on average (Bartlett 2007; Elder this volume). However, while gibbons may feed more heavily on fruits than other primates labeled as frugivores, the undifferentiated use of this label may mask variation at the individual, group, population, and species level, and may imply the presence of behavioral correlates generally associated with frugivory (Bartlett 1999, 2007; Lambert 2007). Further, the distribution and nutritional properties of the so-called fall-back foods may be equally informative in deciphering patterns of behavior (e.g., range size and resource defense). Figs (*Ficus* spp.) constitute a substantial portion of many gibbons' diets (23% on average), and are quite common in many Southeast Asian forests (e.g., large crown volume and high tree density: Bartlett 1999, 2007). Figs represent a reliable year-round food source for gibbons, are high in readily digestible monosaccharides and low in secondary compounds, and appear to be especially important when other fruit species are less abundant (Vallayan 1981; Leighton and Leighton 1983; Bartlett 1999; Marshall et al. this volume). For these reasons, the characterization of gibbons as small-patch fruit specialists may be an overgeneralization (Bartlett 2007).

Fruit selection for specific traits may be influenced by the ability to manipulate and digest fruit, as well as the abundance of fruit in space and time. For example, McConkey et al. (2002) report that hybrid Bornean gibbons (*Hylobates muelleri* x *agilis/albibarbis*) mostly ate the pulp of ripe fruit, but also consumed seeds and unripe fruit. According to McConkey et al. (2002), the ideal gibbon fruit is 6–30 g, seedless, yellow-orange with a soft-juicy pulp, a thin skin, and available in dense crops. Gibbons virtually always swallowed seeds and seed width was a strong determinant of selection (seeds <21 mm were consistently selected). Gibbons were most selective during periods when fruit was abundant whereas when fruit was neither abundant nor scarce no specific trait had a strong influence on selection. Selection patterns may vary intraspecifically in response to pressure from frugivorous primate competitors (McConkey et al. 2002). Throughout their range, gibbons can be in direct competition from other primates (e.g., *Presbytis* spp., *Trachypithecus* spp., *Macaca* spp., and *Pongo* spp.), as well as both nonprimate mammalian orders (e.g., Rodentia and Carnivora) and avifauna (e.g., hornbills: Marshall et al. this volume).

Examples of Variation Among the Four Hylobatid Genera

We will briefly review salient data on variability from each of the four hylobatid genera. Partitioning of family-wide variation in this manner (i.e., by genus) is followed for organizational purposes and should not be mistaken for an assumption of within-genus homogeneity with regard to feeding and socio-ecology (refer to Table 12.3 for an overview of salient data by species).

Hylobates

Gibbon species within the genus *Hylobates* are the most studied of hylobatid taxa. Over a period of four decades, comparative data on the feeding ecology of several *Hylobates* species have been published (Ellefson 1974; Raemaekers 1979; MacKinnon and MacKinnon 1980; Gittins 1982; Kappeler 1984; Srikosamatara 1984; Whitten 1984; Leighton 1987; Palombit 1997; Bartlett 1999, 2007; Suwanvecho 2003). Fruit consumption averages 64.33% in this genus. However, dietary patterns vary both between species and within species (Elder this volume). For example, Palombit (1997) reports percentages of feeding time for white-handed gibbons on Sumatra as: 71% fruit, 24% leaves, 4% insects, and 1% flowers, whereas Raemaekers (1979) reported feeding percentages for the same species on the Malay Peninsula as: 50% fruit, 29% leaves, 13% insects, and 7% flowers. This intraspecific variation is compelling. Indeed, this species displays a range of variation in fruit feeding time (50–72%) approaching that of the genus as a whole (Bartlett 2007).

The foraging strategies necessary for the efficient exploitation of *Hylobates'* non-fruit food items are distinct from those associated with the exploitation of high-quality patches (i.e., fruiting trees). As feeding on leaves requires a different set of feeding patterns (spatial-temporal) and digestive parameters (Waterman and Choo 1981), the overall *suite* of foraging strategies should be considered in models of social organization. Specifically, hypotheses posited for pair-bonding behavior (e.g., females as a limited or widely dispersed resource) should not rely solely on the theoretical predictions of female distribution in relation to resource stress (and the resulting effects on male ranging), but rather

Table 12.3 The Hylobatidae: summary of studies (adapted from Fuentes, 2000)

Species	Location	Duration of study	# Groups (surveyed)	Mean group size	Density (inds/km2)	Day range	Home range	Citations[a]
Hoolock hoolock	Jorhat, Assam, India	62 days	7 (24)	3.2	7	NA	22 ha (18–30) ($N = 7$)	1
Hoolock hoolock	Tripura, India	2 months	9	3	5	600 m (300–1000)	300–400 ha	2
Hylobates agilis	W. Malaysia	11 months	7	4.4	18.9	1217 m (650–2200)	29 ha ($N = 1$)	3
Hylobates agilis	W. Kalimantan, Indonesia	19 months	8 (28)	4.1	14.9	NA	NA	4
Hylobates klossi	Siberut, Indonesia	3 months	11	3.4	24.8	NA	5–8 ha ($N = 13$)	5
Hylobates klossi	Siberut, Indonesia	22 months	2 (10)	3.7	10.4	1,514 m (885–2150)	31–35 ha ($N = 3$)	6
Hylobates klossi	Siberut, Indonesia	21 (10[b]) months	4 (15)	4.1	24.8	NA	8.8–12.5 ha ($N = 10$)	7
Hylobates lar	Khao Yai, Thailand	18 years (1665 days)	4 (12)	4.3[c]	34.4[c]	1245 m (672–1791)	21–40 ha ($N = 12$)	8
Hylobates lar	Kuala Lompat, Malaysia	12 months	6	3.3	2	1490 m (450–2900)	50–58 ha ($N = 2$)	9
Hylobates lar	Tanjong Triang	15 months	4	3.3	6.6		59 ha ($N = 4$)	10
Hylobates lar	Ketambe, Sumatra, Indonesia	72 months	3 (7)	4.1	4.7	NA	NA	11
Hylobates lar	Doi Dao, Thailand	3 months	21	4.3	NA	NA	16–32 ha ($N = 3$)	12
Hylobates moloch	Ujung-Kulon, West Java, Indonesia	11 months	6 (31)	3.3	8.9	1400 m	11.9–22 ha ($N = 6$)	13
Hylobates moloch	Leuweung Sancang, West Java, Indonesia	10 months	8	3.3	2.2	835 m (400–1100)	14.86 ha ($N = 8$)	14
Hylobates muelleri	Kutai, Kalimantan, Indonesia	15 months	7	3.4	10.2	850 m (350–1890)	33–43 ha ($N = 6$)	15
Hylobates pileatus	Khao Soi Dao, Thailand	9 months	1 (14)	6(3.8)	30	833 m (450–1350)	36 ha ($N = 1$)	16
Nomascus concolor	Xiobahe, Yunana, China	8 months	4	5.25	2.6	NA	NA	17
Nomascus concolor	Hainan, China	60 months	4	5.25	1.8	NA	200–500 ha ($N = 4$)	18

Table 12.3 (continued)

Species	Location	Duration of study	# Groups (surveyed)	Mean group size	Density (inds/km2)	Day range	Home range	Citations[a]
Symphalangus syndactylus	Ulu Sempan, Malaysia	14 months[d]	1 (3)	4	6	778 m (485–1390)	14.7 ha (*N* = 1)	19
Symphalangus syndactylus	Kuala Lompat, Malaysia	14 months[d]	1	5	5	969 m (320–2860)	32.4 ha (*N* = 1)	20
Symphalangus syndactylus	Kuala Lompat, Malaysia	12 months[e]	1 (6)	3	5	738 m (200–1700)	48 ha (*N* = 1)	21
Symphalangus syndactylus	Ketambe, Sumatra, Indonesia	72 months	3 (7)	3.8	4	NA	NA	22
Symphalangus syndactylus	Way Canguk, Sumatra, Indonesia	23 months	5	4 (N = 26)	16.44	1147 m (1067–1289)	20.2 ha[f] (*N* = 5)	23

[a] 1. Tilson 1979, Gittins and Tilson 1984; 2. Mukherjee 1986; 3. Gittins and Raemaekers 1980; 4. Mitani 1987, 1990; 5. Tenaza 1975; 6. Whitten 1980; 7. Tilson 1981; 8. Brockelman, et al. 1998, Bartlett 1999, Reichard 1995; 9. Gittins and Raemakers 1980; 10. Ellefson 1974; 11. Palombit 1992, 1994a; 12. Carpenter 1940; 13. Chivers 1984, Kappeler 1984; 14. Malone and Oktavinalis 2006; 15. Leighton 1987; 16. Srikosamatara 1984; 17. Sheeran 1993, Lan and Sheeran 1995; 18. Zhenhe et al. 1989; 19. Chivers 1974; 20. Chivers 1974; 21. Gittins and Raemaekers 1980; 22. Palombit 1992, 1994; 23. Lappan, 2005; O'Brien et al., 2003.

[b] Majority of observations from a 10-month period.

[c] Extrapolated from data provided in reference.

[d] 173–190 days each site.

[e] Same study group (TS1) as Chivers 1974.

[f] This figure is for siamang habitat outside of the area damaged by the El Niño-Southern Oscillation fires of 1997.

include the actual distribution of resources in a population of hylobatid groups (van Schaik and Dunbar 1990; Fuentes 2000).

Patterns of dispersal, pair formation, and both intra- and intergroup social organization of most members of the genus *Hylobates* have been little studied. However, the white-handed gibbon (*Hylobates lar*) is especially well known from two sites: Khao Yai National Park in Thailand (e.g., Reichard 1995, 2003, this volume; Brockelman et al. 1998) and Ketambe Research Station in Gunung Leuser National Park, Sumatra (Palombit 1992, 1994, 1996). Detailed observations of reproduction, natal dispersal, pair formation, and group structure in the Khao Yai population from 1978 to the present represent the largest data set available with which to address questions about hylobatid social organization. Specifically, the static model of highly territorial, monogamous pairs living in nuclear family groups can be assessed with the data encompassing the life histories for individuals in several neighboring social groups. A genetic relationship between adults and immatures in social groups is usually assumed in the nuclear family model, but our ability to test this assumption is dependent upon the knowledge of dispersal, pair formation, and mating patterns. The findings of the many researchers at Khao Yai raise questions about this assumption (Brockelman et al. 1998; Reichard this volume).

While knowledge of life histories and familiarity with migrating individuals are rare, as are actual genetic data, genetic relatedness in hylobatid social units may also be assessed by comparing the estimated ages of offspring to a known interbirth interval (IBI). Long-term observations at Khao Yai by Brockelman et al. (1998) and others indicate a minimum IBI of about 3 years (along with short dispersal distances). Data from a sample of 64 white-handed gibbon groups at Khao Yai reveal that 33% of the groups contained young estimated to be less than 2 years apart in age (Brockelman et al. 1998). These data suggest that more than one female may have produced the group's offspring or that related individuals may reside in neighboring groups. The potentially large number of non-nuclear families in this population stands in stark contrast to the conclusions of earlier researchers (summarized in Leighton 1987) as to the invariably monogamous social and reproductive behavior of hylobatids (Fuentes 2000). Further challenges to the nuclear family model come from the direct observation of partner turnover and extrapair copulations (EPCs), reported to comprise up to 12% of all copulations (Reichard 1995; this volume). The implications of these observations for the nature of intergroup interactions are great. Given the potential interrelatedness of gibbon groups, aggressive interactions with neighbors may in fact be detrimental to an individual's own fitness. Indeed, Bartlett (2003) reports that while a majority of intergroup encounters were considered agonistic, 20% consisted of vocal exchanges only, 6% were neutral, and 16% were actually affiliative.

Symphalangus

Like the white-handed gibbon, the siamang (*Symphalangus syndactylus*) is also relatively well known from Sumatra, as well as the Malay Peninsula. The siamang is the largest of all gibbon species and is found in primary and secondary, lowland, and montane forests up to 3800 m. Palombit (1997) reports the percentages of overall feeding time for the insular (Sumatran) subspecies of siamang as: 61% fruit, 17% leaves, 21% insects, and 1% flowers, while the average percentages reported from the mainland subspecies were: 40% fruit, 49% leaves, 6% insects, and 5% flowers (Chivers 1974; Raemaekers 1979; MacKinnon and MacKinnon 1980). This is similar to the pattern of intraspecific variation noted for the genus *Hylobates* (see above).

Palombit (1996) used quantitative measurements of social interactions and spatial relationships of adult pairs to make interspecific comparisons between pair-bonding behavior in siamangs and white-handed gibbons at Ketambe. Analyses of close proximity and (non-grooming) physical contact were used to evaluate the time spent in affiliation by males and females, and to compare the male and female investment in social relationships with opposite-sex adults. The results indicate that siamang pairs demonstrate greater spatial cohesion than do pairs of white-handed gibbons. Further, interspecific differences in the contributions of the sexes toward maintenance of the male–female social relationship suggest the presence of variable selective pressures affecting the importance of these relationships in different social and ecological contexts.

A recent long-term study of siamang groups at the Way Canguk Research Station in southern Sumatra, Indonesia, provides new insight into the social complexity of siamang populations (Lappan 2005, 2007). The occurrence of cohesive, greater-than-two-adult groups (multimale/unifemale composition) in 80% of the focal groups ($N = 5$), and the observation of polyandrous mating patterns in 75% of the groups with more than a single adult male ($N = 4$), provided an opportunity for the examination of male–infant, male–male, and male–female relationships (Lappan 2007). Relevant to our discussion here is the potential for insight into underlying ecological factors (i.e., distribution of resources) that are predicted, by current models of hylobatid social organization, to ultimately result in the evolution of gibbon pair bonds. In the multimale groups at Way Canguk, Lappan (2007), reports low rates of overall aggression, mutual tolerance among males, and variability in the strength and signaling of male–female bonds. Further, Lappan's (2007) research indicates that genetic relatedness cannot always be predicted from the observable social relationships.

Nomascus

Relatively few studies of the genus *Nomascus* have been conducted (Haimoff et al. 1987; Zhenhe et al. 1989; Bleisch and Chen 1991; Sheeran 1993), and these studies are limited to only a portion (China) of the entire range for the genus. Species in this genus range in montane forests up to 2900 m. With the exception of the siamang, this represents the highest recorded altitude for a gibbon species (Bleisch and Chen 1991). The diet of the black-crested gibbon (*Nomascus* *concolor*) has been reported to be more folivorous than those of other gibbons of similar size, and black-crested gibbons have been observed to come to the ground to forage on bamboo shoots. Early reports of group structure reported one male–multifemale groups of up to four females, and average group sizes of 5.25 individuals (Haimoff et al. 1987). Overall, published reports indicate that approximately 25% of *Nomascus* spp. groups have greater than two adults, including the observations of groups of up to ten individuals, groups with up to four adult females, and multiple females with dependent infants (Haimoff et al. 1986; Bleisch and Chen 1991; Lan and Sheeran 1995).

Bleisch and Chen (1991) report that black-crested gibbon (*N. concolor concolor*/*N. c. jingdongensis*) habitat in the Wu Liang Mountain and Ai Lao Mountain Natural Protected Areas in the center of the Yunnan Province, China, consists of low-stature mixed broadleaf evergreen and deciduous trees. This seasonal subtropical habitat differs from the tropical forests usually associated with gibbons. Day range sizes are generally larger than those found for other gibbon species. Group size/composition was determined for seven groups. Groups were no larger than five individuals and well within the usual range for gibbons. Three groups consisted of a single male and multiple individuals who produced female vocalizations (Bleisch and Chen 1991). The presence of multiple female singers in a single group has been offered as evidence that these gibbons live in polygynous groups. However, as immature individuals produce female songs in this species, this conclusion is tenuous. It is important to note that polygyny is one of the many mating patterns that may exist within a social system in which groups are predominantly characterized by only two adults (Fuentes 2000, 2002). Direct observations of mating behavior, genetic data, and long-term studies of this and other gibbon species are needed before interspecific comparisons can be considered complete.

Hoolock

The hoolock gibbon (*Hoolock hoolock*) inhabits rainforests and semi-deciduous forests in tropical and subtropical areas of India, Myanmar, China, and Bangladesh. Very little is known about the behavioral ecology of this genus. The hoolock gibbon is the second-largest hylobatid species and is the only gibbon species that ranges substantially outside of the tropics (Mootnick et al. 1987). A predicted dietary response to a seasonal environment might include increased reliance on leaves as fruit availability decreases. However, Gittins and Tilson (1984) report stable consumption of fruit throughout the year at a level comparable to species of *Hylobates*.

The hoolock gibbon has been observed to occur in greater-than-two adult groups, including: two adult males and a female (Siddiqi 1986); two adult females and a male (Ahsan 1995); and up to 5 adult males in a bachelor group in northeast India (Mukherjee et al. 1991–1992). Overall, four of the 34 hoolock groups on which studies have been published (12%) had a composition that runs counter to the traditional view of hylobatid social organization (Tilson 1979; Siddiqi 1986; Choudhury 1990; Mukherjee et al. 1991–1992; Ahsan 1995).

Comparison Between Genera: Hylobates and Symphalangus

It is evident that a substantial amount of variability exists in the feeding and grouping behavior of the hylobatids. These differences may arise from ecological variation in resource abundance related to latitude, altitude, rainfall, and the effects of island biogeography. It is very difficult to separate the relative impacts of these variables. Fortunately, two species (white-handed gibbons and siamangs), from two different genera, live in sympatry on both insular and mainland Southeast Asia, which facilitates direct comparisons between the two best-known hylobatid genera.

Palombit (1997) examined intra- and interspecific variation in diets, and the factors underlying such variation in two groups of siamang and two groups of white-handed gibbons at Ketambe in northern Sumatra, Indonesia. In this study, Palombit tested two hypotheses: (a) that interspecific dietary segregation derives from the adaptive consequences of contrasting body sizes; and (b) that the levels of fruit consumption observed at Kuala Lompat in Malaysia represent the upper metabolic limits of frugivory for these two species because of limits on energetic efficiency (*S. syndactylus*) and biochemical intolerance (*H. lar*).

Palombit's (1997) results indicate that white-handed gibbons spent a greater percentage of time feeding on fruit (71%) than did siamangs (61%). The diets of both species included similar proportions of figs and liana fruits. However, white-handed gibbons spent nearly 50% more time eating non-*Ficus* tree fruit than did siamangs. Time spent feeding on young leaves was over four times higher for siamangs than white-handed gibbons. Both siamangs and white-handed gibbons at Ketambe were more frugivorous than their Malaysian conspecifics. The lower total amount of time spent feeding by Ketambe hylobatids suggests that this *Ficus*-dominated diet is of higher quality than that of Malaysian conspecifics. Individuals of different species supplemented fig consumption in different ways: the siamangs focused more on young leaves and less on non-fig fruit while the white-handed gibbons relied more heavily on the pulpy fruit of trees and lianas, further augmented by insects. These findings support a dietary segregation hypothesis (but see Elder this volume). Finally, contrasting intraspecific strategies of folivory may be generated in part by differences in leaf biochemistry at the two sites (Palombit 1997).

Palombit's research suggests that interspecific differences are affected by ecological variation. Specifically, while both species are predominantly frugivorous on Sumatra, the differences that exist between the sympatric mainland species (e.g., types of foods used to supplement a fig-dominated diet) are further exaggerated in the insular populations. The implications of body size differences are apparent here. Due to their larger body size, siamangs expend more energy searching for small patches of scattered fruits than for abundant leaves. Raemaekers (1984) predicted that siamangs could overcome this constraint by increasing the consumption of figs, as long as these patches were large enough and temporally consistent. Siamangs on the island of Sumatra are more frugivorous than their Malayan conspecifics, and this increase is directly related to the fact that they eat nearly twice as many *Ficus spp.* fruits (43 vs. 22%). A floristic comparison of the two sites reveals a substantial difference in the density of fig trees.

The result of this comparison is increased understanding of the ecological underpinnings of both intra- and interspecific variation. This understanding highlights the active and emergent relationship between the individuals and the environment. This perspective is compatible with an increasing acknowledgement in evolutionary biology that a dialectical relationship exists between organisms and their environment through niche construction (Laland et al. 2001; Odling-Smee et al. 2003). The ability for organisms to not only impact their environment but also, in part, shape the selective forces that they face, may result in more plastic or variable behavioral profiles (West-Eberhardt 2003; Fuentes 2004). Therefore, the observable patterns of interaction are always in the context of *site-specific* historical environmental fluctuations, as well as *population-specific*, and demographically defined parameters.

From Ecological Variation to Variable Social Organization

The Family Hylobatidae began diversifying from a common ancestor at least 5 million years ago (Brockelman and Suwanvecho 2002), a time period sufficient for the evolution of behavioral and morphological variability. Detailed studies of all species have yet to be conducted, and this remains a major challenge to a thorough understanding of diversity within the family. Group size appears to have been subject to selective pressures, as small (approximately 5 individuals/group) groups are common throughout the ranges of all hylobatid species. The composition of these groups, as well as intra- and intergroup behavior, may be flexible, however. Given the substantial dietary and behavioral flexibility that gibbons display, especially under variable ecological conditions, further research is necessary before accurate evolutionary models of hylobatid social organization can be developed. A realization that our current understanding is incomplete may have important implications for the conservation of these organisms. The design and management of protected areas, rehabilitation, captive breeding, and reintroduction of hylobatids will be most effective if our knowledge of all free-living species is increased.

As outlined in this chapter, habitat differences can result in marked variation in social behavior and organization. This relationship does not appear to be isolated within a subset of taxonomic categories in the Hylobatidae, but is evident throughout the family. Fuentes (2000) demonstrated that approximately 10% of all gibbon

Table 12.4 Percentage of greater-than-two-adult groups in gibbon species (based on citations in text)

Species	Percentage of total groups observed with > 2 adults
Hoolock hoolock	12%
Hylobates agilis	No reports of greater-than-two-adult-groups
Hylobates klossii	(At least two greater-than-two-adult groups observed)
Hylobates lar	10–18%
Hylobates moloch	(At least one greater-than-two-adult group observed)
Hylobates muelleri	No reports of greater-than-two-adult groups
Hylobates pileatus	(At least three greater-than-two-adult groups observed)
Symphalangus syndactylus	(At least five greater-than-two-adult group observed)
Nomascus concolor	25–27%

groups studied (representing a minimum of six species) have been observed in greater-than-two adult groups. This percentage rises to 18% when only groups from the six species where greater-than-two-adult groups have been observed were considered (Fuentes 2000). Since the time of that review, a seventh species, the Javan gibbon (*Hylobates moloch*), has been observed in a multimale/unifemale group composition (Malone and Oktinavalis 2006) and additional reports of such groups have been made for species in which they had been previously observed (Lappan 2005; Reichard this volume, Table 12.4).

These observations of gibbon grouping patterns and dietary behavior reinforce previous suggestions of an inherent variability in the social organization of the hylobatids (Fuentes 2000). This suggests that the presence of an additional adult does not have a sufficient net cost in terms of within-group feeding competition to prevent greater-than-two adult grouping, at least in some cases. In habitats with abundant resources, constraints on group size may be relaxed. Interestingly, in the case of the Javan gibbon, the observed greater-than-two-adult group ranged within an area of 6.25 ha, the smallest range within the sample (mean = 14.86, SD = 3.89, N = 8: Malone and Oktinavalis 2006; Malone 2007). While this particular observation is in the context of severe anthropogenic habitat disturbance, such a behavioral response is indicative of plasticity at both the individual and the group level. This plasticity in grouping and mating potential may play a role in the geographical success and phylogenetic diversity of the hylobatids relative to other nonhuman hominoids.

Human Impacts, Social Organization, and Population Viability

Primates might gain fitness benefits from an evolved plasticity to respond to variable environmental and social conditions (such as changes in density, overlap with neighboring groups, the presence of unpaired adults, etc.). A social system consisting of relatively behaviorally plastic individuals would be expected to be variable. The variability in social organization (reviewed above) supports the variable community hypothesis for the evolution of hylobatid social organization

(Fuentes 2000, Table 12.2). Additionally, the tendency of males to assist females in resource defense is consistent with the male defense of resources hypothesis (Wittenberger and Tilson 1980, Table 12.2). Thus, group structural plasticity, feeding plasticity, and short dispersal distances (resulting in localized kin-networks) form the basis for variation in the historical and ecological circumstances of specific communities that may elicit variable demographic and behavioral responses in gibbons.

Anthropogenic disturbance, including habitat degradation and hunting pressure, may lead to changes in densities and group sizes, and perhaps drive ecological, and subsequently social, systems into a state of disequilibrium (Struhsaker 1997, 1999; Nijman 2001). Such anthropogenic conditions may result in behavior consistent with the predictions generated from hypotheses for the evolution of social systems in the Hylobatidae. For example, if habitat degradation alters group density, the amount of territorial overlap, or both, the resulting crowding may lead to an increase in time allocation to the defense of resources. The selective hunting of females with dependent offspring (for the pet trade) could lead to an increase in unpaired males, thereby increasing the competition for access to mating opportunities. Rapid departures from equilibrium, and the subsequent breakdown of female counterstrategies, may also substantially increase the risk of infanticide (Palombit 1999).

The specific nature of anthropogenic disturbances (e.g., location and intensity of logging, or hunting frequency/effectiveness) may alter typical behavioral patterns in predictable ways. While both intra- and intergroup social behavior in primates appear to be highly variable (Rylands 1993; Treves and Chapman 1996; Fuentes 1999), the degree to which primates are able to adapt to rapid environmental or population alteration will be a function of the degree of plasticity at the individual, and subsequently the group, level (Fuentes 1999). Therefore, observations of inter- and intragroup behavior in the context of anthropogenic habitat disturbance generate data sets that are conducive to testing predictions from the variable community hypothesis, as well as other population-level models of gibbon social systems (Fuentes 2000; Bartlett 2003; Reichard 2003). Specifically, the ecological aspects of these hypotheses (e.g., correlations between resource distribution, ranging patterns, group size, and the distribution of variation in the Hylobatidae) can be assessed within the context of disturbance.

While this discussion focuses on anthropogenic disturbance, similar demographic shifts could arise through stochastic events such as deaths, uneven sex ratios at birth, and population-level responses to fluctuations in resource abundance. Perhaps, most salient for this discussion are irregular and unpredictable fruiting intervals (masting) by dipterocarps and many other tree taxa that result in periods of either the absence or the super-abundance of foods for frugivores in Southeast Asian forests (Caldecott and Kapos 2005). Additionally, fires associated with El Niño/Southern Oscillation (ENSO) events often affect primary forest located within protected areas, and hence result in large-scale changes to keystone species in ecological communities. The documented impacts of these processes include reductions to infant and juvenile survival rates for siamang groups and the subsequent loss of seed dispersal services in burned forest (O’Brien et al. 2003). While the burning of gibbon habitat, especially when resulting in a reduction of reproductive-sized primary resources (i.e., *Ficus* spp.), may constitute an immediate threat to population viability, the combined (and historical) effects of these two factors (masting and fires) would suggest that the persistence of hylobatid species in Southeast Asia is tied to evolved dietary and social flexibility. Thus, it is the *response* to the ecological disturbance and not the ecological disturbance per se, that ultimately determines the viability of post-disturbance populations. Therefore, the question becomes, how well are hylobatid *populations* able to respond to disturbance? For example, O’Brien et al. (2003, p. 118) demonstrate reduced reproductive success for siamang groups occupying burned habitat as compared to “normal groups” (a potential source-sink relationship), and note that “monogamy and territoriality may limit the range of possible responses to fire (and other severe disturbances) by siamang”. However, home-range overlap and polyandrous mating have been observed within the behavioral profile of siamang groups (O’Brien et al. 2003; Lappan 2005). What are the implications of these (and other) patterns of variation for population viability and conservation?

Caldecott and Kapos (2005) suggest that the pattern of fruit and seed availability in Southeast Asian (dipterocarp) forests favors two specific areas of adaptation: mobility (high) and reproductive rate (rapid). Hylobatids exhibit one of these adaptations: high mobility. As habitually (and often ricochetally) brachiating, small-bodied hominoids, the hylobatids occupy a unique phylogenetic position with respect to ecology and reproductive biology. Several energy-economizing aspects of hylobatid locomotion and postural biomechanics have been identified, including: access to resources near the outer periphery of trees, the alternating transformation of potential energy into kinetic energy (the mathematical pendulum model), and increasing horizontal velocity via relatively long forelimbs (Preuschoft and Demes 1984). Therefore, the costs of additional travel (increases in day range) resulting from larger group sizes or more frequent monitoring (and defense) of widely dispersed resources are arguably minimal (Chapman and Chapman 2000; Steudel 2000; Sussman and Garber 2007).

Insight from life-history theory and the relevant indices of fecundity, mortality, and interbirth intervals may be useful in understanding the rate at which populations can respond to an unpredictable food supply. Kelley (1997) argues that life-history parameters, rather than morphological features, most clearly distinguish the hominoid clade from non-hominoid primates. In this respect, the hylobatids, while clearly within the hominoid range for parameters such as gestation length, age at first reproduction, and IBI, arguably occupy a more favorable position with regard to vulnerability to extinction via small-population processes than other hominoids (e.g., orangutans, with even slower maturation and reproductive rates). Therefore, the conclusion drawn by O’Brien et al. (2003) that the lower survival rates for infant and juvenile siamang in groups affected by fires is tantamount to an insufficient reproductive effort to sustain *groups* may only be one factor affecting the long-term viability of the *population*. That is, variation in the allocation of energy between survival and reproduction will only become apparent through long-term ecological and demographic observations of study populations (assuming that groups are differentially affected by disturbance events: O'Brien et al. 2003).

Here again, social and mating system variants have direct conservation ramifications. For example, generalizations about mating systems (and their biological implications) can impact our assessment of the minimum population size required to maintain genetic heterozygosity, which can in turn affect the prioritization of areas for protection. As such, calculations of population viability should be informed by estimates of the effective population size ($N_e = 4/\mathrm{N}\ /[2 + s^2]$), due to the sensitivity of the latter measure to individual variance in lifetime reproductive success (s^2). A minimal amount of polygyny skew (i.e., inequality in male genetic contributions to future generations) is assumed within monogamous mating systems resulting in N_e being more or less equivalent to the number of reproductive-aged adults (Cowlishaw and Dunbar 2000). Therefore, the biological implications of EPCs and greater-than-two-adult groups become paramount to our modeling of population viability and, subsequently, our conservation tactics.

Perhaps even more pressing with regard to the development of species-specific conservation strategies is the accurate estimation of the total number of individuals (in a given taxon) that remain in both protected and unprotected areas. Exhaustive surveys of fragmented forest blocks throughout a species' range are both time- and resource-intensive. However, these "ground check" methodologies are critical given the complexity and variability of inter- and intragroup social compositions and relationships. A striking example is provided by the distribution (and size) of *H. moloch* territories in the highly fragmented Cagar Alam Leuweung Sancang, West Java. Within this nature reserve are fragments that are of unequal sizes and gibbon group densities. The first fragment (*Cipangisikan*) of approximately 200 ha and the second fragment (*Cipalawah*) of 400 ha are inhabited by six and two gibbon groups, respectively (Malone and Oktinavalis 2006; Malone 2007). This inverse relationship between fragment size and the number of gibbon groups can only be understood historically in the context of the patterning of forest loss and the size/composition of territories and territory holders. Therefore, attempts to derive estimates of remaining individuals based on superficial habitat assessments and extrapolations from average group and territory sizes may produce inaccurate results and limit options for the deployment of conservation tactics.

Potentially related to the use (and realities) of conservation tactics (e.g., the rehabilitation of displaced hylobatids or the reintroduction/translocation of hylobatids within fragmented ecosystems) are the patterns of behavior among individuals in semi-free ranging, or rehabilitative conditions (Esser et al. 1979; Cheyne 2004; Cheyne adn Brulé 2004). Esser et al.'s (1979) study of a provisioned free-ranging group of six white-handed gibbons (*Hylobates lar*) on Hall's

Island, Harrington Sound, Bermuda, provides some insight into the range of gibbon potential behavioral responses to unusual circumstances. The three males and three females ranging on the 1.5 acre island were approximately 5 to 8 years of age, and were observed for an average of 30.5 days during two consecutive years. Approximately one-quarter of all social interactions observed involved three or more individuals, and complex dominance relationships emerged within the population.

Esser et al. (1979) argued that due to the forced aggregation on Hall's Island, the individual gibbons interacted socially, and the development of complex dominance relationships was a behavioral response to this specific social and ecological situation.

Brockelman et al. (1998) discussed several aspects of white-handed gibbon sociality that are inconsistent with a static model of gibbon groups as isolated social units, including low levels of intergroup aggression and even instances of play and affiliation between neighboring-group adults at Khao Yai. Observations of sexual interactions during agonistic intergroup encounters have also been recorded, suggesting that these encounters provide opportunities for maturing subadults to identify potential mates (Bartlett 2002). The emerging view of intra- and intergroup variability in interactions and the example of Hall's Island suggest that it is vital to analyze individual relationships throughout a population as we attempt to understand group compositions and intergroup relationships.

Conclusion

Continued observation of populations of hylobatids, especially long-term studies that yield information about life histories, can help us to develop a better understanding of gibbon social organization at the group, community, or population level. The evidence for complexity and variability emphasizes the need for an integrated focus on intra- and intergroup interactions and relationships. For example, the short dispersal distances, substantial percentages of intergroup affiliative encounters, and EPCs reported by some field researchers (Paeombit 1994; Reichard and Sommer 1997; Brockelman et al. 1998; Reichard this volume) challenge the traditional assumptions of nuclear families, reproductive monogamy, and the importance of intergroup competition underlying previous attempts to model the costs and benefits of different group compositions and mating strategies. Consideration of this information is critical when developing testable hypotheses with reference to social organization.

The results of long-term field studies may be especially helpful for active conservationists attempting to best provide for the behavioral repertoires of displaced organisms. Captive breeding programs, reintroduction, and rehabilitation efforts, considered important in situ conservation tools if adequately implemented (Hannah and McGrew 1991; Cheyne this volume), should consider such potential variation in their management strategies. If further research confirms the dynamic nature of intergroup relationships and encounters, our general outlook on gibbon sociality may expand to encompass life at the community level. Dispersal, pair formation, and reproductive success may all depend greatly on social and ecological interactions with conspecifics. A better understanding of gibbon ecology, life histories, and intra- and intergroup relationships are crucial to our definition of "preferred social units," or viable community compositions, in any strategy involving the conservation of social organisms.

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Chapter 13

Seasonal Home Range Use and Defendability in White-Handed Gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand

Thad Q. Bartlett

Introduction

Gibbons are unique among hominoids in that they form small, socially monogamous groups that defend stable home ranges against encroachment by neighboring conspecifics. The evolution of this combination of traits, and the role of foraging ecology in its emergence, has long been the subject of speculation and research (Leighton 1987; Chivers 2001; Bartlett 2007). Early models focused on the highly frugivorous diets of gibbons and the consequent inability of adult females to share feeding resources. Social and reproductive monogamy, it was argued, resulted from the inability of males to defend areas large enough to support more than one adult female and her offspring. While males of monogamous species might willingly associate with multiple females (and experience increased reproductive success as a result), the distribution of females into separate territories was thought to limit a male's ability to defend access to more than one female, leaving males no other option but to travel with a single female at a time (Ellefson 1974; Emlen and Oring 1977; Wrangham 1979; Raemaekers and Chivers 1980; Leighton 1987).

According to van Schaik and Dunbar (1990), one weakness of this model as applied to gibbons is that long daily path lengths (DPL) relative to home range size in most populations indicate that gibbon males could readily defend the territories of multiple females simultaneously. Based largely on these finding, van Schaik and Dunbar reject what they refer to as the *female dispersion model*, paving the way for alternative explanations for social monogamy in gibbons that highlight the role of sexual competition [e.g., infanticide prevention (van Schaik and Dunbar 1990) and mate guarding (Palombit 1999)] rather than ecological selection pressures (but see Brockelman 2005, this volume). However, in my view, the rejection of the female dispersion model is premature.

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Prior attempts to assess the territorial potential of male gibbons have failed to take into account the seasonal variation in range use and therefore have overestimated the total area a gibbon male can defend. Although gibbon territories are stable year round (and even from year to year), DPL varies seasonally in response to the abundance of preferred resources (Raemaekers 1980; Bricknell 1999; Bartlett 2009). As a result, the hypothetical maximum number of female territories a single male can defend should also fluctuate over course of the year (i.e., on a monthly or seasonal basis). In this paper I examine the monthly changes in range use by white-handed gibbons (*Hylobates lar*) in seasonal evergreen forest to investigate the claim that gibbon males routinely travel far enough to defend territories of sufficient size to maintain exclusive access to multiple females or the resource base necessary to support them.

Methods

Study Site and Animals

Observations were made as part of a yearlong study of the feeding ecology of white-handed gibbons at the Mo Singto study area in Khao Yai National Park, Thailand (Bartlett 2009). Khao Yai, which is Thailand's third-largest national park (2,169 km^2), is located approximately 150 km northeast of Bangkok (101°22′ E, 14°26′ N). The park consists primarily of a sandstone plateau ranging from 600 to 1000 m above sea level. The study area was first established in 1979 by Warren Brockelman and has remained an active center for gibbon research since that time (e.g., Raemaekers et al. 1984; Brockelman et al. 1998; Reichard 2003; e.g., Barelli et al. 2007; Savini et al. 2008). The site, which is located near the park headquarters, is situated in an extensive tract of tropical evergreen forest that receives between 2000 and 3000 mm of rainfall annually (Tangtham 1991), the majority of which typically falls during a 4–5 month period, June through October, during the southwest monsoon or wet season. There is a distinct cool season from November though February, followed by a resource-rich hot season from March through May (Graham and Round 1994).

Resource Abundance and Rainfall

Resource abundance during the study period was determined by monitoring the phenology of 252 trees with a diameter at breast height $\geq$20 cm. Trees were selected without knowledge of species. Once per month all trees were scored for the presence of flowers, ripe fruit, and young leaves. The stage of development for fruit and leaves was assessed visually based on size and color using binoculars (for additional details see Bartlett 2003, 2009). The park weather station was located in an open field approximately 1 km south of the headquarters. Rainfall data were collected daily by park employees and made available to me at the end of each month.

Behavioral Data Collection

Prior to the onset of this study, two gibbon social groups had been habituated by other observers (see Brockelman et al. 1998). The two groups, A and C, were first described by Raemaekers and colleagues (1984) and retain their designations. From February 1994 through January 1995, I conducted systematic observations on both groups, each of which was composed of five animals including an adult pair and three immatures. Each of the two study groups was followed from night tree to night tree, whenever possible, for a period of five consecutive days per month. To document the ranging behavior of the study animals, the location of the focal animal was recorded every half hour, but to recreate day ranges with as much accuracy as possible, the 30-min location samples were combined with the location of all feeding and night trees used during a given day. Location samples took the form of an estimated distance and compass bearing from a known trail location or some other previously identified landmark.

Data Analysis

All location points from all full-day follows were entered into *Pathfinder*, a cartographic database manager developed by Michael E. Winslett (Austin, TX). *Pathfinder* uses mapped location points to calculate the DPL and home range areas (Overdorff 1996; Vasey 2006). The results reported here are based on 109 full-day follows of the two groups conducted during the 12 consecutive months from February 1994 to January 1995.

Defendability. The relationship between home range area and DPL is described using Mitani and Rodman's (1979) *defendability index* (D-index), which describes the likelihood that a group will encounter its own range boundary as it moves around its range on an average day:

$$D = d/d'$$

where d is equal to the average DPL and d' is equal to the diameter of a circle with an area (A) equal to that of the observed home range:

$$d' = (4A/\pi)^{0.5}$$

Mitani and Rodman determined that territorial species invariably have a D-index of at least 1.0, which represents the ability to cross the full width of the home range during an average day's normal travel.

Maximum defendable females. To estimate the maximum number of female territories a male could defend given his observed, van Schaik and Dunbar (1990) invert the formula for the D-index to derive the maximum area ($A_{\max}$) that a male could potentially defend:

$$A_{\max} = 0.25\ \pi d^2$$

The maximum number of females with offspring this area could support ($N_{\max}$) is determined by dividing the total defendable area by the area needed to support a single female and her offspring (A_{fem}):

$$N_{\max} = A_{\max}/A_{\text{fem}}$$

As reported by Reichard (2003: Table 13.4), the mean group size for gibbons at Mo Singto is 4.0 ($N = 107$ social units). Based on this value, Reichard estimates that an adult male requires 25% of the home range to support himself. Thus, A_{fem} is assumed to be 75% of the annual home range. Because Mitani and Rodman (1979) found that no species of primate defends an area larger than 1 km^2, I follow van Schaik and Dunbar (1990) and Reichard (2003) and calculate the maximum number of defendable females under the assumption that males cannot defend an area larger than 1 km^2. This estimate is designated $N_{\min}$. Finally, to investigate intra-annual variation in defendability, I calculate the D-index and $N_{\min}$ for each month based on the average DPL for that month.

Results

Resource Abundance and Rainfall

The availability of ripe fruit was greatest during the hot and wet seasons. During the 12 months of study, fruit abundance showed a bimodal pattern with the first peak in May, when 12% of trees bore fruit, and a second less-pronounced peak in September, with 8% of trees in fruit. In contrast, trees in flower were most abundant from November to February when 9–20% of sample trees were in flower (Fig. 13.1). New leaves were available in all months. The month with the lowest availability was June when only 5% of sample trees had young leaves, as compared to February and November when 31% had young leaves. Total rainfall for 1994 was 2,695 mm; 75% of total rainfall fell in the wet season and there was little rain (2% of the annual total) from November through February (Fig. 13.1).

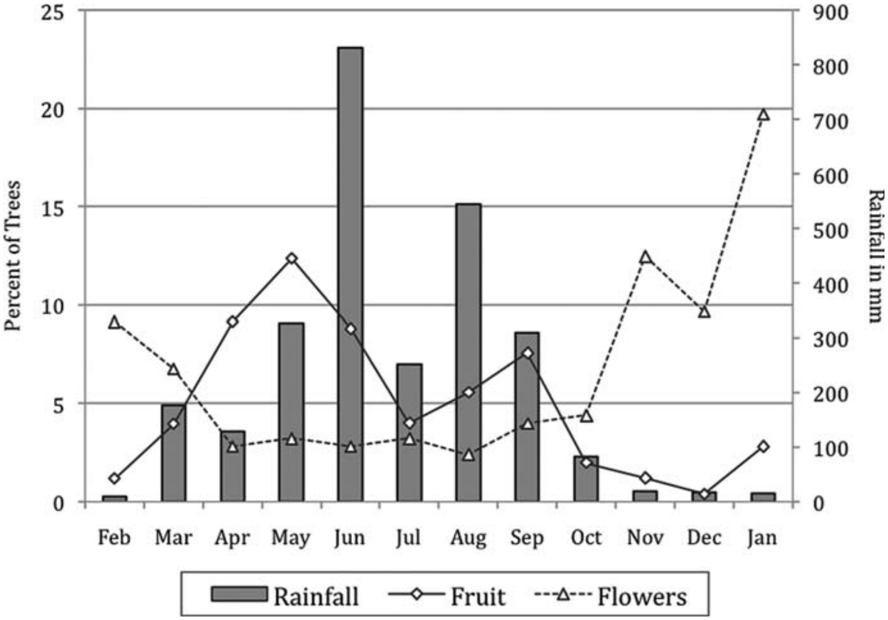

Fig. 13.1 Monthly variation in rainfall and the abundance of reproductive plant parts (i.e., fruit and flowers) in Khao Yai National Park from February 1994 to January 1995

DPL and Home Range Size

The mean DPL for the two groups was 1.24 km per day. DPL was greatest in April, 1.79 km, and lowest in November, 0.67 km (Table 13.1). Group C (mean = 1.33 km, S.D. = 0.42, $N = 12$) traveled farther than group A (mean = 1.16 km, S.D. = 0.32, $N = 12$) in all but 2 months, but the monthly pattern of fluctuations in range use was the same ($r_s = 0.94, p = 0.002$). Over all months there is a significant positive correlation between DPL and fruit abundance ($r_s = 0.64$, $p = 0.033$). There was no significant relationship between DPL and the abundance of flowers or young leaves.

Annually, there was no significant difference between the distance traveled on dry ($N = 71$) versus wet ($N = 28$) days ($U = 970.0, Z = -0.186, p = 0.852$). Nor was there a significant relationship between monthly rainfall and DPL when compared across months ($r_s = 0.35, p = 0.246$).

Home range sizes for the two groups were calculated from the cumulative day range map of each group. Day ranges were drawn from 62 night tree-to-night tree follows for group A and 38 for group C. Minimum convex polygons circumscribing the range maps of each of the two groups yielded annual home range sizes of 0.25 and 0.21 km^2 (mean = 0.23 km^2).

Table 13.1 Mean *DPL*, Defendability (*D-index*) and maximum number of defendable females (N_{min}) in two gibbon social groups

	Group A			Group C			Mean		
	DPL (km)	D-Index	N_{min}	DPL (km)	D-Index	N_{min}	DPL (km)	D-Index	N_{min}
Feb	1.12	1.97	4.80	1.58	3.02	6.20	1.35	2.50	5.50
Mar	1.50	2.64	5.20	1.70	3.25	6.20	1.60	2.95	5.70
Apr	1.66	2.91	5.20	1.93	3.69	6.20	1.79	3.30	5.70
May	1.61	2.83	5.20	1.61	3.08	6.20	1.61	2.96	5.70
Jun	1.22	2.14	5.20	1.42	2.71	6.20	1.32	2.43	5.70
Jul	1.42	2.49	5.20	1.84	3.53	6.20	1.63	3.01	5.70
Aug	1.03	1.80	4.00	1.18	2.27	6.20	1.10	2.04	5.10
Sep	0.92	1.61	3.10	1.23	2.35	6.20	1.07	1.98	4.70
Oct	0.76	1.34	2.10	0.80	1.53	2.80	0.78	1.43	2.40
Nov	0.72	1.27	1.80	0.62	1.19	1.50	0.67	1.23	1.70
Dec	0.91	1.60	3.10	1.02	1.95	4.70	0.96	1.77	3.90
Jan	1.06	1.86	4.30	1.04	1.99	4.90	1.05	1.93	4.60

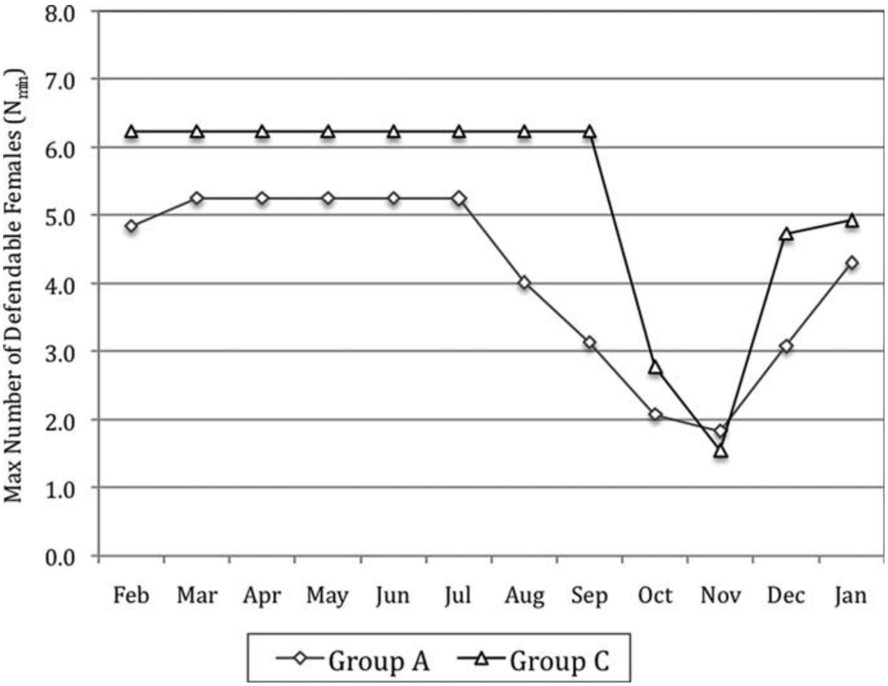

Fig. 13.2 Monthly variation in the maximum number of defendable females, assuming a maximum defensible area of 1 km^2

Defendability

The annual DPL and home range values yield a D-index of 2.04 and 2.55 for groups A and C, respectively (mean = 2.30). D-index values calculated based on mean monthly DPL for each group never fell below 1.0 (Table 13.1).

Based on annual means, the number of defendable females, $N_{\min}$, for the two groups were 5.2 and 6.2, respectively (mean = 5.7). Calculated monthly, the maximum number of defendable females is quite high over most of the year, but there is a steep decline beginning in August for Group A and October for Group C, with the maximum number of defendable females falling below 2.0 for both groups during November (Fig. 13.2).

Discussion

Variation in DPL

In the seasonal forest of Khao Yai National Park, the average distance traveled per day varied considerably over the annual cycle. For example, gibbons traveled over two and a half times farther in April than in November. While it is possible that heavy rainfall limits group travel on occasion, the main factor influencing daily travel distance at Khao Yai was the abundance of preferred resources. Both gibbon social groups traveled least from October to January when ripe fruit was scarce. This conclusion is consistent with the observations made by Raemaekers (1980), who studied range use by white-handed gibbons and siamangs (*Symphalangus syndactylus*) in the Krau Game Reserve, Malaysia. Raemaekers concludes that the strong correlation between food abundance and travel distance suggests that gibbons follow a “loss-cutting policy” when it comes to range use. This finding raises the possibility that gibbon territory size is limited by periods when resource abundance is low. Thus, while it might be possible for gibbon males to defend much larger ranges when resources are abundant, the same range boundaries could not be defended effectively at other times of the year.

Defendability

The D-index describes the likelihood that a group will encounter its own range boundary as it moves around its home range on an average day. Mitani and Rodman (1979) reason that primate groups that routinely approach their range boundary during normal travel will be able to monitor encroachment by neighboring animals with little extra cost. Accordingly, Mitani and Rodman found that all territorial species have a D-index of at least 1.0. While some *non*territorial species were also shown to have a *D* of 1.0 or greater, the authors suggest that not all species derive energetic benefits from defending their range, perhaps due to differences in resource distribution. In a subsequent analysis, Lowen and Dunbar (1994) were better able to distinguish territorial from *non*territorial species by employing an index based on the kinetic theory of gasses, which (unlike the Mitani-Rodman index) takes into account the length of the boundary to be defended and the number of independently foraging parties. Nevertheless, Lowen and Dunbar conclude that the Mitani-Rodman index is largely accurate, and the latter index continues to be used to assess territorial potential in primates (e.g., Müller 1995; Price and Piedade 2001; Reichard 2003). In the present study, the average value of the D-index for the two study groups was 2.30, which is nearly identical to the value Mitani and Rodman (1979) themselves report ($D = 2.29$) for white-handed gibbons based on the data from Chivers (1972). Given the monthly fluctuations in DPL, it follows that defendability too must fluctuate. In fact, while D was well above 1.0 in most months, the value of the D-index approached the threshold below which territoriality is theoretically impracticable during November for both study groups. This finding has important implications for the female dispersion hypothesis.

Maximum Number of Defendable Females

The female dispersion hypothesis for monogamy rests on the premise that females are an “over-dispersed resource” that males are unable to monopolize. Using data from 11 gibbon populations, van Schaik and Dunbar (1990: 36) calculated the maximum number of defendable females ($N_{\min}$) for each group, concluding, “most males could expect to have exclusive access to 2–5 females” (mean = 3.1, $N = 11$, range = 0.9–8.3; *H. lar*: mean = 2.9, $N = 3$; range = 2.1–3.3). Based primarily on these findings, they reject the female dispersion hypothesis in favor, ultimately, of the infanticide defense hypothesis. In the years since van Schaik and Dunbar’s original analysis, observations of extrapair copulations between individuals in neighboring groups (e.g., Palombit 1994; Reichard 1995) and polygamous mating in gibbon groups with >2 adults (e.g., Bricknell 1999; Lappan 2007; Bartlett 2009; Reichard this volume) have underscored the importance of examining reproductive systems independently of social systems. Nevertheless, because social monogamy limits reproductive opportunities in ways that social polygamy does not, investigators continue to examine gibbon social systems in relation to defendability. Recently, for example, Reichard (2003) revisited van Schaik and Dunbar’s critique of the female dispersion model using data from the gibbon population at Mo Singto. Based on a larger sample, Reichard reports an $N_{\min}$ of 5.6 for Khao Yai gibbons, comparable to the $N_{\min}$ of 5.7 reported here. Like van Schaik and Dunbar (1990), Reichard concludes that the failure of male gibbons to pursue a polygynous socioreproductive strategy implicates alternative selective pressures: “it has to be assumed that males choose social monogamy because they gain higher fitness returns from staying with one female than from trying to stay with several females" (Reichard 2003: 201).

The analysis presented here suggests that a male's options may be more constrained than these authors allow. When calculated on a monthly rather than annual basis, the maximum number of females a male can hypothetically defend falls below 2.0 during November. In other words, for Khao Yai gibbons the maximum number of female ranges a male could defend is consistent with social monogamy. These findings suggest that ecological constraints play a central role in limiting gibbon group size, a conclusion consistent with the female dispersion hypothesis. Nevertheless, female dispersion alone is insufficient to account for other elements of gibbon social organization, such as the socio-spatial proximity exhibited by gibbon pair mates (van Schaik and Dunbar 1990). So while feeding competition likely represent the primary pressure limiting group size in gibbons, the close bond between males and females is likely the outcome of secondary selective pressures, potentially including those identified by critics of the female dispersion hypothesis [e.g., mate guarding (Palombit 1999); infanticide protection (van Schaik and Dunbar 1990); foraging efficiency (Fuentes 2000; Reichard 2003)]. A key difference in the view presented here, however, is that it does not regard the two-adult social structure exhibited by gibbons as a unique socioecological mystery yet to be solved. Rather—extrapolating from the finding described above—I argue that the two adult groups exhibited by most hylobatids are the result of energetic constraints imposed by territoriality. Indeed, in black-crested gibbons (*Nomascus concolor*), the one gibbon species for which groups with extra adult females appear to be common, extremely large range sizes make territorial defense improbable (Jiang et al. 1999; Fan et al. 2006). In contrast, the addition of extra adult males should not be expected to impose the same ecological costs because extra adult males are not associated with dependent offspring and they can compensate for increased intragroup feeding competition by contributing to territorial defense (Brockelman et al. 1998; Lappan 2007). So in conclusion, although the evolutionary origins of close socio-spatial proximity among gibbon pairs remains to be established, the hypothetical ability of males to defend multiple female territories should no longer be used as a justification for favoring the explanations rooted in sexual competition over those based on ecological selection pressures.

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Part V
Mating Systems and Reproduction

Chapter 14
Monogamy in Mammals: Expanding the Perspective on Hylobatid Mating Systems

Luca Morino

Introduction

Hylobatids are among the few primate species that live primarily in monogamous (two-adult) groups (Rutberg 1983; Fuentes 1999). Nonetheless, some of their physiological and behavioral characteristics, including their slow life histories (Leighton 1987), a generalized lack of paternal care (Fuentes 1999), and their apparent ability to efficiently defend large territories (Mitani and Rodman 1979), differ from those of most other purportedly monogamous primates (and mammals). Given the relative paucity of monogamous primate species, it may be worthwhile to consider other monogamous mammal species as a valuable additional source of comparative data, as well as of new ideas, innovative methodologies, and theoretical developments.

At the time of the last comprehensive reviews of monogamy in mammals (Kleiman 1977; Wittenberger and Tilson 1980), genetic data were not yet available and long-term field data had not been collected for most species. Subsequent research has provided more information on rare events and behaviors, such as copulations, and paternity has been assessed for several taxa. These studies showed that a social (who lives with whom) as well as mating (who copulates with whom) system does not always reveal the genetic structure of a population. Extrapair paternity (EPP) has been shown to be much more common than expected in many mammalian species previously thought to be strictly monogamous.

In this chapter, I review recent data on monogamous mammals to suggest how approaches and problems far from the field of gibbon socioecology can contribute to the study of hylobatid communities. Some of the issues that I cover include incidence of EPC (extrapair copulations) and EPP; expressions of mate choice and fidelity; flexibility of grouping and mating patterns; proximate

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mechanisms maintaining monogamous grouping; reproductive success of alternative groupings; and multiple pathways leading to social monogamy and mating exclusivity. For each topic, I describe results or methods that may be of interest, while a more comprehensive presentation of the data is provided in the tables and Appendix.

The last column of the Appendix summarizes how new data modify our understanding of monogamy in mammals (see also Table 14.1). Data are available for 29 species not included in previous reviews, including 17 primate species. Of these, 22 have a predominantly monogamous social system, 5 are polygynous, 1 is polyandrous, and 1 (*Microtus ochrogaster*) shows variation at the subspecific level. In 12 cases, recent investigations have confirmed the social system of species already considered monogamous. The Milne-Edward's potto (*Perodicticus potto edwardsi*) is shown to live in (dispersed) pairs. On the other hand, new data do not support a strictly monogamous social system in the common marmoset (*Callithrix jacchus*), the mongoose lemur (*Eulemur mongoz*), and the Mentawai leaf monkey (*Presbytis potenziani*); multi-male groups are also reported in the siamang (*Symphalangus syndactylus*), the silvery gibbon (*Hylobates moloch*), and the white-handed gibbon (*H. lar*). Sixteen of the monogamous species from which data are newly available are small and nocturnal, and fourteen are arboreal. New information on monogamous prosimians also reveals that the *dispersed pairs* described in some species, e.g., the spectral tarsier (*Tarsius spectrum*), maintain closer spatial proximity than previously thought. These data redress the dearth of information on hard-to-study taxa, and are thus valuable for the development and testing of hypotheses on the evolution of mating systems in mammals.

Definition of Monogamy

The words *monogamous* and *pair-bonded* are widely used in the literature, yet the lack of agreement on a definition has generated misunderstanding and ambiguity. Wittenberger and Tilson (1980: 198) define a monogamous mating system as "a prolonged association and essentially exclusive mating relationship between one male and one female" (see also Komers and Brotherton 1997; Kappeler and van Schaik 2002). Several terms have been offered to better identify the specific characteristics of "monogamous groups" (Fuentes 1999; Fuentes 2000; Sommer and Reichard 2000; Kappeler and van Schaik 2002). Data presented in this review reveal that EPPs are widespread across purportedly monogamous species, and that in many species there is a high degree of individual behavioral plasticity. An overly strict definition of monogamy, therefore, while correct from a formal point of view, presents the same practical inconveniences that it was meant to solve: restricting the term *monogamous* (or *pair-bonded*) to lifelong genetically exclusive relationships rules out the great majority of species. Moreover, alternative terms such as *primarily two-adult group* (Fuentes 1999) do not remove subjectivity, since the point of the matter is

Table 14.1 Summary of the new data on monogamous mammals presented in this review

Order/Family/ Species	Monogamous	Evidence for or against monogamy	Number of Study Groups (Grouping Pattern)†	Hypothesized Evolutionary Cause	Hypothesized Proximate Cause	Methods	Ref.
MARSUPIALIA							
Pseudocheiridae							
Petropseudes dahli	y		16 (15 FM; 1 FFM)	Paternal care? Inability of M to guard more than one F		O,T	38
Macropodidae							
Petrogale assimilis	y		131 individuals		IS aggression, F aggression of extragroup Ms	O,T,G	47
RODENTIA							
Muridae							
Hypogeomys antimena	y	For: genetics	157 individuals	?		O,T,G	44
Mus spicilegus	y?	For: F sexual preference; paternal care. Against: spatial association	25 (6 FM; 9 F; 4 FF; 2 M; 2 FFM; 1 FFF); 1 FFFM (spatial association)	Paternal care?	IS aggression	CO,CX, G,O	3,11,15, 30,31
Apodemus argentous	n	Against: no home-range overlap, polygynous mating	64 individuals (no FM groups)			MR,G	27
Microtus ochrogaster	y‡	For: optimal group composition is FM (captive experiment, [19]). Against: optimal group composition is FMM (in the wild, [23]); lack of F preference for social partner	639 (solitary: 30%; FM: 47%; 3 individuals: 10%; >3 individuals:13%) [23]	Predation risk	Mate guarding; IS aggression	O,CO, CX	12,19, 23,52

Table 14.1 (continued)

Order/Family/ Species	Monogamous	Evidence for or against monogamy	Number of Study Groups (Grouping Pattern)†	Hypothesized Evolutionary Cause	Hypothesized Proximate Cause	Methods	Ref.
Cricetidae							
Peromyscus californicus	y	For: genetics; paternal care		Paternal care		O,G,CX	16,35,36
Peromyscus polionotus	y	For: genetics	(FM: 50.5%; F + I: 13.4%; single adults: 25.2%; M + I: 1.2%; other: 9.7%)	Paternal care?		O,G	10,36
Sciuridae							
Marmota marmota	y?	For: social partner sired 80% of the offspring	35			O,MR,G	14
Castoridae							
Castor fiber	y	For: no division of labor [41]. Against: marked division of labor [2]	6 (6 FM)	Paternal care		O,T	2,44
Castor canadensis	y	For: sexual monomorphism, limited territory overlap, stable "family groups"	22 (22 FM)	paternal care	Genetic kin recognition? Predation risk	O,MR	48
PRIMATES							
Loridae							
Perodicticus potto edwardsi	y	For: home-range overlap; spatial association; sleeping in proximity; small testes size	10 individuals (8 in FM dispersed pairs; 2 solitary)			O,T	32
Nycticebus coucang	y	For: group composition; small testes	4 (4 FM, dispersed)	Need for allogrooming? Exchange of information on food sources?		O,T	50

Table 14.1 (continued)

Order/Family/ Species	Monogamous	Evidence for or against monogamy	Number of Study Groups (Grouping Pattern)†	Hypothesized Evolutionary Cause	Hypothesized Proximate Cause	Methods	Ref.
Megaladapidae							
Lepilemur edwardsi	y	For: (some) stable FM sleeping associations	8 (4 FM, sleeping association)	Defense of limited sleeping sites		O,T	34
Lepilemur ruficaudatus	y	For: home-range overlap; no sexual size dimorphism. Against: canine size dimorphism	6 (4 FM; 2 FFM)	Resource distribution? Infanticide prevention?	M mate guarding?	O,T	53
Lemuridae							
Hapalemur griseus alaotrensis	n	Against: genetics	22 (42.3% FM; 11.5% FMM; 19.2% FFM; 26.9% multi F-multi M)			O,MR,G	26
Hapalemur aureus	y	For: group composition	2 (2 FM)			O	49
Eulemur mongoz	y	For: (two-adult) group composition stable over time	2 (2 FM)			O	4
Eulemur rubriventer	y	For: paternal care	1 (1 FM)	Paternal care		O	29
Varecia variegata	n	For: core group composition, reproduction by multiple females, polyandrous and polygynous mating	1 community (fission-fusion with FM and FFM core groups)			O	24
Varecia rubra	n	Against: core group composition, reproduction by multiple females	1 community (fission-fusion with FM and FFM core groups)			O	51

Table 14.1 (continued)

Order/Family/ Species	Monogamous	Evidence for or against monogamy	Number of Study Groups (Grouping Pattern)†	Hypothesized Evolutionary Cause	Hypothesized Proximate Cause	Methods	Ref.
Cheirogaleidae							
Cheirogaleus medius	y (social, not genetic)	For: sleeping in contact, shared babysitting. Against: genetics	9 (8 FM; 1 FFM)	Paternal care?		O,MR,G	8,9
Phaner furcifer	y	For: home-range overlap; group composition; territoriality. Against: genetics	8 (8 FM)	Strong IS and ES feeding competition	Mate guarding?	O,T,G	40,41,42,43
Tarsiidae							
Tarsius spectrum	y	For: home-range overlap	3 (3 FM)	Predation risk		O,T	17,18
Callitrichidae							
Callithrix jacchus	n	Against: group composition; genetics	3 (1 FFM; 2 FFM)			O,MR,G	5,25
Cebidae							
Aotus sp.	y	For: strong infant-putative father bond		Paternal care (as mating effort?)	IS competition	O,T	6
Cercopithecidae							
Presbytis potenziani	n	Against: group composition	12 (5 FM; 3 FFM; 1 FMM; 3 FFMM)			O	39
Hylobatidae							
Hylobates muelleri	y	For: genetics	3 (3 FM)			G	28
Symphalangus syndactylus	y?	For: paternal care. Against: group composition	5 (1 FM; 4 FMM)	paternal investment?		O	22
ARTIODACTYLA							
Bovidae							
Madoqua kirkii	y	For: genetics; no EPC	11 (11 FM)		M mate guarding	O,T,G	1

Table 14.1 (continued)

Order/Family/ Species	Monogamous	Evidence for or against monogamy	Number of Study Groups (Grouping Pattern)†	Hypothesized Evolutionary Cause	Hypothesized Proximate Cause	Methods	Ref.
Capricornis crispus	y?	For: home-range overlap. Against: no pair-bonding behavior, sexual interactions with non-mates	159 individuals§	energetically too costly for M to defend an additional F	strict IS territoriality	O	20,21
CARNIVORA							
Canidae							
Vulpes macrotis mutica	y	For: adults in "two-individual groups" are not genetically related	12 (10 FM; 1 FFM; 1 FMM)			O,T	33
Lycaon pictus	y	For: genetics	9 (communal)	high F IS competition for resources	F competition, F infanticide	O,G	13
Canis simensis	n	Against: high extra-group copulation rate	9 (communal)			O,T	45

†Some studies do not provide data on sample size or grouping pattern.

‡Intraspecific variation, Kansas vs Illinois populations (Roberts et al. 1998).

§Solitary: 79.3%; 2 individuals ("usually mothers with a kid or adult FM pairs"): 17.6%; 3 individuals ("usually pairs with a kid"): 3%; 4 individuals: 0.1% (spatial association) (Kishimoto and Kawamichi 1996).

References: 1. Brotherton et al. 1997; 2. Buech 1995; 3. Carter and Getz, 1993; 4. Curtis and Zaramody 1998; 5. Digby 1999; 6. Fernandez-Duque et al. 2008; 7. Fernandez-Duque et al. 2000; 8. Fietz 1999; 9. Fietz et al. 2000; 10. Foltz 1981; 11. Garza et al. 1997; 12. Getz et al. 2003; 13. Girman et al. 1997; 14. Goossens et al. 1998; 15. Gouat et al. 2003; 16. Gubernick and Teferi 2000; 17. Gursky 2002; 18. Gursky 2005; 19. Hodges et al. 2002; 20. Kishimoto 2003; 21. Kishimoto and Kawamichi 1996; 22. Lappan 2005; 23. McGuire et al. 2002; 24. Morland 1993; 25. Nievergelt et al. 2000; 26. Nievergelt et al. 2002; 27. Ohnishi et al. 2000; 28. Oka and Takenaka 2001; 29. Overdorff 1996; 30. Patris and Baudoin 1998; 31. Patris and Baudoin 2000; 32. Pimley et al. 2005; 33. Ralls et al. 2001; 34. Rasoloharijaona et al. 2003; 35. Ribble 1991; 36. Ribble 2003; 37. Roberts et al. 1998; 38. Runcie 2000; 39. Sangchantr 2004; 40. Schülke 2003; 41. Schülke 2005; 42. Schülke and Kappeler, 2003; 43. Schülke et al. 2004; 44. Sharpe and Rosell 2003; 45. Sillero-Zubiri et al. 1996; 46. Sommer and Tichy 1999; 47. Spencer et al. 1998; 48. Sun 2003; 49. Tan 1999; 50. Vasey 2006; 51. Wiens and Zitzmann 2003; 52. Wolff et al. 2002; 53. Zinner et al. 2003.

This table only includes data from the listed studies. Previous studies may provide additional information (Kleiman 1977; Rutberg 1983; Komers and Brotherton 1997; Fuentes 1999; Fuentes 2000). Abbreviations: CO: Captive Observations; CX: Captive Experiment; ES: Intersexual; F: Female; G: Genetic; I: Infant; IS: Intrasexual; M: Male; MR: Capture Mark and Release; n: No; O: Field Observation; T: Radio-tracking; y: Yes; y?: Data within the study or from different studies are conflicting.

how much flexibility, if any, is allowed, when we are considering how often extrapair individuals co-reside in the group or are involved in sexual interactions. Tolerating sporadic EPCs in a monogamous mating system seems more practical than conforming to an excessively stringent definition that applies to very few mammal (or bird) species. In any case, a basic distinction that should always be made explicit is that between social monogamy (or a monogamous social system: an adult male and female sharing a territory), genetic monogamy (an adult male and female sharing parentage of all offspring), and sexual monogamy (or a monogamous mating system: an adult male and female mating exclusively) (Kappeler and van Schaik 2002).

Incidence of EPC and EPP

Observational and genetic evidence demonstrate that the great majority of mammals described as monogamous engage in some level of extrapair mating (Tables 14.1 and 14.2). In fact, only three of the reviewed studies report results consistent with pure reproductive monogamy, and in these cases the data are still inadequate to support firm conclusions. Sommer and Tichy (1999) caution about the low polymorphism in the locus they examined, and Brotherton et al. (1997) and Oka and Takenaka (2001) determined paternity of only twelve and five juveniles, respectively, from a single population.

While there are a number of methodological barriers that must be overcome to allow parentage and relatedness analyses in some taxa, in the absence of genetic information few reliable conclusions can be drawn regarding the actual mating or reproductive patterns of a population, or the relationship between relatedness and social structure. These conclusions directly relate to a shift in our knowledge of gibbon mating systems: initial observations suggested strict monogamy, while subsequent long-term studies allowed the detection of EPCs (Palombit 1994b; Reichard 1995). Parentage analyses are badly needed in this taxon, to correctly quantify the impact of these EPCs on individual reproductive success and to understand the factors determining the observed mating patterns (see below). Extrapair mating provides males with the obvious advantage of increased potential reproductive success (though associated costs require careful study), whereas the benefits for females are at the center of a lively discussion. Studies of other taxa may suggest some of the potential factors affecting female (and male) strategies.

Females may benefit from EPCs if the EPCs result in improved offspring genetic quality. In a population of Allied rock-wallabies (*Petrogale assimilis*), faithful females had higher reproductive success than those who only had young fathered by extrapair males, but females adopting a mixed strategy had the highest success (Spencer et al. 1998). Because of intense female–female competition, females may benefit from EPCs with genetically superior males they failed to acquire as stable pair-bonded mates (H.D. Marsh, pers. comm.).

Table 14.2 Summary of new molecular data on monogamous mammals

Order/Family/ Species	% of offspring fathered by social partner (sample size)†	Method	Ref.
MARSUPIALIA			
Pseudocheiridae			
Petrogale assimilis	66.0 (63)	5 microsats	15
RODENTIA			
Muridae			
Hypogeomys antimena	100.0 (39)	1 MHC locus	14
Mus spicilegus	inconclusive in relation to monogamy (167)	4 autosomal, 4 X-linked microsats	4
Apodemus argenteus	no stable social partner (6)	5 microsats	10
Cricetidae			
Peromyscus californicus	100.0 (82)	DNA minisatellites	12
Peromyscus polionotus	98.0 (147)	5 proteins	3
Sciuridae			
Marmota marmota	80.6 (134)	6 microsats	6
PRIMATES			
Lemuridae			
Hapalemur griseus alaotrensis	91.5 (56)‡	10 microsats, mtDNA	9
Cheirogaleidae			
Phaner furcifer	42.9 (7)	6 microsats	13
Cheirogaleus medius	56 (16)	7 microsats	2
Callitrichidae			
Callithrix jacchus	81.8 (11)	11 microsats	8
Saguinus mystax	92.9 (28)	12 microsats	7
Hylobatidae			
Hylobates muelleri	100 (5)	16 microsats	11
ARTIODACTYLA			
Bovidae			
Madoqua kirkii	100 (12)	7 microsats	1
CARNIVORA			
Canidae			
Lycaon pictus	90 for M (29 offspring), 92 for F (51 offspring)	14 microsats, mtDNA	5

† Except when noted, the sample size indicates individuals (either offspring, infants, or juveniles).
‡ Only 60% of males were in monogamous group, the others in polygynous or polyandrous groups.
MHC = Major Histocompatibility Complex; mt = Mitochondrial.
References: 1. Brotherton et al. 1997; 2. Fietz et al. 2000; 3. Foltz 1981; 4. Garza et al. 1997; 5. Girman et al. 1997; 6. Goossens et al. 1998; 7. Huck et al. 2005a; 8. Nievergelt et al. 2000; 9. Nievergelt et al. 2002; 10. Ohnishi et al. 2000; 11. Oka and Takenaka 2001; 12. Ribble 1991; 13. Schülke et al. 2004; 14. Sommer and Tichy 1999; 15. Spencer et al. 1998.

In this way, they accrue the practical advantages conferred by being pair-bonded, e.g., help with territory defense and predator detection, but may gain genetic advantages as well. This mixed female mating strategy has also been described in several bird species (e.g., Gray 1997).

A parentage analysis of wild fat-tailed dwarf lemurs (*Cheirogaleus medius*) revealed that 44% ($N = 16$) of infants were sired by a male other than the mother's social partner at the time of conception (Fietz et al. 2000). In all cases, the sire was a nearby territory owner. *Floaters*, i.e., males not defending a stable territory, are thought to be of lower quality (they have smaller testes and regularly lose aggressive interactions); thus, the preference of non-monogamous females for territory-holders suggests they are seeking good genes. The high proportion of EPP is surprising, given the apparently obligate paternal care suggested to promote pair-bonding in this species (Fietz 1999). Males have been observed investing in litters containing extrapair young; therefore, it is possible that these males are incapable of detecting relatedness, or may gain inclusive fitness benefits from raising the offspring of related individuals (Fietz et al. 2000). Similarly, 55% of captive female prairie voles (*Microtus ochrogaster*) copulated polyandrously when presented with the opportunity to do so (Wolff et al. 2002). Social preference (time spent near a stimulus male) was found to be a good predictor of sexual preference (number of copulations with that male). One evolutionary advantage of polyandrous mating in this species could be paternity confusion, since infanticide has been observed in the wild (Mahady and Wolf 2002). In Wolff et al. (2002) study, however, litters of females who deserted their previous mate and re-paired were not harmed by the new partner.

African wild dogs (*Lycaon pictus*) are a highly social species, in which a dominant pair is thought to found and reproduce within a pack. In a recent genetic study, paternity could not be attributed to the alpha male for 10% (3 out of 29) of the pups analyzed (Girman et al. 1997). In one of two cases of documented EPP for which actual paternity could be determined, paternity was attributed to a resident brother of the dominant male. Eight percent (4 out of 51) of pups were not the offspring of the alpha female. While it is possible that dominants are unable to detect or prevent EPP, indirect reproductive benefits could also justify tolerance by the dominant male of a few fertilizations by closely related subordinates, and may underlie the communal rearing by the subdominants.

Inbreeding avoidance has been suggested to explain high rates of EPP under certain conditions. One example is the extreme scarcity of dispersal opportunities among the social groups of Ethiopian wolves (*Canis simensis*). Seventy percent of female copulations involved extragroup males, and genetic data suggest high rates of EPP (Sillero-Zubiri et al. 1996). Within packs, females mated only with the alpha male, while they accepted lower-ranking outside males for extragroup copulations. Sillero-Zubiri et al. (1996) speculate, on the basis of their results and studies on African wild dogs (Reich 1981) and gray wolves (*Canis lupus*) (Packard et al. 1985), that the risk of inbreeding could be widespread in canids, and that extragroup mating could be a common, albeit rarely documented, behavioral response to it, leading to the conclusion "that the monogamy supposedly fundamental to the family may be more sociological than genetic" (Sillero-Zubiri et al. 1996: 331). Inbreeding avoidance seems to promote extragroup copulation in the Alaotran gentle lemur (*Hapalemur* *griseus alaotrensis*) as well: of the five cases of extragroup paternity documented in a study of 22 groups ($N = 59$), three involved maturing female offspring in the group, i.e., a likely daughter or sister of the resident reproducing male (Nievergelt et al. 2002).

Other factors playing a role in determining the frequency and extent of EPPs in birds and mammals are breeding density, genetic variation in the population, the intensity of sexual conflict, the need for helpers at the nest, the costs of mate loss, and direct benefits such as access to additional foraging areas, increased protection from predators, or knowledge of potential new mates (Petrie and Kempenaers 1998).

Proximate Mechanisms Maintaining Monogamy

Intrasexual aggression and mate guarding are often indicated as important proximate factors maintaining monogamous social organization (Table 14.1). Evidence for intrasexual aggression within both sexes is suggested for Allied rock-wallabies (*Petrogale assimilis*: Spencer et al. 1998), prairie voles (*Microtus ochrogaster*: Hodges et al. 2002), red-tailed sportive lemurs (*Lepilemur ruficaudatus*: Zinner et al. 2003), Japanese serows (*Capricornis crispus*: Kishimoto and Kawamichi 1996), mound building mice (*Mus spicilegus*: Gouat et al. 2003), douroucoulis (*Aotus spp.*: Fernandez-Duque 2007; Fernandez-Duque et al. 2008), and, only among males, in the slow loris (*Nycticebus coucang*: Wiens and Zitzmann 2003). Male Kirk's dik-diks (*Madoqua kirkii*) display mate-guarding behaviors such as overmarking females' scent, aggressively keeping them inside the defended territory, and increasing proximity during estrus (Brotherton et al. 1997). The sexual harassment received by females from both their partners and extrapair males during the few contended copulations observed suggests that females may abstain from seeking EPCs to avoid such harassment (Brotherton et al. 1997). In the fork-marked lemur (*Phaner furcifer*), an increase in intrapair agonistic interactions during the mating season seems to suggest mate guarding, although this is contradicted by the absence of sexual size or canine dimorphism (females are slightly larger than males) and female dominance over males (Schülke et al. 2004). Within nine communal breeding African wild dog (*Lycaon pictus*) packs, subordinate females rarely reproduced, and when they did, all of their pups died within 6 months (Girman et al. 1997). The cause of death was usually unknown, but the alpha female was observed killing some of the subordinate females' pups, in a pattern resembling that of callitrichids (see Digby 2000). This is interpreted as indicating strong competition between females for resources, and the ability of the dominant female to thwart subordinate reproduction.

The affiliative behaviors typical of pair-bonded dusky titi monkeys (*Callicebus moloch*) were studied by experimental manipulation of social context: captive mated pairs had significantly stronger reactions to the presence of other adults than did unfamiliar pairs and differed in the quality of their affiliative interactions (Fernandez-Duque et al. 2000). Moreover, male responses were substantially stronger than those of females, and this difference was more pronounced in mated pairs than unfamiliar pairs. The authors argue that this sex difference is functionally related to male mate guarding and cuckoldry prevention. In an experimental test of partner preference in the mound-building mouse (*Mus spicilegus*), estrous females spent significantly more time with the male with which they were paired than with an unfamiliar male (Patris and Baudoin 1998). On the other hand, female *M. musculus domesticus*, a closely related polygynous species, significantly favored unfamiliar mates (the difference between the species was also significant). The authors suggest that the sexual preference showed in these experiments indicates the presence of a pair-bond in *M. spicilegus*. The sexual preference for the familiar mate is thought to increase paternity certainty and secure male parental contribution (Patris and Baudoin 1998). Since this female sexual preference was not complete, however, questions remain about the factors influencing female choice in this species.

Several fish studies revealed the ability to recognize kin through olfactory cues (Moore et al. 1994; Neff and Sherman 2003). This mechanism would allow a male to detect possible extrapair offspring and withhold his parental contribution, and may thus promote mate fidelity. Recent data suggest that such mechanism could function in North American beaver males (*Castor canadensis*), through a genetically controlled kinship pheromone contained in anal gland secretions (Sun 2003). This is an exciting avenue for future research, because at present there are only a few confirmed mechanisms of genetic kin recognition in mammals, and because of the potential for further exploration of the relationship between certainty of paternity and social systems.

Studies of territorial behavior in gibbons have suggested an important role of intrasexual aggression in both sexes for the maintenance of monogamous mating (Mitani 1984; Raemaekers and Raemaekers 1985), and preliminary data suggest that male white-handed gibbons (*Hylobates lar*) guard their mates (Morino, Barelli and Reichard unpubl. data). Duets have also been interpreted in this context (Mitani 1985; Raemaekers and Raemaekers 1985; Mitani 1987) although other functions, such as advertising a pair-bond's strength, have been proposed as well (Cowlishaw 1992; Geissmann 1999; Geissmann and Orgeldinger 2000).

Ultimate Causation

Although it is beyond the scope of this chapter to address the theoretical debate surrounding the evolution of the monogamous mating system, I will review here some recent data relevant to this issue. The possible evolutionary causes of monogamy have been reviewed in more detail by Komers and Brotherton

(1997) for mammals in general, and for primates specifically by Rutberg (1983), van Schaik and Dunbar (1990), Palombit (1999), Kappeler and van Schaik (2002), and van Schaik and Kappeler (2003).

Paternal Care

Table 14.1 lists hypothesized evolutionary factors promoting monogamy, that have been proposed in the past 15 years. Eleven out of the eighteen studies that address this issue emphasize the importance of male parental care for infant survival (Table 14.3).

An analysis of the time spent covering the young (thermal protection) and in pup retrieval behavior (after artificial displacement) revealed that males of the monogamous *Mus spicilegus* invested significantly more time in these activities than males of the polygynous *M. m. domesticus* (Patris and Baudoin 2000). Male contributions to allogrooming, babysitting, and antipredator protection are also thought to have affected the evolution of monogamy in the rock-haunting possum, *Petropseudes dahli* (Runcie 2000). Similarly, douroucouli (*Aotus* spp.) males are heavily involved in the care of offspring, taking over the task of carrying the infant after the first two weeks of its life. The bond between an infant and its putative father is so strong that in some instances juveniles stayed with their fathers after their mother was evicted (Rotundo et al. 2005). Nonetheless, the evolutionary reasons underlying monogamy and male parental care in douroucoulis are still unexplained, and the benefits to the infant or mother have not yet been quantified. A possibility is that pronounced paternal care functions as mating effort, since male owl monkeys have been observed to care for infants they are unlikely to have sired (Fernandez-Duque et al. 2008). Obligate monogamy (*sensu* Kleiman 1977) is hypothesized in the other typically monogamous New World primate genus, *Callicebus*, and the absolute requirement for male care is clearly a factor affecting the variable mating and grouping patterns in the callitrichids. Fietz (1999) showed that fat-tailed dwarf lemurs (*Cheirogaleus medius*) sleep mostly in heterosexual pairs and share babysitting tasks (warming the offspring and guarding it from predators). She argued that babysitting is the main driving force leading to monogamy, since in the two observed cases of male desertion, the offspring died after only 2 days. The fast developmental rate of rufous lemur (*Eulemur fulvus rufus*) infants (compared to closely related, group-living species such as the red-bellied lemur *Eulemur rubriventer*) is thought to generate a need for additional parental care, thus promoting social monogamy in this species (Overdorff 1996). In fact, males held and carried their putative offspring in two groups of rufous lemurs (Overdorff 1996). Any form of direct paternal care, however, is excluded in the cases of the Allied rock-wallaby (*Petrogale assimilis*), dik-dik (*Madoqua kirkii*), and Malagasy giant jumping rat (*Hypogeomys antimena*). Recent studies have emphasized the importance of male parental care in some monogamous

Table 14.3 Summary of new data on paternal care in monogamous mammals

Order/Family/ Species	Paternal care	Protection from: predators infanticide	Food provisioning	Carrying	Grooming/ Socializing	Retrieval	Thermal protection	Shelter building	Ref.
MARSUPIALIA									
Pseudocheiridae									
Petropseudes dahli	y	y	y	y	y				12
Macropodidae									
Petrogale assimilis	n								16
RODENTIA									
Muridae									
Hypogeomys antimena	n								15
Mus spicilegus	y					y	y		9
Cricetidae									
Peromyscus californicus	y						y		11
Peromyscus polionotus	y							y	11
Castoridae									
Castor fiber	y		y					y	14
PRIMATES									
Lorisidae									
Perodicticus potto edwardsi	n								10
Nycticebus coucang	n								17
Lemuridae									
Eulemur rubriventer	y			y					8

Table 14.3 (continued)

Order/Family/ Species	Paternal care	Protection from: predators infanticide	Food provisioning	Carrying	Grooming/ Socializing	Retrieval	Thermal protection	Shelter building	Ref.
Cheirogaleidae									
Phaner furcifer	n								13
Cheirogaleus medius	y						y		3
Cebidae									
Aotus sp.	y			y	y				2
Hylobatidae									
Symphalangus syndactylus	y			y	y				7
ARTIODACTYLA									
Bovidae									
Madoqua kirkii	n								1
Capricornis crispus	n								6

n: No; y: Yes.

References: 1. Brotherton et al. 1997; 2. Fernandez-Duque et al. 2008; 3. Fietz 1999; 4. Gursky 2002; 5. Gursky 2005; 6. Kishimoto and Kawamichi 1996; 7. Lappan 2005; 8. Overdorff 1996; 9. Patris and Baudoin 2000; 10. Pimley et al. 2005; 11. Ribble 2003; 12. Runcie 2000; 13. Schülke and Kappeler 2003; 14. Sharpe and Rosell 2003; 15. Sommer and Tichy 1999; 16. Spencer et al. 1998; 17. Wiens and Zitzmann 2003; 18. Zinner et al. 2003.

mammal species. In the two monogamous species of *Peromyscus*, male contributions seem to be necessary for successful breeding (Ribble 2003). Gubernick and Teferi (2000) experimentally demonstrated that the presence of the father has a substantial positive effect on offspring survivorship (81% of offspring survived in the father-present condition versus 26% in the father-absent condition) in wild California mice (*P. californicus*). The thermal contribution of *P. californicus* males is a direct, depreciable commodity (*sensu* Kleiman and Malcolm 1981), since it cannot be allocated simultaneously to multiple litters. This constraint should favor a monogamous social system. *P. polionotus* fathers, on the other hand, help in digging and maintaining the extensive burrows typical of this species (Ribble 2003).

In their phylogenetic analysis, Komers and Brotherton (1997) concluded that paternal care is not a fundamental force leading to monogamous systems in mammals. It is possible, however, that inclusion of information from these recent studies might alter the results of their analysis.

Among the hylobatids, most species do not display biparental care, but male siamangs (*Symphalangus syndactylus*) carry infants for a considerable (and variable) amount of time (Chivers 1974; Gittins and Raemaekers 1980; Palombit 1996). Lappan (this volume) suggests that male siamang paternal contribution may not have a positive impact on the offspring, but rather benefits the female by reducing her energetic costs of reproduction. Given the rarity of direct paternal care in most gibbon taxa, male care is unlikely to have been an important factor promoting monogamy in this family, although the importance of other male services, such as territorial defense, predator defense, and defense from hostile conspecifics, should be given careful consideration (Lappan this volume; Reichard this volume).

Ecology

The distribution of resources strongly affects grouping patterns, and is invoked to explain monogamous social structure for several mammals. The strepsirhine species *Avahi occidentalis* and *Lepilemur edwardsi* are both described as being monogamous, but the former lives in family groups, while the latter is usually observed alone during the active period (but sleeps in pairs, see Rasoloharijaona et al. 2003). A comparison of the food resources used by *Avahi* and *Lepilemur* suggests that *Avahi* may have a more specialized diet, and so group living is advantageous for the defense of rare, larger, and high-quality food sources (Thalmann 2001; Thalmann 2002). *Lepilemur*, on the other hand, seems to be less specialized; males may not be under the same ecological constraint as *Avahi* males, so the reason for their monogamous social organization must be sought elsewhere. The monogamous social systems of the rock-haunting possum, *Petropseudes dahli* (Runcie 2000), and the serow, *Capricornis crispus* (Kishimoto and Kawamichi 1996), are thought to be determined by the inability of a male to guard more than one female. Similarly, ecological constraints may shape the behavior of the North American beaver: the mating season is in winter, which limits males' search for potential mates, since beavers need lodges for warmth and protection against predators and traveling in unknown areas is potentially dangerous (Sun 2003). Wiens and Zitzmann (2003) describe the social system of the slow loris (*Nycticebus coucang*) as monogamous, on the basis of data on ranging, sleeping, social interactions, dispersal, and morphometrics. Individuals, however, spent only 8% of the time within 20 m of conspecifics and slept alone on 79% of days. Discussing the evolution of this social system, the authors reject most common advantages of group living (predator defense, joint defense of food resources, alloparenting), suggesting instead that alternative factors such as the need for allogrooming and transfer of information on rapidly depletable resources may underlie this social system. Resource availability and population density also affect the grouping pattern of prairie voles (*Microtus ochrogaster*), mound-building mice (*Mus spicilegus*), and prairie dogs (*Cynomys gunnisoni*), as will be discussed in the next section.

Rasoloharijaona et al. (2003) found dispersed but stable (lasting up to 4 years) sleeping-site-related associations between male and female Milne-Edwards sportive lemurs (*Lepilemur edwardsi*). Sleeping sites are thought to be the important and limited resources that are defended by socially monogamous pairs (although there was no direct observation of territorial behavior in this study). An analysis of the possible evolutionary explanation for pair-living in the fork-marked lemur (*Phaner furcifer*) found no support for protection from predators or infanticidal males, need for paternal care, male coercion of females, or male defense of valuable resources (Schülke 2005). Instead, Schülke (2005) proposes that females compete among themselves for resources, and defend territories from other females. Males are tolerated in their territories to keep out other males, although they are competitors for valuable food resources. According to this scenario, both males and females would benefit if one male was able to defend a territory encompassing those of two females, but this only rarely occurs because males are limited by strong competition with their (dominant) mates for access to quickly depleted food sources: a male needs knowledge of the female's movements to avoid her in his foraging itinerary.

The effect of ecological factors on gibbon social systems is still unclear: previous arguments suggest that feeding competition forces females to defend exclusive territories, and that males are not able to defend a territory large enough to encompass those of more than one female (Wrangham 1980; Mitani 1984). Nonetheless, on the basis of Mitani and Rodman's (1979) defendability index, as well as data on day range length, home range size, and the expected frequency of encounters with cycling females, gibbon males should be able to defend much larger territories (van Schaik and Dunbar 1990; Reichard 2003; but see Bartlett this volume). Many additional parameters are likely to play an important role in shaping gibbon male reproductive tactics, and need to be quantified in future analyses.

Infanticide

Sexually selected infanticide has been hypothesized to serve as a powerful evolutionary force favoring monogamous grouping in some species (van Schaik and Dunbar 1990). Accordingly, infanticide has been observed in wild populations of prairie voles (Mahady and Wolf 2002), where it has been interpreted as a possible explanation for polyandrous, rather than monogamous, mating of the females in this species (Wolff et al. 2002, see above). Infanticide is unlikely to benefit *Cheirogaleus medius* males, since the infanticidal male would not be able to sire a new offspring before the onset of hibernation (Fietz 1999). Infanticide risk is also excluded in the Malagasy giant jumping rat, *Hypogeomys antimena* (Sommer and Tichy 1999), and the wild California mouse (Gubernick and Teferi 2000), in light of the tolerance shown by newly immigrated adult males toward unrelated immatures. Similarly, no evidence for an important role of infanticide was found in douroucoulis (Fernandez-Duque et al. 2008) or fork-marked lemurs (Schülke 2005). Sexually selected infanticide has been proposed instead as the primary evolutionary pressure underlying hylobatid social systems (van Schaik and Dunbar 1990). Palombit (1999), however, notes a number of features of gibbon societies that are inconsistent with this explanation, including the rarity of male floaters and the absence of sexual dimorphism in body or canine size. Good data by which the role of sexually selected infanticide in gibbons can be evaluated are still lacking.

Other Factors

Predation avoidance and intragroup aggression have been proposed as factors affecting social and mating systems of some monogamous mammal species. Studies of the relationship between grouping pattern and reproductive success in voles have produced contradictory results. In a wild population of prairie voles, the optimal group composition in terms of reproductive success (measured by infant survival) was two adult males and one adult female (McGuire et al. 2002). Predation risk was considered to be the main cost of smaller (single females or male-female pairs) or larger (communal, up to sixteen individuals – typically retained offspring) groups, since two adults need to leave the nest unattended when foraging, and too many individuals attract the attention of predators. Hodges et al. (2002), however, compared the reproductive success of captive social groups composed of one female and one male (1F:1 M), two females and one male (2F:1M), and one female and two males (1F:2M), and found the highest conception rates, litter sizes, and offspring survival in 1F:1 M groups. Female infanticide was only observed in 2F:1 M groups (in 35% of the litters), and these groups had the lowest infant survival. When two breeding males were present, litters could be sired by both males. Two females, on the other hand, never produced litters in the same group.

Spectral tarsiers (*Tarsius spectrum*) were generally thought to be solitary, in spite of the observation of individuals sleeping together during the day (MacKinnon and MacKinnon 1980). However, Gursky (2005) demonstrated that encounters between group members (i.e., individuals sleeping together) during their nocturnal activity are more frequent than would be expected if they were due to chance alone, and that proximity to other individuals causes a decrease in foraging efficiency. This disadvantage of gregariousness may be offset by antipredatory benefits (Gursky 2002). Similar data on home range overlap and social networks are reported for the Milne-Edward's potto, *Perodicticus potto edwardsi* (Pimley et al. 2005).

Social Structure and Mating Patterns

An important insight revealed by recent studies on gibbons is the remarkable flexibility in their grouping patterns. Most long-term studies have reported varying proportions of multifemale and multimale groups (Palombit 1994a; Brockelman et al. 1998; Lappan 2005; Reichard this volume). Enlarging the perspective to consider other mammals reveals patterns that could help direct future studies on hylobatids. In this section I review novel data on the social structure of monogamous species, and the factors that influence it.

Flexible Grouping and Mating

In the studies contained in this review, the most common deviation from largely monogamous social systems is one male–two female groups (Table 14.1). This is consistent with the prevalence of polygyny among mammals. Several surveys also report polygynous groupings in hylobatids, although the only non-monogamous groups that have been shown to be stable over time were polyandrous (Lappan 2005; Reichard this volume).

Once thought to be strictly monogamous, marmosets (*Callithrix* spp., *Cebuella pygmaea*) and tamarins (*Saguinus* spp., *Leontopithecus* spp.) have been shown to display remarkable flexibility in their mating systems (Goldizen 1987). In particular, Goldizen (1987) showed that in 33 group-years, no monogamous pair (without helpers) ever attempted a breeding cycle, that helpers (mainly infant carriers) suffered costs in terms of reduced feeding and resting, and that males living polyandrously with a female equitably split copulations with her and shared infant carrying equally. In fact, it is difficult to draw generalizations about association patterns even within callitrichid species, and many studies now focus on single populations. Digby (1999) and Nievergelt et al. (2000) collected behavioral and genetic data on three groups of wild common marmoset (*Callithrix jacchus*). While all groups contained two breeding females, one group had only one adult male, and the other two included several males, and mating behavior ranged from monogamous to polygynous. Within-group mating always involved only a single male, whereas 24 out of 101 mounts involved individuals from other social groups, and 65% of adults were involved at least once in an EPC (Digby 1999). Parentage data reveal that the dominant male sired 9 out of the 11 infants studied, and in many cases both adult females could not be excluded as mothers (Nievergelt et al. 2000). The authors therefore categorize mating in these groups as polygynmonandrous. On the other hand, a genetic study of six groups of moustached tamarins (*Saguinus mystax*) showed that in spite of extensive polyandrous mating, only 2 out of 28 infants were not sired by the main breeding male, and only one female bred in each group (Huck et al. 2005b).

A genetic analysis of 22 groups of wild Alaotran gentle lemur (*Hapalemur griseus alaotrensis*) revealed considerable variation in grouping and mating patterns (Nievergelt et al. 2002). All but one of the infants and juveniles ($N = 56$) resided in groups with at least one parent. Groups comprised two to nine individuals, with an even sex ratio and variable composition: 1M:1F (42%), 1M:2F (19%), 2M:2F (12%), and >2M:>2F (27%). When more than one male was present in the group, only one reproduced at a time. Sixty percent of groups contained only one breeding female (hence forming a monogamous unit) while the remaining 40% had two breeding females. Male reproductive success was doubled in two-breeding-female groups, while female reproductive output did not differ between one- and two-breeding-female groups.

In a long-term field study of the Japanese serow (*Capricornis crispus*), <20% of sightings ($N = 3259$) were of male–female dyads (Kishimoto and Kawamichi 1996). Nonetheless, male territories overlapped extensively with those of one or two females. Most males displayed dispersed social monogamy, whereas every year an average of 18.6% of the males appeared to be polygynous. These males had to defend much larger territories than monogamous ones, although as in dik-diks (Brotherton et al. 1997), the home ranges of females mating with a polygynous male tended to be smaller than the ranges of females mating with a monogamous male. Sexual behavior was observed in 57% of encounters with the social mate ($N = 170$) and 50% of those involving nonmates ($N = 8$). Although the number of extragroup interactions was relatively small, it suggests a lack of pair-bonding or affiliative behaviors in this species. Females did not seem to need a male to defend their territories, because even after the disappearance of their mates they were able to retain them. This suggests that males and females might be defending the home range for different purposes. Females living in polygynous groups had similar reproductive rates to monogamous females, thus suggesting a nearly twofold success for polygynous males (assuming no EPP). Polygynous groups, however, appeared to be less stable over time, rarely lasting more than one year (Kishimoto 2003: 156).

Dispersal has profound effects on population structure. Several theoretical papers have addressed this issue in primates (Sterck et al. 1997; Isbell 2004), proposing factors that lead individuals to leave their natal group, e.g., lack of appropriate mates, inbreeding avoidance, and intrasexual competition for resources or mates. Field data on dispersal are often difficult to obtain, especially in long-lived, fast-moving, unmarked animals. Although in most bird and mammal species at least one sex disperses from the natal territory, some monogamous species exhibit philopatry by both sexes and communal breeding. Two models have been put forth to explain the evolution of this pattern. The Habitat-Saturation Hypothesis (Emlen 1982) states that offspring retention is more common where resources are too scarce to support many breeding territories, which reduces the chances of successful dispersal. Conversely, the Benefit-of-Philopatry Hypothesis (Stacey and Ligon 1987) posits that philopatry is associated with high food habitats since in these conditions offspring can successfully reproduce in the natal territory. A 25-year field study on the monogamous prairie vole provides support for the Habitat-Saturation Hypothesis, although high levels of communal nesting were present in some populations in high resource territories (Getz et al. 2003). The authors suggest that the social organization and mating system of voles living in poor or rich habitats are the same, and they provide a proximate explanation for the observed pattern: in areas with a high density of individuals, male mate guarding is less effective, and females that would be reproductively suppressed by mate guarding are instead sexually activated in response to contact with unfamiliar males.

Similarly, Travis et al. (1995) found that prairie dogs (*Cynomys gunnisoni*) are monogamous at low or intermediate resource patchiness and densities below saturation. As patchiness increases, they shift their social system to polygynous or polyandrous groups at intermediate densities, and to multimale/multifemale groups at higher densities (thus supporting the Benefit-of-Philopatry model).

An analysis of the sociospatial distribution of wild mound-building mice revealed that while the two most common social units were single females (nine out of 25 recaptures) and male-female pairs (six recaptures), there were also several spatial associations involving two or more females (2F, 3F, 2F:1M, 3F:1M), but none with two males (Gouat et al. 2003). These findings, unlike the results of laboratory studies (Patris and Baudoin 1998, 2000, see above), suggest a territorial polygynous mating system. Gouat et al. (2003) suggest high density as a possible reason for multifemale grouping. Other possible advantages of communal nesting are improved thermoregulation and predator avoidance (Garza et al. 1997).

In some species, individuals appear to show considerable variation in their responses to similar conditions [e.g., *Callithrix jacchus* (Digby 1999; Nievergelt et al. 2000), *Hapalemur griseus* (Nievergelt et al. 2002), *Capricornis crispus* (Kishimoto and Kawamichi 1996)]; other species seem instead to respond to specific ecological or social stimuli in a stereotyped way [e.g., *M. spicilegus* (Gouat et al. 2003), *M. ochrogaster* (Roberts et al. 1998; Hodges et al. 2002; McGuire et al. 2002; Getz et al. 2003), *Cynomys gunnisoni* (Travis et al. 1995)]. Thus, it is important to explicitly investigate the nature of flexibility in the taxon under study. As the rodent data demonstrate, an increase in the sample of groups, populations, and species will allow the detection and evaluation of broader patterns, such as how habitat variability and richness and population density influence grouping patterns. Data on ecology and spatial distribution should therefore be collected keeping in mind this broader perspective. At present, the scarcity of long term studies on hylobatids limits comparative analyses. In the few species for which data are available from different sites, however, they suggest substantial variation in ecology and behavior. For example, three long-term studies on the siamang (*Symphalangus syndactylus*) from different sites report substantial differences in diets, social structure, and mating patterns (Chivers 1974; Palombit 1994a, 1996; Lappan 2005).

Relatedness Within Groups

To better understand the causal factors promoting monogamy, it is also useful to consider large groups containing several adults of both sexes, but where breeding by a single adult pair renders the system genetically monogamous. In some cases, the extra adults are older offspring of the original pair who did not disperse. In other cases, the extra adults might be related to either breeding individual, but not to all other individuals in the group. Several studies on group-living mammals support the prediction that breeding pairs are not close genetic relatives, whereas additional co-residing adults are offspring of one or both members of the pair (*Lycaon pictus*: Girman et al. 1997; *Marmota marmota*: Goossens et al. 1998; *Vulpes macrotis*: Ralls et al. 2001). Studies on primates with variable social structure reveal the same pattern. Nievergelt et al. (2002) reports that the additional (nonreproducing) males in groups of Alaotran gentle lemurs were genetically related (either brothers or sons) to the reproductive female. Similarly, in the two cases of multifemale grouping documented in red-tailed sportive lemurs (*Lepilemur ruficaudatus*), the extra females are thought to be mature offspring (Zinner et al. 2003). On the other hand, Lappan (2007) documents a high proportion of multimale groups of siamangs (four out of five study groups). In three of these groups, both males were observed copulating with the female, and mitochondrial DNA evidence confirmed that the males are not matrilineally related to each other or to the female, indicating true polyandry. The other published genetic analysis of a hylobatid species, the wild Bornean gibbon (*Hylobates muelleri*), assigned all immature individuals ($N = 5$) to their putative parents (Oka and Takenaka 2001). The authors, however, underline that two out of five subadults were found living in groups other than their natal group.

Broader Social Networks

Genetic data will also help to elucidate the broader, community-level social networks in which gibbons live, which may be similar to those of some canids.

Dispersing African wild dogs (*Lycaon pictus*) tend to establish territories near close relatives (Girman et al. 1997), and Ralls et al. (2001) described sharing of kit fox (*Vulpes macrotis*) dens by individuals who did not belong to the same social group but were genetically related, testifying to the maintenance of social relationships among related individuals after dispersal.

Many authors have underlined the enduring relationship between parents and offspring in several hylobatid species (e.g., Tenaza 1975; Tilson 1981; Brockelman et al. 1998), and suggested that individual strategies should be viewed in the context of the community (Palombit 1999; Bartlett 2003; Reichard 2003). Lappan (2007) provides preliminary genetic data on dispersal patterns in siamangs.

Future Directions

Additional data or novel approaches may shed light on a number of the remaining questions about hylobatid socioecology highlighted in this review. Data on relatedness among members of a social group (and on the mechanisms by which relatives are identified) will help researchers to understand and evaluate inbreeding avoidance, costs and benefits of tolerating additional adult or subadult individuals in the group, and patterns of interactions among group members. Male contributions to parental care should be quantified in terms of costs to the male (energy expenditure from which the female is released, risks in defending offspring from predators or infanticidal individuals), and benefits to the offspring or mother (e.g., Price 1992; Lappan in press).

Several ecological factors could potentially have a strong impact on male reproductive tactics and could be added to Mitani and Rodman's (1979) elegant analysis of territory defendability, including, for example, the ability to monitor a longer perimeter (Lowen and Dunbar 1994), the energetic costs and risks associated with larger territories, the number of neighboring groups and male floaters, the rate of aggressive encounters [which are costly in terms of time and energy, and potentially dangerous (Palombit 1993)], and the time devoted to each defended female. New data from different hylobatid populations could be used to develop a new model accounting for these factors, thus improving our estimate of the impact of ecological variables on gibbon social systems. Work on other taxa could also help to address the issue of whether resource-defense models are appropriate for analyses of mate-defense in gibbons (e.g., Davies and Lundberg 1984; Fashing 2001).

Many studies have focused on the coordination and strength of hylobatid pair-bonds (Carpenter 1940; Geissmann 1986; Leighton 1987; Fischer and Geissmann 1990; Palombit 1996; Geissmann and Orgeldinger 2000). Nonetheless, it would be fruitful to independently analyze male and female reproductive strategies, using a cost/benefit approach, since the activities of each sex may be determined and constrained by different forces (e.g., Kishimoto and Kawamichi 1996). An explicit comparison of male and female time budgets and ranging patterns (e.g., Sharpe and Rosell 2003) should now be feasible also for several gibbon populations. Future studies should consider this when planning their data collection. For many other species, however, even basic behavioral and ecological data are still badly needed, and it must be underlined that many of these species are critically endangered, and thus the highest priority should be placed on conserving the areas in which they live.

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Appendix

List of the mammalian species catalogued as monogamous by Kleiman (1977), Rutberg (1983), Komers and Brotherton (1997), and the present review. Species for which the initial evaluation has been revised on the basis of new data are indicated in the last column.

Order	Family	Species	KL (1977)	R (1983)	KB (1997)	LM (2007)	Impact of new data
MARSUPIALIA							
	Pseudocheiridae	*Petropseudes dahli*	–	–	–	M	N
	Macropodidae	*Petrogale assimilis*	–	–	–	M	N
	Phalangeridae	*Tarsipes spencerae*	M	–	–	–	–
INSECTIVORA							
	Solenodontidae	*Solenodon paradoxus*	M	–	–	–	–
	Tenrecidae	*Microgale talazaci*	M	–	–	–	–
	Macroscelididae	*Elephantulus rufescens*	M	–	–	–	–
		Rhynchocyon chrysopygus	M	–	–	–	–
	Soricidae	*Suncus etruscus*	M	–	–	–	–
RODENTIA							
	Cricetidae	*Ondatra zibethicus*	M	–	–	–	–
		Peromyscus californicus	M	–	–	M	C
		Peromyscus polionotus	M	–	–	M	C
		Peromyscus maniculatus	M	–	–	–	–
		Peromyscus eremicus	M	–	–	–	–
		Baiomys taylori	M	–	–	–	–
		Onychomys leucogaster	M	–	–	–	–
		Onychomys torridus	M	–	–	–	–
	Gliridae	*Graphiurus murinus*	M	–	–	–	–

(continued)

Order	Family	Species	KL (1977)	R (1983)	KB (1997)	LM (2007)	Impact of new data
	Muridae	*Hypogeomys antimena*	–	–	–	M	N
		Apodemus argenteus	–	–	–	P	N
		Microtus ochrogaster	–	–	–	M/P	N
		Microtus californicus	–	–	M	–	–
		Microtus montanus	–	–	M	–	–
		Notomys alexis	M	–	–	–	–
		Mus minutoides	M	–	–	–	–
		Mus spicilegus	–	–	–	M?	N
		Lemniscomys barbarus	M	–	–	–	–
		Grammomys dolichurus	M	–	–	–	–
		Myomyscus fumatus	M	–	–	–	–
		Thallomys paedulcus	M	–	–	–	–
		Mastacomys fuscus	M	–	–	–	–
	Sciuridae	*Marmota flaviventris*	–	–	–	P	N
		Marmota marmota	–	–	–	M	N
		Cynomys gunnisoni	–	–	–	M	N
	Castoridae	*Castor fiber*	M	–	–	M	C
		Castor canadensis	–	–	–	M	N
	Hystricidae	*Hystrix cristata*	M	–	–	–	–
		Atherurus africanus	M	–	–	–	–
	Capromyidae	*Capromys melanurus*	M	–	–	–	–
		Plagiodontia aedium	M	–	–	–	–
	Caviidae	*Dolichotis patagonum*	M	–	–	–	–
	Dasyproctidae	*Myoprocta pratti*	M	–	–	–	–
		Dasyprocta punctata	M	–	–	–	–
	Cuniculidae	*Cuniculus paca*	M	–	–	–	–
	Dinomyidae	*Dinomys branickii*	M	–	–	–	–
	Pedetidae	*Pedetes capensis*	M	–	–	–	–
LAGOMORPHA							
	Leporidae	*Caprolagus hispidus*	–	–	M	–	–
CHIROPTERA							
	Phyllostomatidae	*Vampyrum spectrum*	M	–	–	–	–
	Nycteridae	*Nycteris hispida*	M	–	–	–	–
		Nycteris arge	M	–	–	–	–
		Nycteris nana	M	–	–	–	–
	Emballonuridae	*Saccolaimus peli*	M	–	–	–	–
		Taphozous mauritianus	M	–	–	–	–
	Hipposideridae	*Hipposideros galeritus*	M	–	–	–	–
		Hipposideros beatus	M	–	–	–	–
	Rhinolophidae	*Rhinolophus luctus*	M	–	–	–	–
	Megadermatidae	*Lavia frons*	M	–	–	–	–
	Vespertilionidae	*Kerivoula* sp.	M	–	–	–	–
PRIMATES							
	Loridae	*Nyticebus coucang*	–	–	–	M	N

(continued)

Order	Family	Species	KL (1977)	R (1983)	KB (1997)	LM (2007)	Impact of new data
		Perodicticus potto	–	–	–	M	N
	Megaladapidae	*Lepilemur edwardsi*	–	–	–	M?	N
		Lepilemur ruficaudatus	–	–	–	M	N
	Lemuridae	*Hapalemur griseus*	–	–	–	M	N
		Hapalemur aureus	–	–	–	M	N
		Eulemur mongoz	–	M	–	M	C
		Eulemur fulvus rufus	–	–	–	M	N
		Varecia variegata	–	–	–	P	N
		Varecia rubra	–	–	–	P	N
	Cheirogaleidae	*Cheirogaleus medius*	–	–	–	M	N
		Phaner furcifer	–	M	–	M	C
	Indridae	*Indri indri*	M	M	–	–	–
		Avahi laniger	–	–	–	M	N
		Avahi occidentalis	–	–	–	M?	N
	Tarsiidae	*Tarsius spectrum*	–	–	M	–	–
		Tarsius bancanus	–	M	–	–	–
	Callitrichidae	*Cebuella pygmaea*	M	M	–	–	–
		Callithrix jacchus	M	M	–	M/P	R
		Saguinus oedipus	M	M	–	–	–
		Saguinus geoffroyi	M	M	–	–	–
		Saguinus mystax	M	M	–	–	–
		Saguinus fuscicollis	M	M	–	–	–
		Saguinus nigricollis	M	M	–	–	–
		Saguinus midas	M	M	–	–	–
		Saguinus imperator	M	M	–	–	–
		Leontopithecus rosalia	M	M	–	–	–
	Callimiconidae	*Callimico goeldii*	M	M	–	–	–
	Cebidae	*Aotus trivirgatus*	M	M	–	M	C
		Aotus azarai	–	–	–	M	N
		Aotus nigriceps	–	–	–	M	N
		Callicebus moloch	M	M	–	M	C
		Callicebus torquatus	M	M	–	M	N
		Pithecia pithecia	M	M	–	–	–
		Pithecia monachus	M	M	–	–	–
	Cercopithecidae	*Presbytis potenziani*	M	M	–	M/pa/MM	R
		Nasalis concolor	–	M	–	–	–
	Hylobatidae	*Hylobates lar*	M	M	–	M/Pa	R
		Hylobates muelleri	–	–	–	M	N
		Hylobates concolor	M	M	–	–	–
		Hylobates klossii	M	M	–	–	–
		Hylobates agilis	–	M	–	–	–
		Hylobates hoolock	–	M	–	–	–
		Hylobates pileatus	–	M	–	–	–
		Hylobates moloch	–	–	–	M/Pa	N
		Symphalangus syndactylus	M	M	–	M/Pa	R
MYSTICETI							
	Balaeniidae	*Balaena mysticetis*	M	–	–	–	–
ARTIODACTYLA							
	Bovidae	*Cephalophus maxwelli*	M	–	–	–	–
		Silvicapra grimmia	M	–	–	–	–
		Madoqua kirkii	M	–	–	M	C
		Oreotragus oreotragus	M	–	–	–	–

(continued)

Order	Family	Species	KL (1977)	R (1983)	KB (1997)	LM (2007)	Impact of new data
		Raphicerus campestris	M	–	–	–	–
		Redunca arundinum	M	–	P	–	–
		Redunca redunca	M	–	P	–	–
		Philantomba monticola	–	–	M	–	–
		Capricornis crispus	–	–	–	M	N
CARNIVORA							
	Canidae	*Canis lupus*	M	–	–	–	–
		Canis latrans	M	–	–	–	–
		Canis aureus	M	–	–	–	–
		Canis mesomelas	M	–	–	–	–
		Canis simensis	–	–	–	P	N
		Alopex lagopus	M	–	–	–	–
		Vulpes vulpes	M	–	–	–	–
		Vulpes macrotis	M	–	–	M	C
		Vulpes velox	M	–	–	–	–
		Urocyon cinereoargenteus	M	–	–	–	–
		Fennecus zerda	M	–	–	–	–
		Nyctereutes procyonoides	M	–	–	–	–
		Otocyon megalotis	M	–	–	–	–
		Cerdocyon thous	M	–	–	–	–
		Dusicyon culpaeus	M	–	–	–	–
		Dusicyon griseus	M	–	–	–	–
		Speothos venaticus	M	–	–	–	–
		Lycaon pictus	M	–	–	M	C
	Mustelidae	*Meles meles*	M	–	P	–	–
		Lutrogale perspicillata	M	–	–	–	–
		Amblonyx cinereus	M	–	–	–	–
	Herpestidae	*Suricata suricatta*	M	–	P	–	–
		Helogale parvula	M	–	–	–	–
	Viverridae/ Eupleridae	*Fossa fossana*	M	–	–	–	–
		Eupleres goudotii	M	–	–	–	–
		Galidia elegans	M	–	–	–	–
		Mungotictis decemlineata	M	–	–	–	–
PINNIPEDIA							
	Phocidae	*Phoca vitulina*	M	–	–	–	–
		Halichoerus grypus	M	–	–	–	–
		Lobodon carcinophagus	M	–	–	–	–
		Cystophora cristata	M	–	–	–	–

KL = Kleiman (1977); RU = Rutberg (1983); KB = Komers & Brotherton (1997); LM = the current review; C = the new data confirm previous evaluations; M = monogamous; MM = multimale/multifemale; N = new data (absent in previous reviews); P = polygynous; Pa = polyandrous; R = new data do not support previous evaluations.

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Chapter 15
Monitoring Female Reproductive Status in White-Handed Gibbons (*Hylobates lar*) Using Fecal Hormone Analysis and Patterns of Genital Skin Swellings

Claudia Barelli and Michael Heistermann

Introduction

Recent field research on white-handed gibbons (*Hylobates lar*) has focused predominantly on questions regarding their social organization, mating systems, and life histories under different socioecological conditions (Sommer and Reichard 2000; Reichard 2003). However, due to difficulties in accurately determining female reproductive status in free-ranging animals, a number of questions concerning gibbon reproductive biology in their natural setting have remained unanswered. In the past, assessment of reproductive status in wild female gibbons has been restricted to observations of menstruation, sexual behavior, and presence/absence of clinging infants (Morino, Barelli, and Reichard unpubl. data); these parameters provide only rough and mostly indirect information on female reproductive condition. Endocrine monitoring, in contrast, permits a more reliable and direct assessment of female reproductive status and thus enables more detailed studies into the reproductive biology of wild-living gibbons. For example, reliable information on a female's cycle stage and timing of ovulation would allow for the mating patterns observed in free-ranging individuals to be better interpreted. This, in turn, could help elucidate the reproductive strategies of males and females and thus aid in better understanding the evolutionary significance of the species' flexible mating system (Sommer and Reichard 2000; Barelli and Reichard 2004). In addition, methods for monitoring gibbon female reproductive physiology under natural conditions would enable the examination of the characteristics, endocrine correlates, and functional significance of female genital skin swelling, information that is limited in general, and completely lacking for free-ranging individuals. Available data on pair-housed captive animals have indicated a close association between the changes in swelling characteristics and female estrogen levels (Dahl and Nadler 1992a, b; Nadler et al. 1993). Since swelling

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patterns have not been characterized for free-ranging gibbons, it remains unclear if and how swelling patterns differ between reproductive conditions (cycling, pregnant, lactating) in wild-living individuals and if and how changes in swelling characteristics are related to female cycle stage and female sex hormone profiles.

To address these questions, researchers require a reliable method for non-invasive assessment of female reproductive status, suitable for application in the field. Although urinary estrogen measurements have proven useful in monitoring female reproductive processes in captive animals (Nadler et al. 1993), regular collection of urine is not a feasible option in the wild. A more practical alternative is measuring hormone levels in feces (Whitten et al. 1998; Hodges and Heistermann 2003), and several studies, in a variety of primate species, have demonstrated this method's reliability for assessing female reproductive status under field conditions (e.g., Strier and Ziegler 1997; Ziegler et al. 2000; Engelhardt et al. 2004). To date, no published information exists on the excretion of estrogen and progesterone metabolites in the feces of female white-handed gibbons (or any other species of gibbon), and the applicability of fecal hormone analysis to the assessment of female reproductive function in the gibbons has not been evaluated.

Against this background, the aims of the present study were (1) to establish reliable methods for fecal estrogen and progestogen measurement for assessing female reproductive status based on the samples collected from captive individuals, (2) to obtain information on the usefulness of these methods for monitoring female reproductive condition in wild-living subjects, and (3) to provide data on patterns of genital skin swelling and their association with female cycle stage in both captive and wild animals.

Since recent studies have shown that storage of fecal samples in ethanol (the method of choice in most previous field studies on primates) can cause marked changes in steroid hormone concentrations over time (Khan et al. 2002; Hunt and Wasser 2003), we also examined whether estrogen and progestogen levels in gibbon feces as well as their temporal pattern during the ovarian cycle changed as a result of storing samples in ethanol.

Methods

Subjects and Study Sites

For the establishment of fecal hormone analysis techniques, five captive adult female white-handed gibbons, differing in reproductive condition, served as subjects. Four animals (2 multiparous: Hexe and Hekti, 1 primiparous: Barbel, 1 nulliparous: Minna) were housed in the Wuppertal Zoo (Germany), while a fifth one (nulliparous: Lucy) was maintained at the Berlin Zoo (Germany).

Two of the females in Wuppertal were housed in family groups together with an adult male and their offspring (Barbel had one dependent offspring and

Hekti had three offspring), while the other two females (Hexe and Minna) were housed as a mother–daughter pair. Lucy, from Berlin, was housed together with an adult male partner. Hexe and Minna were cycling (as indicated by a regular menstruation history), Hekti was pregnant, Barbel was lactating, and Lucy was assumed to be cycling. All animals lived in indoor cages with access to outdoor enclosures. In both zoos, a mixture of fruit and vegetables, supplemented weekly with eggs, nuts, meat, or different carbohydrates, were fed to the gibbons twice daily and water was available ad libitum.

To examine the feasibility of fecal hormone analysis for reproductive assessment in wild females, C.B. collected samples from four individual white-handed gibbons at Khao Yai National Park, Thailand (for description of the study site see Reichard 2003). Of the selected females, two were assumed to be cycling and one was lactating while the fourth is known to have been in the late stages of pregnancy since she gave birth 2 months after collection.

To assess the relationship between female reproductive condition and its hormonal correlates, we measured estrogen and progestogen levels, which characterize the primates' menstrual cycle and pregnancy. During the follicular phase, defined as the interval between the first day of menstruation and the day of ovulation, estrogen concentrations increase, peaking around the time of ovulation; they drop soon after, while progestogen levels rise immediately after ovulation and stay elevated throughout the luteal phase until the onset of menstruation, or if pregnancy occurs, throughout the pregnancy.

Fecal Sample Collection

C.B. collected fecal samples from each of the four females in Wuppertal for a period of approximately 6 weeks, thus spanning about 2 cycle lengths (typical cycle length 19–22 days, Nadler et al. 1993). Animal keepers at the Berlin Zoo collected fecal samples from Lucy over a period of 7 weeks. We collected samples on a daily basis for the cycling and pregnant females and twice per week for the lactating one. We collected fecal samples in the early morning between 7:30 and 9:30 after the animals left their sleeping place and were observed defecating. Only samples that were not contaminated with urine were collected.

Before collection, we homogenized fecal samples using a gloved hand. We then placed one thumb-nail sized aliquot in a plastic tube and stored it immediately by freezing at −20°C. For the cycling females in Wuppertal, we transferred a second aliquot into a polypropylene tube containing 10 ml of 95% ethanol and stored it at 4–5°C for 10 months (for female Hexe) or 25 months (for female Minna) before extraction and analysis. These samples were used to examine the potential effects of storing fecal samples in alcohol on hormone concentrations. We collected daily records of menstruation by checking the females' urine for the presence of blood using a stick test (Combur-3-Test E, Roche Diagnostics Mannheim, Germany).

C.B. collected fecal samples from wild females in the early morning after the animals were observed defecating at a night tree or during the first hours of activity. Over a period of approximately one month, we collected samples on a daily basis from the cycling and pregnant females and weekly from the lactating one. We placed fecal samples in tubes with 10 ml of 95% ethanol and stored them at 4–5°C within 10 h of collection. We took daily records of menstruation using the same methods used for the captive animals.

Hormone Analysis

We lyophilized and pulverized the frozen fecal samples and extracted an aliquot (~0.05 g) of the resulting fecal powder with 3 ml of 80% methanol in water by vortexing for 10 min (Heistermann et al. 1995). We then stored the extract at −20°C until analysis. For fecal samples stored in ethanol, we homogenized the samples in their original ethanolic solvent and subsequently extracted them twice as described by Ziegler et al. (2000), with the modification that samples were vortexed twice for 10 min instead of shaking them overnight on a horizontal shaker. Following extraction, we dried the remaining fecal pellets in a vacuum oven and measured the dry weight of the samples. All hormone concentrations are expressed as mass per gram of dry weight.

For hormone determination in fecal extracts, we conducted group-specific assays for the measurement of immunoreactive 5α-reduced 20-oxo pregnanes (5-P-3OH) and total estrogen (Et; a combined measure of estrone and estradiol). Both groups of hormones are known to represent quantitatively abundant fecal metabolites of estradiol and progesterone in mammals (Schwarzenberger et al. 1996), including the white-handed gibbon (Nadler, pers. comm.), and their measurement has been shown to accurately reflect female reproductive function in a variety of primate species (e.g., Curtis et al. 2000; Heistermann et al. 2001; Ostner and Heistermann 2003; Möhle et al. 2005). We measured the hormone levels using microtiterplate enzymeimmunoassay (EIA) procedures already described by Hodges et al. (1997) and Ostner and Heistermann (2003). Sensitivity of the assay at 90% binding was 39 pg/well for 5-P-3OH and 1.9 pg/well for Et. Intra- and inter-assay coefficients of variation, calculated from replicate determinations of high- and low-value quality controls, were 7.4% ($n = 16$) and 12.9% ($n = 8$) (high) and 8.2% ($n = 16$) and 17.3% ($n = 8$) (low) for 5-P-3OH measurements and 6.1% ($n = 16$) and 16.4 ($n = 8$) (high) and 7.9% ($n = 16$) and 14.5% ($n = 8$) (low) for Et determinations.

Genital Swelling Score

C.B. conducted daily visual inspections of genital skin swellings on the four females housed in the Wuppertal Zoo. Due to the presence of a glass pane between the observer and the animals and the natural tendency of captive animals to approach the observer and show their hind ends (Mootnick et al. 2004), it was possible to generate data on vulval size. From a distance of approximately 10–15 cm, C.B. determined the size of the vulva by comparing it with a series of white cards of known sizes used as references (Dahl and Nadler 1992b). In addition to size measures, C.B. recorded changes in swelling appearance by evaluating color and degree of turgidity of the labia minora, urethral eminence, and dorsal lining of the vaginal wall. These measures were always taken even when it was not possible to get the animals to come close enough to measure changes in swelling size.

In the wild, C.B. conducted daily visual inspections of female swellings from an approximate distance of 10 m. Since it was not possible to apply the detailed swelling score method used with captive females, C.B. assessed the size of the swelling in the wild animals intra-individually in comparison to the size of the female's ischial callosities (Fig. 15.1), which are a constant size, measuring approximately 4×5 cm (Matthews 1946). C.B. also systematically recorded

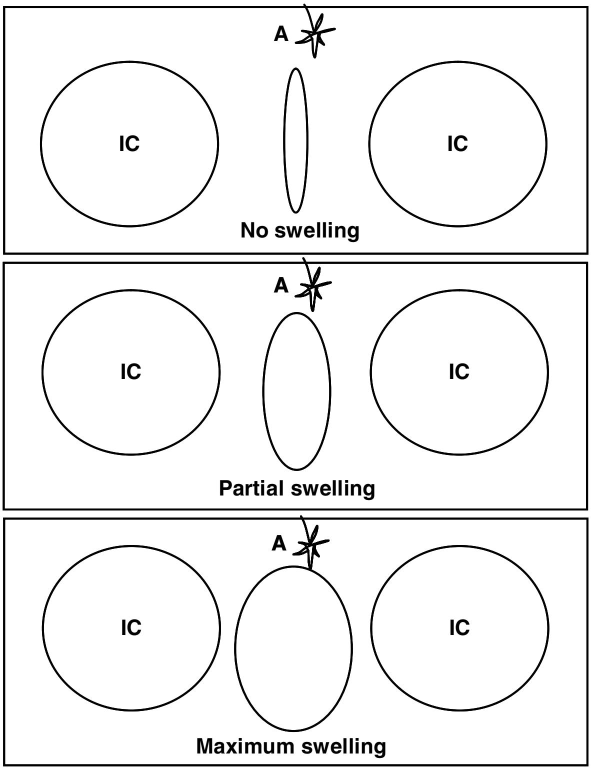

Fig. 15.1 Schematic drawing of the genital swelling categories. The genital swelling sizes were classified by comparison with the size of the ischial callosities. A: anus and IC: ischial callosity

qualitative characteristics of the appearance of the vulva (shape, tumescence, and color). To allow a better comparison of swelling changes between captive and free-ranging animals, we converted swelling characteristics and size measures to a 3-stage score defined as follows: *No swelling*: minimum size of outer genital structures and maximal degree of wrinkling. The vulva was almost not visible or appeared as a pink mass of less than 2 cm in length or approximately ¼ of one ischial callosity (stages 0 and 1 of the scale described in Dahl and Nadler 1992b); *Partial swelling*: any intermediate stage between no swelling and maximum swelling. The lobes of the vulva were smooth and measured between 2 and 2.5 cm or approximately ½ of one ischial callous size (stages 2–3 of Dahl and Nadler's scale); *Maximum swelling*: The lobes of the vulva had no wrinkles and maximum levels of protrusion and turgidity. The size of the vulva could reach its maximum length of 3.5–4 cm or around ¾ of one ischial callous (stages 4–7 of Dahl and Nadler's scale).

Results

Hormone Profiles and Concentrations in Relation to Female Reproductive Status

Figure 15.2 shows the profiles of immunoreactive fecal 5-P-3OH and Et in relation to changes in genital skin swelling size for Hexe and Minna. The hormone profiles for Lucy were similar. In each of the three females, 5-P-3OH followed a cyclic pattern in which the presumed follicular (low progestogen concentrations) and luteal (high progestogen concentrations) components of the ovarian cycle could be clearly distinguished. Moreover, in all females there was a well-defined late follicular phase rise in fecal Et, with a distinct peak occurring 0–2 days before the defined luteal phase progestogen increase, clearly suggesting that the cycles were ovulatory. Specifically, mean levels of Et increased about three- to sixfold during the follicular phase, from baseline levels of around 20–30 ng/g to presumed pre-ovulatory peak values of up to 180 ng/g (Fig. 15.2). Following a marked drop in Et levels thereafter, levels remained at low baseline concentrations for the remainder of the cycle with no obvious elevation during the luteal phase. In contrast, fecal 5-P-3OH levels were consistently low during the follicular phase (mean±SD = 1.6±1.4 μg/g), but rose significantly after the Et peak, reaching markedly elevated (on average 5–6 fold higher) concentrations during the luteal phase of the cycle (mean±SD = 9.08±4.20 μg/g; Fig. 15.2). In each of the three cycling females, 5-P-3OH levels began to decline around 10 days after the Et peak, which was followed by menstruation.

The two cycling free-ranging females exhibited fecal 5-P-3OH profiles that were similar to those obtained for the captive cycling individuals (Fig. 15.3) in terms of both absolute hormone levels and temporal changes. In contrast to the

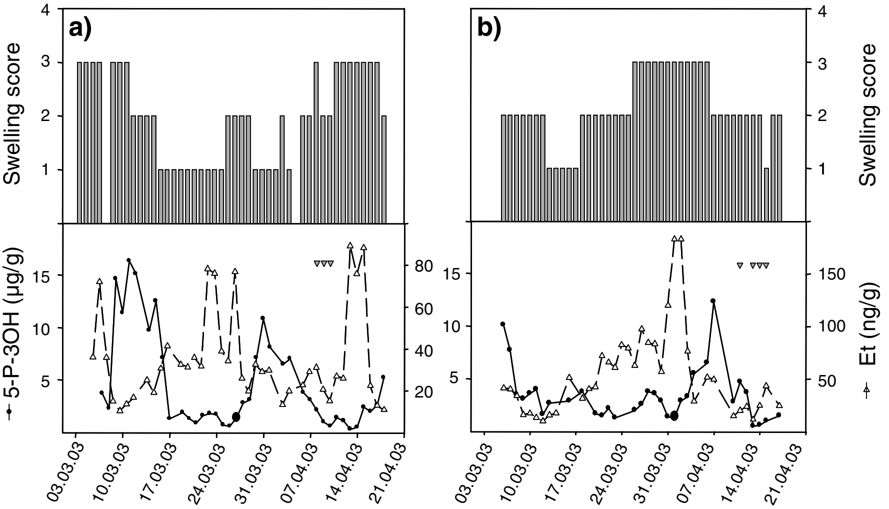

Fig. 15.2 Individual profiles of fecal immunoreactive progestogen (5-P-3OH) and estrogen (Et) excretion and the scores of genital swelling size of two white-handed gibbon females from Wuppertal Zoo. *Gray triangles* indicate periods of menstruation, *big black dots* along the progestogen profiles indicate the presumed day of ovulation. (**a**) female Hexe; (**b**) female Minna

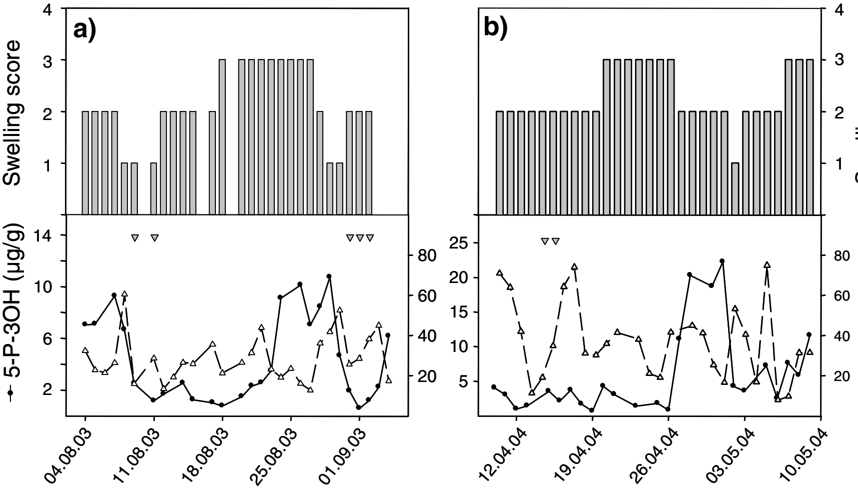

Fig. 15.3 Individual profiles of fecal immunoreactive progestogen (5-P-3OH) and estrogen (Et) excretion and the scores of genital swelling size of two wild white-handed gibbon females. *Gray triangles* indicate periods of menstruation. (**a**) female Natasha; (**b**) female Hannah

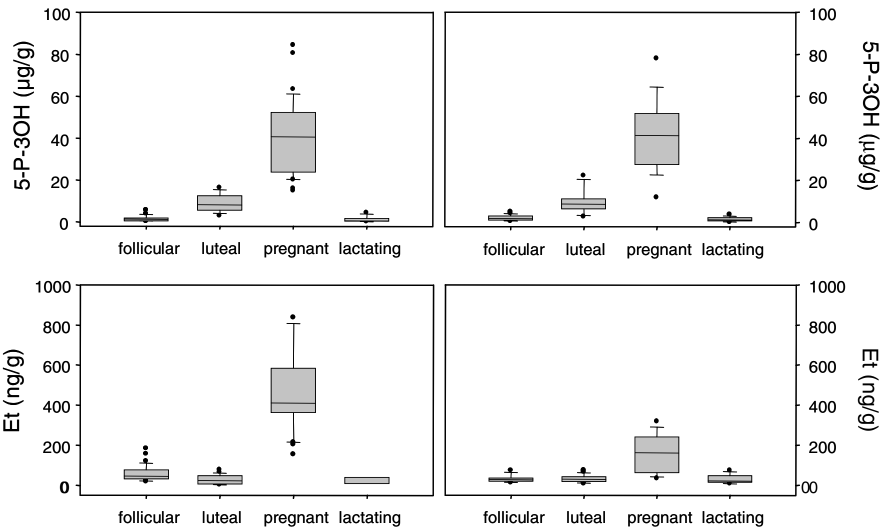

Fig. 15.4 Boxplots of concentrations of fecal immunoreactive progestogens (5-P-3OH) and estrogens (Et) during different reproductive conditions in captive-housed (*left graphs*) and wild (*right graphs*) female white-handed gibbons. The boxes show the median value and the upper and lower quartile values; bars show the 10th and 90th percentiles of the values

captive animals, Et profiles in both wild females were, however, less clear due to more pronounced day-to-day variation and the lack of a distinct pre-ovulatory estrogen peak.

Figure 15.4 compares median fecal 5-P-3OH and Et levels during the ovarian cycle to those obtained for the pregnant and lactating females (both captive and free-ranging). Although the data are preliminary and based on just one pregnant and one lactating animal in each condition (captive and wild), concentrations of both hormones were clearly substantially elevated in the pregnant females, although the elevation in Et was less pronounced for the individual sampled in the wild. In contrast and as expected, progestogen and estrogen levels during lactation were consistently low, and were in the range of the follicular phase concentrations of cycling animals for both the captive and the wild females.

Changes in Genital Skin Swelling

Both captive and free-ranging females showed clear fluctuations in swelling size during the ovarian cycle (Figs. 15.2 and 15.3). Females were partially swollen for a period of 5–8 days before reaching the stage of maximum tumescence, which lasted for 7–12 days in the two captive animals and 7–10 days in the two wild females. In both captive and wild females there was a clear association between swelling size and female cycle stage, with the highest swelling scores being generally confined to the peri-ovulatory period of the cycle. Furthermore, in the captive females, maximum swelling scores were associated with elevated estrogen levels relative to the levels associated with the two lowest swelling scores (mean±SD in no swelling stage: 35.5±5.1 ng/g; partial swelling stage: 31.4±8.0 ng/g; maximum swelling stage: 67.1±37.3 ng/g; Fig. 15.2).

Effect of Storage Procedure on Hormone Concentrations

To assess a possible effect of storing fecal samples in ethanol on 5-P-3OH and Et concentrations, we compared hormone levels generated from the samples stored frozen and the samples stored in ethanol. Samples stored in alcohol had markedly elevated progestogen and estrogen concentrations in both females (Table 15.1), with the effect generally being more pronounced for progestogens than for estrogens and in the samples that had been stored for longer (Female 2). However, despite the difference in absolute hormone concentrations, the temporal pattern and magnitude of changes in 5-P-3OH and Et concentrations throughout the ovarian cycle was similar in frozen and ethanol-stored feces in both females (see example in Fig. 15.5), and both measurements were highly significantly correlated in each of the two individuals (Table 15.1).

Table 15.1 Comparison of immunoreactive 5α-reduced 20-oxo pregnanes (5-P-3OH) and total estrogen (Et) concentrations (mean ± SD) in fecal samples stored frozen and in 95% ethanol

	Hexe (Female 1)[†]		Minna (Female 2)[‡]	
	5-P-3OH	Et	5-P-3OH	5-P-3OH
Frozen samples	4.7 ± 4.5	34.8 ± 22.4	3.6 ± 2.5	53.3 ± 41.7
95% Ethanol samples	8.6 ± 8.4	42.0 ± 21.8	12.7 ± 9.7	98.7 ± 63.3
Factorial difference[§]	1.83	1.21	3.53	1.85
Correlation coefficient[+]	0.97	0.72	0.83	0.89

[†] Samples were stored in ethanol for approximately 10 months after collection.

[‡] Samples were stored in ethanol for approximately 25 months after collection.

[§] Ratio between mean values, all significant with $p < 0.001$ (paired t-test).

[+] Pearson Product Moment Correlation coefficient, all significant with $p < 0.001$.

Discussion

This preliminary study provides a first account of the measurement of fecal steroids for noninvasive monitoring of female reproductive status in the white-handed gibbon. Specifically, the results show that the group-specific measurement of immunoreactive fecal progestogen and estrogen metabolites provides reliable information on a female's endocrine status associated with ovarian function, pregnancy, and lactation. Our data also show that the method is effective for the assessment of reproductive status in gibbon females living in

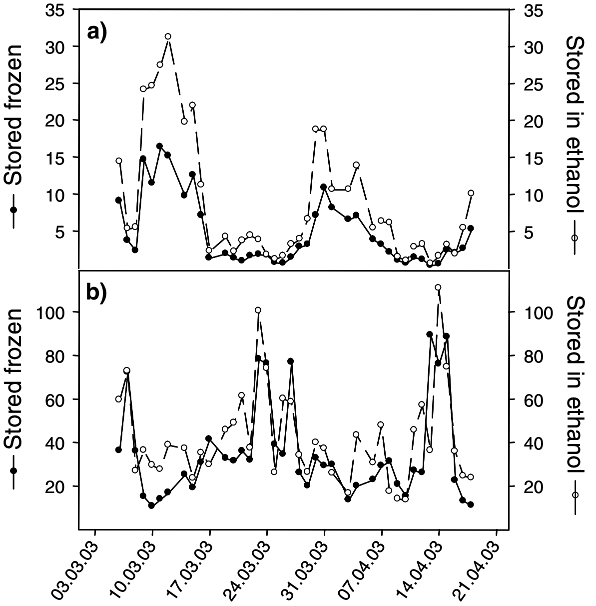

Fig. 15.5 Profiles of fecal (**a**) 5-P-3OH and (**b**) Et generated from frozen-stored samples (*closed circles*) and samples stored in 95% ethanol (*open circles*) throughout two ovarian cycles in female Hexe from Wuppertal Zoo

their natural habitat, thus demonstrating its utility for studying this species' female reproductive physiology under field conditions.

In the absence of published information on the metabolism and fecal excretion of steroids in the white-handed gibbon, we used group-specific assays for the measurement of 5α-reduced 20-oxo pregnanes and total estrogens, an approach that has been successfully applied to monitor endocrine changes associated with female reproductive processes in a variety of other primate species (Heistermann et al. 2001; Ostner and Heistermann 2003; Engelhardt et al. 2004). Our data show that profiles of both groups of hormones demonstrated the expected pattern in the cycling animals, with estrogens exhibiting a clear follicular phase rise, culminating in a distinct pre-ovulatory peak, followed by a post-ovulatory luteal progestogen increase. Since levels of both hormones were markedly elevated in the pregnant (captive and wild) animals and consistently low in the lactating ones, the group-specific measurements of 5-reduced progestogens and estrogens appear to be a useful tool for reproductive assessment in gibbons. However, the assessment of estrogen dynamics had certain limitations when applied to the two free-ranging individuals, in which no clear estrogen profiles emerged although the progestogen profiles indicated the presence of an ovulatory cycle in both females. Therefore, while it is possible to detect and pinpoint the time of ovulation in wild cycling gibbons using progestogen metabolites, the ability of field researchers to predict ovulation based on a pre-ovulatory estrogen surge may be limited. The reason for the less informative estrogen profile is not clear, but may be related to differences in diet (e.g., variability in dietary fiber composition), which is known to affect fecal hormone concentrations (Wasser et al. 1993). Alternatively, although not mutually exclusively, differences in fecal storage methods might have contributed to a higher variance in estrogen levels and a less clear profile in the wild females. Although an effect of storage cannot be excluded, it is relatively unlikely given that the ethanol storage method used in this study has been successfully applied to monitor estrogen dynamics during the ovarian cycle in other primates (e.g., Engelhardt et al. 2005) and, more importantly, our findings on storage effects in white-handed gibbons show that estrogen (and progestogen) measurements in frozen and long-term ethanol-stored samples provide similar profiles.

Our data from white-handed gibbons confirm the results from previous studies on other primate and nonprimate species, and showed that preservation of feces in alcohol for prolonged periods of time can markedly alter hormone concentrations and that this degree of change can differ according to storage duration (e.g., Khan et al. 2002; Hunt and Wasser 2003). However, our data also clearly demonstrate that irrespective of the change in absolute hormone levels, the temporal patterns of progestogens and estrogens during the ovarian cycle generated from the ethanol-stored samples were similar to those generated from the samples stored frozen. This finding has important implications for future studies on the reproductive physiology of wild gibbons as it shows that fecal samples can be stored in alcohol for up to 2 years without impairing the information gained on female reproductive status.

This study provides a methodological basis for future studies aiming to clarify the relationship between changes in genital swelling size, female cycle stage, and endocrine events in free-ranging gibbons. Here, we were able to confirm earlier findings from Nadler et al. (1993) and Dahl and Nadler (1992b) that swelling size shows a cyclic pattern during the ovarian cycle in captive females, and that the maximum swelling size is confined to the periovulatory phase of the cycle in association with elevated estrogen levels. We found a similar relationship between swelling and cycle stage in the two wild females in which the duration of maximum swelling size was also comparable to that of the captive animals studied here and by Dahl and Nadler (1992b). Moreover, in the four study animals, ovulation occurred mainly during the stage of maximum swelling. Thus, although the data are limited, they suggest that female gibbons are similar to the primate species exhibiting exaggerated genital skin swelling in terms of swelling patterns and their relationship to female reproductive condition and endocrine changes (e.g., Deschner et al. 2003; Engelhardt et al. 2005).

However, more comprehensive data from a larger number of females are needed to determine more precisely the relationship between swelling changes, female sex hormone levels, and timing of ovulation and to elucidate the pattern of swelling changes in pregnant and lactating females. This, in turn, will help to improve our understanding of the functional significance of this morphological trait in a species for which the adaptive function of genital swelling is largely unknown.

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Chapter 16
Patterns of Infant Care in Wild Siamangs (*Symphalangus syndactylus*) in Southern Sumatra

Susan Lappan

Introduction

Parental care—parental behavior that is likely to increase offspring fitness (Clutton-Brock 1991)—is an important component of reproduction for many animals. Among mammals, internal gestation and lactation constrain females to be the more investing sex, particularly during the initial stages of a reproductive attempt (Clutton-Brock 1989). The costs and benefits of abandonment or neglect of offspring differ between the sexes for most mammal species due to this heavy early female investment. Therefore, the interaction between male and female reproductive strategies in mammals has generally resulted in male strategies that prioritize mating effort over parental investment (Trivers 1972; Clutton-Brock 1989). Uniparental female care is universal in solitary mammals, and is the most common pattern in social mammals (Kleiman and Malcolm 1981; Clutton-Brock 1991). Nonetheless, biparental care does occur in a minority of mammal species. Biparental care is most common among carnivores, primates, and rodents, and is often associated with social monogamy or cooperative breeding (Kleiman and Malcolm 1981; Clutton-Brock 1991; Jennions and MacDonald 1994), although some male parental care has also been reported in species with other grouping and mating patterns (e.g., Borries et al. 1999; Buchan et al. 2003). In many species displaying biparental care, there is intraspecific variation in the quantity of care provided by males (Webb et al. 1999). Patterns of parental care may affect and be affected by grouping patterns and mating systems (Trivers 1972; Emlen and Oring 1977; Emlen 1995), remating opportunities (Smith 1995; Marlowe 1998), population densities (Kokko and Rankin 2006), and adult sex ratios (Burley and Calkins 1999; Burley and Johnson 2002). Variation in the quantity or quality of male care in biparental mammals has been shown to affect infant survivorship (Gubernick

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and Teferi 2000; McInroy et al. 2000; Wright 2006), interbirth intervals (Cantoni and Brown 1997), and offspring development (McInroy et al. 2000; Bester-Meredith and Marler 2003; Frazier et al. 2006). Thus, in biparental species, male caring behavior may be an important determinant of offspring and female reproductive success.

Many anthropoid primates typically found in unimale–unifemale groups display substantial male care of infants (Kleiman 1985; Whitten 1987; Wright 1989; Fuentes 2002). However, direct male care of infants has not been reported for most gibbon (Hylobatidae) species, despite the prevalence of social monogamy in this family. Siamangs (*Symphalangus syndactylus*) are unusual among the hylobatids in that they exhibit biparental care of infants in the wild (Chivers 1974; Chivers and Raemaekers 1980; Gittins and Raemaekers 1980) and in captivity (Alberts 1987; Dielentheis et al. 1991). Chivers (1974), Chivers and Raemaekers (1980), and Gittins and Raemaekers (1980) describe wild siamangs in peninsular Malaysia as displaying exclusive female care during the early stages of infant development, followed by the gradual transfer of most infant care responsibilities from the female to the male in the second year of infant life. However, Palombit (1992) did not report extensive male involvement in infant care in the single siamang group at Ketambe that contained an infant of appropriate age during his study. This suggests that the pattern of infant care may vary between groups and that biparental care may not be obligate for siamangs.

Gibbons are characterized by slow life histories relative to most other primates of their body size. Maximum female lifetime reproductive output for gibbons is low (Palombit 1992; O'Brien et al. 2003; Barelli et al. 2007), and each infant born represents a substantial portion of potential female lifetime reproductive success. As gibbon gestation periods represent only a small portion of the total IBI, prolongation of the period of infant care and maternal recovery is primarily responsible for long gibbon interbirth intervals. Accordingly, variation in patterns of infant care and resulting differences in infant survivorship may have substantial impacts on adult reproductive success. However, previous studies of the behavioral ecology of wild siamangs provide data from only one or two groups at a given location with dependent infants, and did not document patterns of infant care in detail. Therefore, neither the "typical" pattern of siamang parental care nor the range of variation of siamang parenting behavior has been established. In this chapter, I describe the patterns of infant care and infant development in five groups of wild siamangs at the Way Canguk Research Station in southern Sumatra, describe the range of variation in the timing and extent of male involvement in infant care in siamangs, and examine the hypothesis that biparental care is obligate for wild siamangs. As the study population included both polyandrous and socially monogamous groups, I also examine the hypothesis that the need for infant care is an important factor promoting facultative polyandry in siamangs.

Methods

Study Site and Animals

The Way Canguk Research Area is located in the Bukit Barisan Selatan National Park in southern Sumatra, Indonesia, and encompasses 900 hectares of primary forest interspersed with forest damaged by drought, wind throws, earthquakes, and fire (Kinnaird and O'Brien 1998; O'Brien et al. 2003). The research area is run collaboratively by the Wildlife Conservation Society-Indonesia Program (WCS-IP) and the Indonesian Ministry of Forestry's Department for the Protection and Conservation of Nature (PHKA). Siamangs at this site have been the subjects of behavioral and demographic studies by the WCS-IP staff and students since 1998 (e.g., Nurcahyo 1999; Kinnaird et al. 2002; O'Brien et al. 2003.

Five groups of siamangs were chosen for the study based on proximity to the research camp and the presence of a young infant. All individuals were individually recognizable based on facial and body features. Compositions of the study groups throughout the study period are depicted in Fig. 16.1. I have described the methods by which individual age-classes and were assigned and infant birth dates were determined elsewhere (Lappan 2007a, 2008). The first letter of each individual's name indicates its group membership at the time of first contact (e.g., Amang is from group A, Connie is from group C).

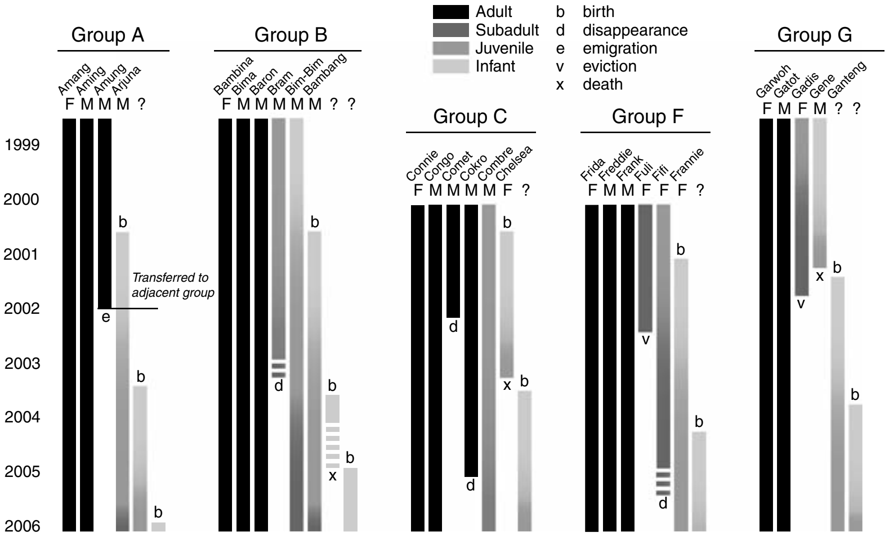

Fig. 16.1 Compositions of the study groups from 1998–2006 (data from Nurcahyo 1999; Lappan 2005; unpubl. data; Jayus, pers. comm.; L. Morino, pers. comm.; A. Elder, pers. comm)

Four of the five study groups contained more than one adult male at the beginning of the study (Fig. 16.1). Multimale groups may form through the retention of adult male offspring in their natal group or by the immigration of an adult male into a group already containing an adult pair (Reichard this volume). Therefore, multimale group composition is not necessarily indicative of polyandrous mating. Mitochondrial DNA (mtDNA) haplotypes for the study adults were determined as a part of a different study (Lappan 2007b), so to classify groups as socially monogamous or socially polyandrous, I considered both mating patterns and the distribution of mtDNA haplotypes (which are indicative of matrilineal relatedness) among adults within a group. Groups A, B, and F contained two adult males at the beginning of the study, and group C briefly contained three adult males. However, the third male, Comet, disappeared from group C very soon after the study was initiated (Fig. 16.1). In groups A, B, and C, both males mated with the female (Lappan 2007a), and each adult had a different mtDNA haplotype, indicating that they were not close matrilineal relatives (Lappan 2007b). Accordingly, groups A, B, and C are described as polyandrous. While group F contained two adult males throughout the study, only one, Freddie, was observed copulating with the female or carrying her offspring, and the second male, Frank, had an mtDNA haplotype matching that of the female (Lappan 2007b). Matching mtDNA haplotypes do not conclusively demonstrate a close matrilineal relationship. However, in light of the high haplotype diversity observed in the neighborhood (Lappan 2007b), the most parsimonious interpretation of these observations is that Frank was a retained adult offspring (or sibling) of the female and was nonreproductive within the group. Accordingly, group F was classified as socially monogamous. Group G contained only a single adult male and a single adult female, and so was also classified as socially monogamous. Prior to the eviction of subadult females Fuli and Gadis from their groups, copulations between these females and the adult males in their groups were observed, which means that the apparent social monogamy in groups F and G was not indicative of strict sexual monogamy, at least for the males.

Behavioral Data Collection and Analysis

Three field assistants and I collected behavioral data during sleeping-tree-to-sleeping-tree follows of the study groups. The study groups were followed on a rotating basis, and each group was followed continuously for either six (groups A, B, C, and F) or four days (group G) until each adult group member had served as a focal adult for two days.

Behavioral data were collected from the focal adult and the infant at 5-min intervals using instantaneous focal animal sampling (Martin and Bateson 1993). Data collected included focal adult activity, estimated interindividual distance between the focal adult and the infant (in meters, to the nearest half-meter), infant activity, infant social partner(s), and any interaction between the adult and the infant. Infant activities included suckling, clinging to another individual, resting (excluding clinging), feeding (on adult foods), social grooming (grooming another individual or being groomed by another individual), traveling, solo play, social play, and other.

Behavioral data were collected from group B from October 2000, from groups A and C from November 2000, from group F from February 2001, and from group G from May 2001. Data were collected from all groups until August 2002.

For all classes of infant care, the quantity of care was expressed as the proportion of infant time spent receiving care, which was estimated as the proportion of instantaneous samples in which caring behavior was observed. Proportional data were arcsine-square-root transformed to approximate a normal distribution prior to the application of parametric statistical tests (Zar 1996). I used daily means of hourly rates (or daily means of hourly means for interindividual distances) for analyses of individual or dyadic behaviors, and means of group means are presented as summary statistics for the population as a whole. Days from which fewer than five hours of data were available were excluded from the analyses.

Results

Lactation

Suckling data were collected from all infant-female dyads throughout the study. However, it was often impossible for the observer to determine whether young infants were merely clinging to the mother or suckling due to small infant size and the positioning of clinging infants on their mothers' bodies. When there was uncertainty, the infant was recorded as clinging to the mother (which it clearly was), but not as suckling; the method employed probably substantially underestimates suckling time for younger infants. For larger infants (≥11 months), it was possible to consistently ascertain the position of the infant's mouth when the infant was visible (infant activity data were not collected when infants were not visible). Therefore, as infant age increased, the error in the estimation of suckling time likely was reduced. Accordingly, only data collected from infants aged ≥11 months, which are likely to represent a reliable estimate of suckling time, are presented (Fig. 16.2).

Fig. 16.2 Mean (± SE) percentage of time that infants spent suckling (from 11 to 24 months of age) and eating plant foods (from 0 to 24 months of age)

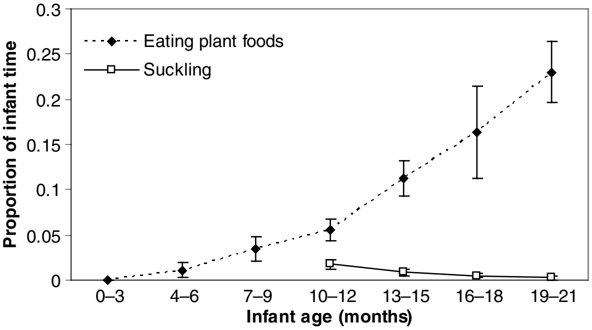

Table 16.1 Infant age (in months) when behaviors were first observed

Behavior	Arjuna	Bambang	Chelsea	Frannie	Ganteng
Not in contact with mother	4	2	3	4	4
>1 m from mother	4	4	6	7–9[a]	5
Eating solid food	6	6	6	7–9[a]	3
Last daytime suckling	15	23	23	≥21[b]	≥15[b]
Social play	4	3	8	13	5
Independent travel	11	9	12	13	10

[a] Frannie was not observed at ages 7 and 8 months.

[b] Frannie and Ganteng were still occasionally observed suckling at the conclusion of the study.

Most infants were not observed consuming solid foods prior to age 6 months (Table 16.1), although younger infants did occasionally handle food items, which suggests that lactation was an important, and probably the only, source of nutrition during the first 6 months of life for most infants. While suckling time between infant ages 6 and 11 months could not be reliably estimated, the consumption of plant foods increased throughout this time (Fig. 16.2). The mean percentage of infant time spent suckling in the second year of life was consistently very low (Fig. 16.2), which suggests that lactation probably does not make a substantial contribution to infant nutrition in the second year of life. It is important to note that suckling behavior is not necessarily a reliable indicator of milk transfer. Non-nutritive suckling—suckling without milk transfer—is common in many mammals, and may serve a social function (Hayssen 1993; Cameron 1998).

Female Time Spent Carrying Infants Declined Consistently Over Time

The most frequently exhibited form of nonlactational infant care was carrying of the infant by adults. Infants were carried by (or clung to) their mothers nearly 100% of the time during the first 2 months of life (Table 16.1), and all infants except Bambang were in physical contact with their mothers 100% of the time prior to age 3 months. From infant age 3 months on, however, the proportion of time that an infant spent being carried by his or her mother declined consistently in all five groups (Fig. 16.3). All females carried infants over 16 months of age less than 20% of the time, and by age 22 months, infants spent as much time traveling independently as did adults.

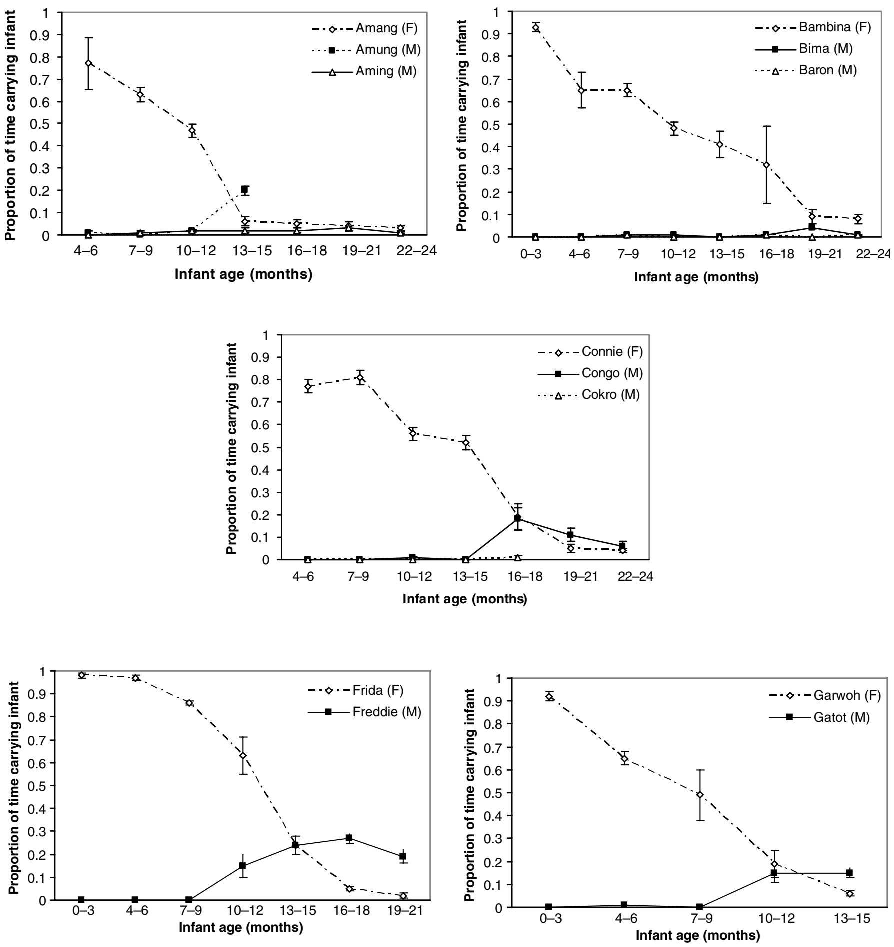

Fig. 16.3 Mean (± SE) percentage of time that each adult spent carrying the infant in their group plotted against infant age

Male Time Spent Carrying Infants Varied Between Groups and Individuals

Adult males in all five groups were observed carrying infants, which suggests that male involvement in infant care is common in this population. However, the proportion of time spent carrying infants varied dramatically among males (Fig. 16.3). For example, in group B, both males occasionally carried the infant, but never more than 3% of the time, whereas in groups F and G, an adult male became the primary provider of infant care by infant age 13 months (Fig. 16.3).

Even among males providing extensive care, there was variation in the timing of onset of male care: male Gatot was the primary carrier of infant Ganteng by age 12 months, whereas male Congo only became the primary carrier of infant Chelsea at age 18 months (Fig. 16.3).

In all three socially polyandrous groups, both males were observed carrying the infant. However, the contribution to infant care varied between males both within and between polyandrous groups. For example, in group C, Congo was the primary carrier for the infant during the second half of her second year of life, whereas Cokro rarely provided infant care (Fig. 16.3) and emigrated from the group in February 2002 (Fig. 16.1), and in group B, neither male provided a substantial contribution to infant care (Fig. 16.3). Only one male in group F, the female's social mate, Freddie, was observed carrying the infant (Fig. 16.3).

Adults Spent Little Time in Social Play with Infants

Social play was defined as play involving two or more individuals, and was easily distinguishable from other behaviors by the nature of the locomotor movements and the frequent display of open-mouth "play faces". Social play was also the only context in which a distinctive infant vocalization, resembling human laughter, was observed. Siamang "laughter" consisted of a high-pitched repetitive "ee ee ee . . ." produced intermittently for several minutes. Only one infant, Chelsea, was observed "laughing" during this study, but previous researchers observed another infant (Gene, from group G) "laughing" during late infancy as well (A. Nurcahyo, pers. comm). Chivers (1974) also reported the emission of characteristic vocalizations during social play by wild siamangs. However, it is unclear whether Chivers' (1974) "strange grunts and growls" correspond to the "laughing" vocalizations observed in this study.

All infants were observed engaging in social play (Table 16.1). While infants and juveniles frequently directed play solicitations at adults, these solicitations were often ignored. Adult males and females both spent an average of only 0.2% of their time in social play with infants. Infants were also observed attempting to initiate social play with mitered leaf monkeys (*Presbytis melalophos*), but their approach invariably resulted in an immediate retreat by the monkeys, which may be typical, but may also have been induced by the presence of human observers. Social play occupied an average of about 2% (mean of individual means) of infant time for infants aged 0–24 months, and all observations of social play involved at least one immature individual.

Differences between infants in the amount of time devoted to social play were pronounced. Bambang spent a much higher percentage of his time (5.0%) in social play between ages 6 and 24 months than did other infants (1.3–2.1%). The number of juveniles in a group may be an important determinant of the percentage of time that an infant is able to spend in social play. Small juvenile male Bim-Bim was Bambang's partner in 84% of social play observations in group B. No other study infant lived in a group also containing a small juvenile. However, Chivers (1974) reported a similar pattern of frequent play behavior in another siamang group (TS1) containing a small juvenile and an infant.

Adults Spent Little Time Grooming Infants

Females were the most frequent social grooming partners of infants, being involved in 46% of infant social grooming interactions. However, the proportion of infant time spent in social grooming interactions with adults of both sexes was very low. Social grooming with adult females and males occupied only 0.3% and 0.1% of the infant's time, respectively.

Female Time in Close Proximity with Infants Declined Over Time

Very young infants were always observed in physical contact with their mothers (Table 16.1). However, as infant age increased, the mean distance between infants and their mothers increased. Changes in infant suckling time or infant time spent being carried by the female may partially explain the change in proximity patterns between the mother and her infant. However, females and infant also spent less time in close proximity with each other (≤ 2 m apart) while not engaged in any form of social or caring interaction as the infant's age increased (Fig. 16.4). By age 16–18 months, infants on average spent 12% of

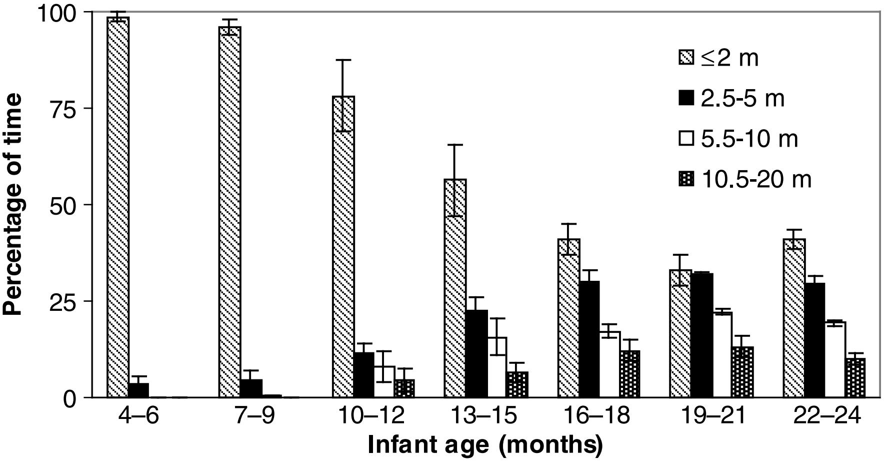

Fig. 16.4 Mean percentage of time that females and their infants spent ≤ 2 m, 2.5–5 m, 5.5–10 m, and 10.5–20 m apart (mean of individual means ± SE). Includes only observations in which the female was not directly providing care for the infant

their time >10 m from their mothers. This suggests that mothers become less able to protect their infants from predators, conspecifics, and other dangers as their infants grow older.

Some Males Spent Most of Their Time in Close Proximity with Older Infants, Even When Not Directly Providing Care

Some males displayed a substantial increase in time spent in close proximity (defined as ≤2 m) with infants as infants grew older. Males Aming and Amung (group A), Congo (group C), Freddie (group F), and Gatot (group G) spent a significantly higher mean percentage of time in close proximity with infants during the second year of life than the first (Table 16.2). This analysis excluded the time spent carrying and socializing with infants, so these data indicate a change in overall patterns of spatial proximity, and not just a change in the rate of direct social interaction between males and infants. Conversely, males Bimo and Baron (group B) and Cokro (group C) spent relatively little time in close proximity with infants of any age, and did not spend significantly different mean proportions of time in close proximity with infants in the first and second years of infant life (Table 16.2). As behavioral data from male Frank (group F) from the infant's first year of life are unavailable, it is unclear whether the pattern of proximity between Frank and the infant changed between the two years.

Table 16.2 Mean (± SE) percentage of time that male–infant pairs spent ≤ 2 m apart in the first and second years of infant life (excluding observations involving direct male care of the infant). Analysis by ANOVA

		Mean percentage of time spent ≤ 2 m from infant				
Group	Male	0–12 months	13–24 months	*F*	*N* (days)	*p*
A	Aming	27.4 ± 4.0	44.2 ± 4.1	8.502	12,12	0.008
	Amung	30.4 ± 4.3	54.8[a] ± 2.6	7.388	7,2	0.030
B	Bima	32.0 ± 3.6	30.0 ± 2.8	0.166	13,13	0.687
	Baron	30.8 ± 4.0	22.8 ± 4.0	2.271	8,8	0.154
C	Congo	32.5 ± 3.3	47.8 ± 4.5	6.505	14,17	0.016
	Cokro	20.1 ± 6.0	17.3[b] ± 2.3	0.266	2,7	0.622
F	Freddie	28.5 ± 3.0	70.9 ± 7.0	34.011	13,10	<0.001
	Frank	–	12.2 ± 2.9	–	0,8	–
G	Gatot	41.0 ± 3.7	70.1[c] ± 6.8	13.074	16,4	0.002

[a] Amung emigrated from group A when the infant was 16 months old.
[b] Cokro emigrated from group C when the infant was 19 months old.
[c] Data from group G are available only through infant age 15 months.

Infants in Polyandrous Groups Received Less Male Care than Infants in Monogamous Groups

The mean proportion of time that males in polyandrous groups spent carrying infants was significantly lower than the mean proportion of time that males in monogamous groups spent carrying infants (Lappan 2008). When the total contribution of all males in each group was considered, infants in monogamous groups received substantially more male care than infants in polyandrous groups (Fig. 16.5). This is the opposite pattern to that predicted if the need for additional male care is an important factor promoting facultative polyandry in this population.

Infants in this population receiving more care from males received less care from females (Lappan 2008), and the proportion of time that infant spent being carried by males was not correlated with the proportion of time that infants spent being carried by all adults (Lappan 2008). This suggests that the primary effect of male care in siamangs is to reduce the energetic costs of infant care for the female.

All Study Infants Survived at Least Two Years

A four-year demographic study of Way Canguk siamangs determined that approximately 26.5% of infants died prior to age 2 years, and a further 16% of individuals died during the juvenile stage (O'Brien et al. 2003). In this population, variation in infant and juvenile mortality may have strong selective effects on adult reproductive strategies.

Siamang infants grow quickly between birth and age 2.5 years (Leigh and Shea 1995). The energetic demands of growth coupled with an immature digestive system may therefore place young siamangs at risk of malnutrition (Altmann 1980; Janson and van Schaik 1993) and predation (O'Brien et al.

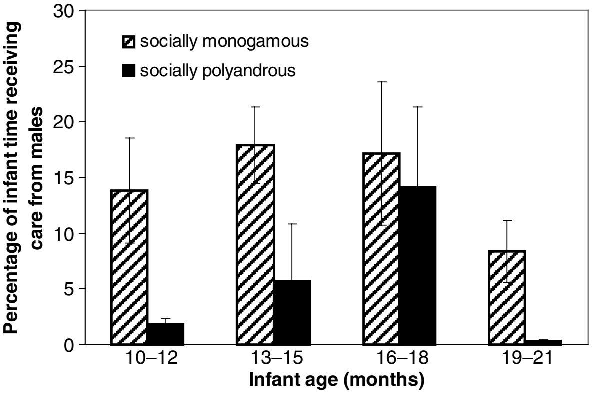

Fig. 16.5 Mean percentage of time that infants in socially monogamous and polyandrous groups spent receiving care from all males in their groups (mean ± SE)

2003) during this period of rapid growth. In this study, all five infants survived to age 2 years, and four of the infants survived into the later stages of the juvenile period (Fig. 16.1). Unfortunately, the sample size is not adequate to directly test the hypothesis that infants receiving more parental care are more likely to survive infancy and juvenility than infants receiving less care, or that there is a relationship between group composition and infant survival. However, longitudinal data from the study groups provide anecdotal support for the argument that there may be a relationship between parental investment and survivorship in the juvenile stage. Between 1998 and 2006, 3 of 13 infants (23%) born in the study groups disappeared before age ~3 years and are assumed to have died (Fig. 16.1). As five of the remaining infants had not reached 3 years of age at the time of writing, this figure may be an underestimate. The exact month of disappearance of one infant is not known, but in the other two cases (Gene and Chelsea), a new infant was born within 2–3 months following the disappearance of its older sibling. Given a mean siamang gestation period of 7–7.5 months (Geissmann 1991), these disappearances must have occurred during the later stages of the mother's pregnancy with the subsequent infant. It is possible that there is an association between withdrawal of female care due to the energetic demands of pregnancy and increased risk of mortality.

Discussion

Previous studies have reported extensive male care in wild (Chivers 1974; Chivers and Raemaekers 1980; Gittins and Raemaekers 1980) and captive (Alberts 1987; Dielentheis et al. 1991) siamangs, with a transition from primarily female to primarily male care between the first and second years of life. The results of this study confirm that male care of infants is common in wild siamangs, and that most males do provide care for infants. In several other biparental primate species, male care is believed to be essential for infant survivorship (Wright 1984; Goldizen 1987a; Dunbar 1988). However, substantial variation in the quantity of care provided by males in this study and the relatively small contribution of most males to infant care caution against the assumption that biparental care is universal in siamangs. These results suggest that the behavior of male and female siamangs is not tightly constrained by an obligate requirement for biparental care.

Carrying of infants was by far the most frequently observed form of infant care by adult males and females, but carrying behavior varied dramatically between males. These differences may be explained in part by the presence of two adult males in some groups. Each group member's decisions about infant care should depend on those of other adults. Where more individuals provide care for infants, each individual may experience fewer opportunities to provide care for infants, infant motivation to solicit care may be lower, and the payoff for each unit of additional care may be reduced relative to groups with fewer helpers. Several studies of wild and captive callitrichids report reduced care by adult males in the presence of additional helpers (McGrew 1988; Tardif et al. 1990; Price 1992; Santos et al. 1997; Santos and Martins 2000). In this study, however, neither male in group B ever displayed significant involvement in infant care, and the emigration of Amung from group A did not result in a substantial compensatory increase in caring behavior by the remaining male Aming. The failure of some males to provide substantial quantities of care for infants cannot be explained simply by reduced opportunity or motivation due to the caring efforts of an additional male.

Proximate cues affecting male parenting behavior in biparental mammals may be physiological, environmental, or social. No research has been conducted to date on the hormonal correlates of male care in siamangs, although studies in other biparental primate species (e.g., Ziegler et al. 2000; Nunes et al. 2001; Fleming et al. 2002; Schradin et al. 2003; da Silva Mota et al. 2006; Gray et al. 2006) suggest that this area of investigation may prove fruitful. Alberts (1987) reported that the transition from primarily female to primarily male care in a group of captive siamangs occurred primarily in response to an increase in the rate of infant-initiated contact with males. In this study as well, siamang infants were obviously attracted to adult males, frequently approaching them and attempting to initiate physical contact. However, a transition to primarily male care did not occur in group B (and was transient in group A), in spite of persistent infant solicitations for male care. In wild siamang groups, male-infant dyads are often physically separated by gaps not easily negotiable by infants, and males sometimes move away when approached by infants. Therefore, while infant solicitations may affect male behavior, frequent infant solicitations for care are not sufficient to guarantee extensive male involvement in infant care. Information about the frequency of approaches by males and infants at Way Canguk is not available, but males often approached infants and picked them up, suggesting that many incidents of male care were initiated by males.

Female behavior may also affect male decisions. In the presence of a restrictive mother, males may not have the option of carrying infants (Schradin and Anzenberger 2003). However, all females in this study allowed male group members to approach and touch young infants, and older infants spent substantial time out of close proximity with their mothers. Therefore, it seems unlikely that the pronounced variation in male carrying behavior resulted simply from the differences in female parenting styles.

Certainty of paternity is a predictor of male parental effort in several vertebrate taxa (Dixon et al. 1994; Lifjeld et al. 1998; Chuang-Dobbs et al. 2001; Neff and Gross 2001; Sheldon 2002; Neff 2003), including some primates (Buchan et al. 2003). Information about the actual genetic paternity of infants in this study is not yet available. However, the reduction of male care in socially polyandrous groups is consistent with the interpretation that reduced certainty of paternity may result in reduced male investment in infant care. However, it is important to consider that females living in unimale groups may also mate polyandrously (Palombit 1994; Reichard 1995, this volume). If the presence of additional males results in more effective mate-guarding against extragroup males, then polyandrous grouping may not be associated with increased loss of paternity by dominant males (e.g., Whittingham et al. 1997). Further study of patterns of relatedness and paternity in polyandrous and monogamous groups will be essential to understanding the factors affecting individual behavioral decisions.

Male activities other than overt infant care may also benefit infants. For example, *babysitting* behavior, wherein one individual remains close to the infant while the others forage or engage in territorial defense, was observed in the study groups, and patterns of spatial proximity between males and infants in this study are consistent with the interpretation that some males frequently babysat infants during the second year of infant life. Passive supervision of the infant by a single group member while others engage in risky or difficult behaviors may reduce the infant's need for transportation, which may in turn reduce the frequency of more overt caring behaviors such as infant carrying, confounding studies of the relationship between the number of males in a group, and the quantity of direct male care received by infants.

Brockelman et al. (1998) suggest that additional adults in white-handed gibbon groups may positively affect infant and juvenile growth and development by providing partners for social play. At Way Canguk, however, the rarity of social play between infants and adults suggests that the effect of social play with adults on infant development may be negligible. However, it is possible that immature siamangs primarily benefit from social play interactions with males during the juvenile period, rather than during infancy.

Several models for the formation of polyandrous groups in cooperatively breeding animals suggest that subordinate males may benefit from polyandrous grouping either through inclusive fitness (if they are genetically related to one or both breeding adults) or through paternity of current or future offspring, and that dominant males can benefit from helping behavior by subordinate males (e.g., Gaston 1978; Emlen 1982a,b; Dunbar 1995; Ihara 2002; Kokko et al. 2002). For example, studies of callitrichid primates suggest that the presence of helpers is critical to offspring survival in the wild (Goldizen 1987b; Sussman and Garber 1987; Garber 1997), and genetic paternity by multiple males has been reported in polyandrous groups of moustached tamarins (Huck et al. 2005), which is consistent with a model of group formation in which dominant males sacrifice a portion of their paternity of the female's offspring in return for the help of subordinate males with infant care. In my study, however, infants in polyandrous groups received substantially less male care (and no more total care) than infants in monogamous groups: a pattern that is difficult to reconcile with a model where additional males are accepted or retained specifically as helpers. Furthermore, while siamangs are the only hylobatid species in which males routinely carry infants, polyandrous grouping and mating have been reported in a number of hylobatid species (e.g., Brockelman et al. 1998; Malone and Fuentes this volume; Reichard this volume). The results of this study suggest that dominant male or female siamangs are unlikely to benefit from the inclusion of an additional male as a helper. Other factors, such as biased sex ratios, habitat saturation, or territorial benefits of large group size, are probably more important in promoting facultative polyandry in some populations of siamangs as well as other gibbon species that do not display paternal care.

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Chapter 17
The Social Organization and Mating System of Khao Yai White-Handed Gibbons: 1992–2006

Ulrich H. Reichard

Introduction

Nonhuman primates are well known among mammals for having a highly social nature and for developing individualized, long-lasting, intimate social relationships (Haimoff and Gittins 1985; Cheney et al. 1986; Rendall et al. 1996; Boesch and Boesch-Achermann 2000; Zuberbühler and Byrne 2006). In both gregarious and semisolitary primates such as orangutans, social relationships are characterized by repeated interactions with the same partners both within and between groups (Singleton and van Schaik 2002; Robbins et al. 2005). It has been recognized (e.g., Dunbar 1998) that a complex social life and long-term individual-based partnerships may require specific cognitive capacities and has been a primary force for the evolution of large brains in primates.

Within the realm of primate social systems, a great diversity of social relationships can be seen across age-sex classes. One component of the social system, commonly denoted as the social organization, describes how groups are organized with respect to the size, sexual composition, and spatiotemporal cohesion of social groups (Kappeler and van Schaik 2002). Another component of the social system involves how sexual relationships are distributed in a community. Sexual relationships represent a specific subset of social contact confined to patterns of mating, which are commonly referred to as a species' mating system (Kappeler and van Schaik 2002). A natural link exists between the mating system and the social organization, because the number of adults present within a social group may influence the availability of potential mating partners (Cords 2000; Müller and Thalmann 2000; Schwab 2000; Kudo and Dunbar 2001; Zinner et al. 2003).

Pair living was once believed to be the same as monogamous mating and vice versa, because individuals living in social pairs were assumed to be "faithful" to one another at least for a breeding season, or in extreme cases for a lifetime (cf. Reichard 2003a). Behavioral and genetic studies of the past two decades,

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however, have shattered the static, simplistic monogamy concept and it has now become evident that pair-living and monogamous mating are not synonymous (Birkhead and Møller 1996, 1998). Transitions between pair-living and polyandrous grouping, as well as monogamous and polygamous mating strategies, can occur in response to environmental and social changes or because the use of multiple, diverse mating strategies maximizes the reproductive success of group members (Davies and Lundberg 1984; Goldizen 1987; Zabel and Taggart 1989; Whittingham et al. 1997; Zinner et al. 2003; Schülke 2005). Hence, mating relationships in pair-living species are best understood as a visible outcome of compromises between the sexes over mating, including flexible responses to changing socioecological conditions (Davies 1992).

Gibbons are Asian apes that have until recently always been portrayed as holistically monogamous, at least in textbooks (e.g., Jolly 1985; Relethford 1996; Boyd and Silk 1997). Differentiation between the social organization and the mating system appeared superfluous: researchers agree that female and male gibbons are commonly found in pairs, they are renowned for their continuous spatiotemporal proximity on coinciding home ranges, and pairs show a high degree of behavioral synchronization and pair-specific behaviors such as duet singing (Chivers 1974; Haimoff 1984a, b). Duetting has been interpreted as a reflection of a particular form of social relationship between a male and a female termed a pair-bond (Geissmann and Orgeldinger 2000). The notion of obligate monogamous pairs of adults with offspring as core social units of gibbon societies was ubiquitous in early field studies after Carpenter's (1940) landmark, although brief study of wild white-handed gibbons in Thailand (Chivers 1974; Ellefson 1974; Tenaza 1975; Tilson 1979; Gittins 1980; Srikosamatara 1980; Kappeler 1984; Mitani 1984; Srikosamatara 1984; Leighton 1987). These consistent reports of pair-living were interpreted as evidence of obligate sexual monogamy despite the paucity of detailed information on sexual behavior in early monographs (e.g., Chivers 1974; Ellefson 1974).

The harmonious nuclear family model of gibbon social organization (Kleiman 1981) met its first challenge when Haimoff and colleagues (1986; 1987) reported multifemale grouping in black-crested gibbons (*Nomascus concolor*) of the remote Wuliang and Ailao Mountains, Yunnan, People's Republic of China, implying a polygynous mating system; however, subsequent studies failed to confirm deviation from both pair-living and monogamous mating (Bleisch and Chen 1991; Sheeran 1993; but see Jiang et al. 1999). Around the same time, Srikosamatara and Brockelman (1987) also reported deviation from the pair-living pattern when they described a multifemale pileated gibbon group (*Hylobates pileatus*) at Khao Soi Dao, Thailand, in which two females carried nursing infants. When two months later one of the females and her offspring had disappeared, Srikosamatara and Brockelman (1987) concluded that they had witnessed an exceptional and instable case of familial polygyny. When deviation from the two-adult pair-living pattern was noticed in early gibbon studies (summarized in Fuentes 1999, 2000; Reichard 2003b) these observations were interpreted, for example, as rare exceptions after long periods of social stability (Chivers and Raemaekers 1980) or as unusual cases of mixed-species group compositions in small hybrid zones between closely related species caused by inadequate female song recognition (Brockelman and Gittins 1984). The possibility of behavioral plasticity – condition-dependent variation in individual mating strategies – and the implications for understanding gibbon reproductive strategies and cognition are only now being addressed.

The slow pace of progress in unraveling gibbon societies is understandable given several factors. Attendant to the inevitable difficulties of observing natural populations, research efforts are hampered by gibbons' small group sizes and slow life histories (Reichard and Barelli 2008), short field studies of few years, and small numbers of habituated individuals (e.g., Chivers 1974; Ellefson 1974; Ahsan 1995) surrounded by intolerant neighbors. All of these factors resulted in unavoidable weaknesses in the early fieldwork, which so persuasively framed gibbons as a prime primate example of strict territoriality and monogamy. The absence of large long-term field studies of gibbons, i.e., studies involving multiple groups and spanning several generations, hindered the discovery of behavioral flexibility and documentation of the full array of gibbon reproductive strategies, including between-group contacts, natal and secondary dispersal (but see Brockelman et al. 1998; Lappan 2007a, b), and non-pair grouping and non-monogamous mating patterns.

More recently, our understanding of the gibbon social and mating system was extended when the results of a 6-year study of three siamang (*Symphalangus syndactylus*) and three white-handed gibbon (*Hylobates lar*) groups in northern Sumatra, Indonesia, were published (Palombit 1992). Palombit (1994a) documented numerous group composition changes and described the first observations of extrapair copulations (EPCs; Palombit 1994b), i.e., sexual contacts between individuals who did not maintain a close spatiosocial pair bond. Despite frequent group composition changes (Palombit 1994a), however, no deviation from the two-adult pair-living pattern was noticed. Shortly thereafter, flexible sexual behavior was reported in white-handed gibbons (*Hylobates lar*) in Thailand's Khao Yai Mountains (Reichard 1995b).

Following rapid advances in studies of pair-living birds (cf. Black 1996; Bennett and Owens 2002), which provided powerful theoretical tools for understanding behavioral flexibility in pair-living species, conceptual progress has begun to penetrate the study of hylobatid social and mating behavior (Brockelman et al. 1998; Fuentes 2000, 2002; Reichard and Boesch 2003; Barelli et al. 2008). In a series of detailed reviews, Fuentes (1999, 2000, 2002) summarized the anecdotes of deviation from pair-living in so-called "monogamous primates." These reviews raised a much-needed awareness of the subtle differences between pair-bonding behavior, a two-adult group composition and a monogamous mating system. However, empirical data that describe and quantify the variability of gibbon social organization and mating strategies are still rare.

It is my aim in this chapter to fill this gap with data from the longest ongoing field study on gibbons to date, which has focused on the Khao Yai white-handed gibbon population. Demographic records for the oldest known individuals in this population span almost three decades: I have followed the fate of many individuals since October 1989, forming the basis for the analyses presented here. I investigate the links between a variable social organization and the mating system of Khao Yai gibbons with new demographic and behavioral data to evaluate behavioral flexibility in social grouping (social organization). I then take a closer look at sexual relationships and the mating system of Khao Yai gibbons. The chapter concludes with a discussion about the possible links between behavioral flexibility in social organization and mating, aspects of resource competition, and the evolution of gibbon cognitive evolution. Information on the genetic mating system of Khao Yai gibbons is not yet available.

The Flexible Social Organization of Khao Yai Gibbons

Anecdotal evidence of variation in the social organization of gibbon groups has accumulated in recent years for some populations (e.g., Brockelman et al. 1998; Fuentes 1999; Sommer and Reichard 2000; Reichard 2003b; Lappan 2007a,b). Based on a literature review, Fuentes (2000) hypothesized that 10% or more of gibbon social groups contain more than two unrelated adults. However, besides sporadic observations of non-pair-living groups, empirical data that will allow confirmation or rejection of Fuentes' (2000) estimate are not yet available.

Mo Singto – Klong E-Tau Study Site

Data on the Khao Yai white-handed gibbon social organization come from the Mo Singto – Klong E-Tau study site, Khao Yai National Park, Thailand (2,168 km^2; 101°22′ E, 14°26′ N; ~ 130 km NE of Bangkok; Fig. 17.1). Khao Yai National Park is part of the Dong Phayayen – Khao Yai Forest Complex (DPKY), which covers an area of 6,199 km^2 (Lynam et al. 2006) and has recently been designated a World Heritage site (UNESCO 2005). The Mo Singto – Klong E-Tau study site is a continuous forest area that covers approximately 8.5 km^2 of slightly hilly terrain (730–890 m above sea level) and is located in the central portion of the Khao Yai Mountains. Population density at the site is high, at ~4 groups and 15.9 individuals/km^2 (Fig. 17.1), but remains within the ranges of population densities reported from other field studies (Leighton 1987; Mitani 1990b; Borries et al. 2002; Bartlett 2007).

The Khao Yai Mountains are largely covered by seasonally wet evergreen forest (Kerby et al. 2000; Kitamura et al. 2004). The park experiences a distinct dry season (November–April) and a wet season (May–October) with an overall average precipitation of ~2700 mm (January 2001–December 2003).

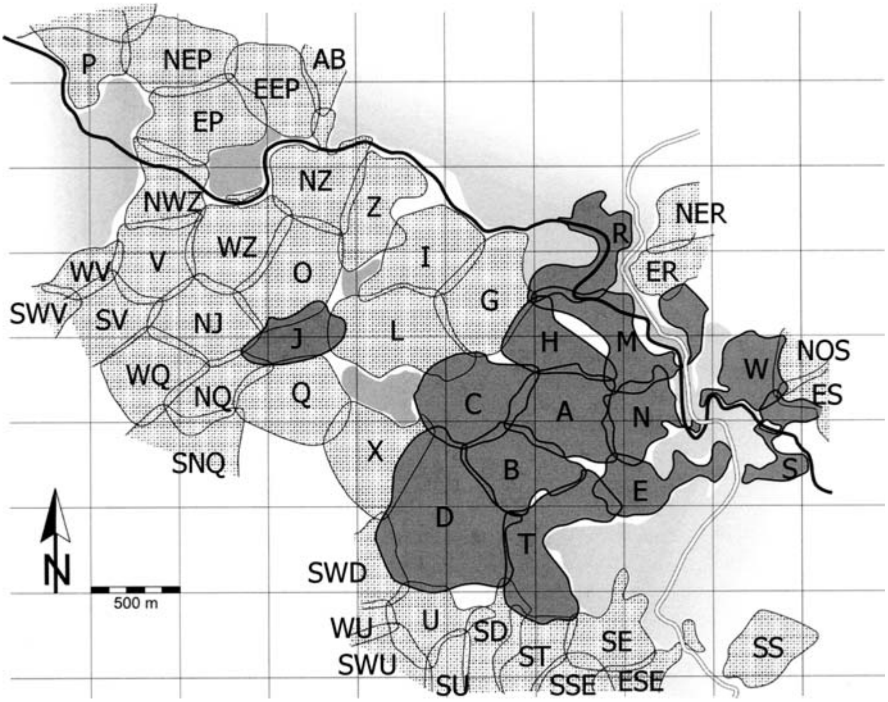


Fig. 17.1 Mo Singto – Klong E-Tau study site with home range outlines of habituated and neighboring study groups, Khao Yai National Park, Thailand. Thick, *solid line* = Lam Takhong river; thick, *open line* = N-S road traversing national park; *letters* = gibbon home range outlines; *dotted home ranges* = approximately known home range outlines; *fading areas* = grassland, patches of open canopy or low canopy regenerating forest along the river

Mixed Species Groups

Gibbon species are commonly allopatric and only few contact and natural hybridization zones between closely related species have been described (Brockelman and Gittins 1984). The Mun River and its tributary, the Takhong, mark the geographic distribution boundary of white-handed (*Hylobates lar*) and pileated gibbons (*H. pileatus*) in Northeast Thailand (Srikosamatara 1984). In the headwaters of the Takhong, around Haeow Suwat waterfall, in Khao Yai National Park, a contact zone exists where mixed-species trios have been described, i.e., a male–female pair and another adult of either species or a hybrid (Marshall et al. 1972, Brockelman and Srikosamatara 1984). The contact zone is narrow and populations only ~10 km away are again dominated by either white-handed or pileated gibbons (Brockelman and Gittins 1984).

The tip of the Mo Singto – Klong E-Tau study site closest to the contact zone is approximately 20–30 km away. In 1997, a single pileated gibbon female migrated into the study site and became resident on one particular home range. Over the years, this female has been involved in various partnerships with white-handed gibbon males and females (see Table 17.1). Because of the

Table 17.1 Frequencies of solitary individuals and social groups in Khao Yai, Thailand, white-handed gibbons

Census year#	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Mean ± SD
Solitary individuals																
females [N]	0	0	0	–	0	0	0	1	1	0	1	0	0	0	0	
males [N]	1	1	0	–	0	0	0	0	1	0	0	0	0	1	0	
[%]	7.1	6.3	0	–	0	0	0	3.8	8.3	0	3.4	0	0	6.3	0	2.5 ± 3.2
Groups																
pair-living [N]	12	14	10	–	12	12	13	20^{∂}	19^{∂}	31^{∂}	23^{∂}	10^{∂}	10^{∂}	9	9^{∂}	
[%]	85.7	87.5	90.9	–	85.7	85.7	81.3	76.9	79.2	88.6	79.3	76.9	66.7	56.3	60.0	78.6 ± 10.7
multimale single-female [N]	1	1	1	–	2	1	1	4	2	3	5	3	5	5	5	
[%]	7.1	6.3	9.1	–	14.3	7.1	6.3	15.4	8.3	8.6	17.2	23.1	33.3	31.3	33.3	15.8 ± 10.4
multifemale single-male [N]	0	0	0	–	0	0	1	1	1	1	0	0	0	1^{∂}	0	
[%]	0	0	0	–	0	0	6.3	3.8	4.2	2.9	0	0	0	6.3	0	1.7 ± 2.5
multimale multifemale [N]	0	0	0	–	0	1^{∂}	1^{∂}	0	0	0	0	0	0	0	0	
[%]	0	0	0	–	0	7.1	6.3	0	0	0	0	0	0	0	0	1.0 ± 2.4
Total units	14	16	11	–	14	14	16	26	24	35	29	13	15	16	15	

= data collected during last quarter of calendar year (Oct–Dec).
∂ = one group included the same pileated gibbon female (H. pileatus) across all years.
_ = no census conducted.

mixed-species status, I interpreted the groups in which this female was involved as exceptional (see below: Social Organizations In Khao Yai Gibbons). She was the only pileated gibbon individual in this sample, although beyond the immediate study site occasionally pileated or pileatus-lar-backcross females were heard singing.

Social Groups

The term "social group" is used to describe the social organization of group-living gibbons and I use "solitary individual" to refer to animals that appeared to be alone or "floating" (Cowlishaw 1996). Individuals were considered adult once they completed physical growth, which in this population does not occur before the age of 7–8 years in females and about 8 years in males (for age-class definitions see Reichard 2003b).

Data Collection

Part of the Mo Singto – Klong E-Tau gibbon population has been studied since the early 1980s (Treesucon 1984; Raemaekers and Raemaekers 1985; Whitington 1990), but behavioral observations and demographic records presented here are based on the observations collected by field assistants and myself between October 1989 and December 2006. In 1989, a single gibbon group was habituated (group A), but by the end of 2006 this number had grown to 14 (Fig. 17.1). Systematic annual censuses (Ross and Reeve 2003) were conducted from 1992 to 2006 and included 44 social groups over the years. Group compositions were irregularly tracked throughout those years, but identification and designation of social groups was confined to the census results collected during the last quarter of each calendar year, except 1995. Instead of a census in late 1995, a census was carried out in early February 1996 to detect composition changes, but those survey results were excluded from the data set. The majority of social groups were contacted repeatedly each year; the habituated study groups in particular were continuously monitored, because they were the focus of intense, systematic data collection for other purposes (Nettlebeck 1993; Neudenberger 1993; Reichard and Sommer 1997; Reichard 1998; Sommer and Reichard 2000; Chambers et al. 2004; Clarke et al. 2006; Fürtbauer 2006; Barelli et al. 2007; Savini et al. 2008).

All individuals encountered during census walks were assigned to one of two categories based on their solitary or group living status. Individuals were designated "solitary" if they were continuously without other gibbons. An individual in the company of other gibbons was considered a "member of a social group." Members of social groups were usually easily identifiable, because they coordinated daily activities, frequently interacted with and stayed more or less continuously in spatial proximity with other individuals (e.g., remaining within view for most of the day). Cohesion is notably high in white-handed gibbons (Nettlebeck 1993; Neudenberger 1993; Reichard

1995a); only mature male offspring occasionally range further than 50 m from others for periods exceeding an hour (Fürtbauer 2006).

Individual Recognition

Individuals were recognized based on three traits: (1) Pelage color: white-handed gibbons at Khao Yai are asexually dichromatic. They are dark or buff, which was recognizable within the first week of life. (2) Shape, size, and "whiteness" of the white face ring, eyebrows, and white areas of the hands and feet; and (3) idiosyncratic markers (scars, stiff or missing fingers or toes, etc.). I distinguished a black (coded: black-dark) and a brown (coded: brown-dark) type of the dark color morph and a light (coded: light-buff) and cream-brown (coded: cream-buff) type of the buff morph to aid individual identification. The white circumfacial pelage marking is a reliable, individually recognizable feature in many hylobatid species including white-handed gibbons (Geissmann 2003).

Field Key to Identify Social Groups and Solitary Individuals

A hierarchical, three-step key was used to determine the composition of social groups and solitary individuals in the field (Fig. 17.2).

Step one: the number of adult individuals present was counted. (i) If an adult was encountered alone and neither joined nor was joined by members of a social group during the observation period, that individual was considered *solitary* (*n* = *7 individuals*). Contact times with solitary individuals were short (range: 10–55 min), because solitary individuals were shy and unhabituated except for one well-known young adult male who had dispersed from its natal group about a year prior to the time when he was found to be solitary. Unfamiliar solitary

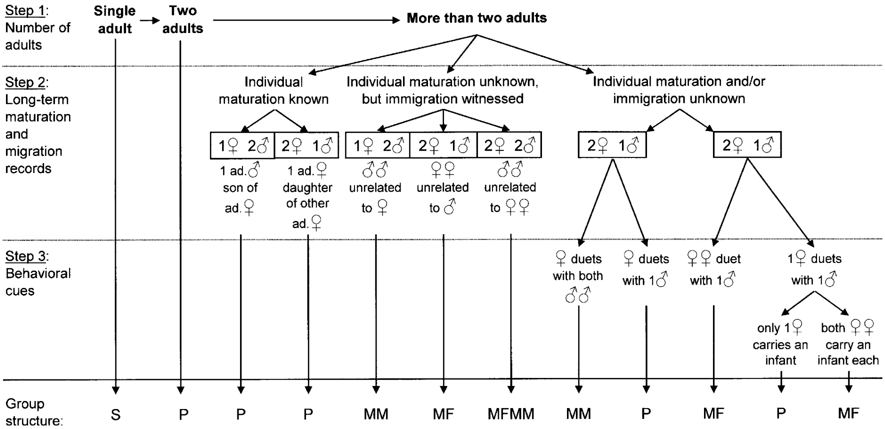


Fig. 17.2 Social organization identification key. ad. = adult; S = solitary; P = pair-living; MM = multimale; MF = multifemale; MFMM = multifemale-multimale

individuals all fled rapidly after having spotted a human observer and thus naturally limited observations could be made while hiding. Despite pursuit of fleeing solitary individuals, none was contacted a second time on the same day or later. (ii) If only two adults were counted as the social group, they were always considered *pair-living* ($n = 155$).

Step two: When more than two adults were counted ($n = 96$ social groups), long-term maturation and migration histories were used to differentiate groups with mature adult offspring (46% of groups) from groups with an additional, unrelated adult (54% of groups). Social histories are known from my own long-term monitoring of the population spanning more than 3200 h of direct observations spread across more than 500 days over 17 years (October 1989–December 2006). These data were complemented with published migration and maturation records of individuals in study groups A, B, and C (Treecuson and Raemaekers 1984; Treesucon 1984; Whitington 1990; Brockelman et al. 1998). (iii) Groups with three adults including a mature offspring were always identified as *pair-living*, based on the assumption that mature offspring were nonbreeders in their natal group and hence would not count as potential mates. In groups where social histories of all offspring were known, no copulation attempt with an offspring has ever been recorded. Hence, for groups with an adult offspring, I assumed that the offspring delayed dispersal, which has been documented for this population (Brockelman et al. 1998). Therefore, such a group functionally resembled a pair-living group. (iv) If more than two adults were present and migration – i.e., emigration or immigration – of an adult had been witnessed, social groups were considered *multimale, multifemale*, or *multimale multifemale*. The combination of social- and migration-history records suggested it was highly unlikely the immigrant was related to the opposite-sex breeding adult in his new group. Designation of social organization was independent of kin relationships between same-sex adults in groups, as I was primarily interested in the number of potential breeding partners within social groups. For example, a group with a (presumed) father–son pair was identified as multimale if the son's mother was replaced by a new female, because both males were potential breeding partners of the new female.

Step three: If more than two adults were present in a group, but individual social histories and migration patterns were unknown ($n = 10$ groups; five groups with two females; five groups with two males), social groups were categorized following behavioral cues. Group structure assignment in the absence of individual social histories or migration was conservative; groups were considered pair-living unless clear deviation from behavioral patterns consistently observed in pair-living social groups strongly suggested a different structure. By definition, this procedure can lead to overestimation of the proportion of pair-living, but not group-living, individuals. The following behavioral cues and procedures were used to identify deviation from patterns seen in pair-living groups: (1) In groups with two adult males, (a) if a female sang duets with both males, the group was classified as *multimale*, because long-term observations of habituated groups revealed that mature sons never sang duets with their mothers (unpublished data). (b) If instead, a female consistently sang duets with only one male, the group was assumed to be pair-living and one adult male was presumed to be the female's mature son. A common singing pattern in known multimale groups featured one male consistently and the other occasionally singing duets with the female. (2) In groups with two adult females, (c) a group was considered multifemale if both females alternated duet singing with a male or both carried a dependent infant. (d) The group was considered pair-living if only one female sang duets and only the same female carried an infant, in which case one female was assumed to be a retained adult daughter.

In social groups with more than two adults where individual social histories were known, an age-difference between same-sex adults was usually noticeable. However, age was not used as a variable in assigning social organization for two reasons: birth dates were unknown for many individuals, and visual age estimates in the absence of known birth dates were subjective.

Social Organizations in Khao Yai gibbons

Two hundred and fifty-one ($n = 251$) social groups and seven solitary individuals ($n = 7$) were recorded over 14 census years (1992–2006). Because gibbon groups at Khao Yai are territorial and spatially stable, most individuals were censused multiple times during consecutive years. In contrast, all solitary individuals were encountered only once. Thus, the sample comprised seven solitary individuals and 44 groups (Table 17.1). Three social groups ("K", "Y", and "WJ") dissolved after 1, 2, and 3 census years, respectively. Of the remaining social groups ($n = 41$), about one-third were censused only once, primarily during extensive census walks in 2001 and 2002. Nearly half (46.3%) were censused over at least 5 years, about one-third were censused over at least 10 years, and six groups (13.6%) were censused each year over the entire 14-year study period.

Solitary individuals of both sexes were infrequently encountered and constituted on average less than 3% of the communities' social groups and solitary individuals across years (Table 17.1). During 57% of census years no solitary individual was discovered. All solitary individuals were shy (average contact time <60 min) and, by definition, had no contact with other gibbons and neither engaged in intergroup encounters nor vocalized loudly. The only exception was one habituated, postdispersal young adult male, who was found singing a loud male solo song in an area of degraded, low-canopy forest bordering grassland, where no gibbons had been previously seen. Solitary animals seemed to lack a defined home range as inferred from single contacts even in areas walked frequently. They were encountered while quietly foraging in peripheral/overlapping areas between the adjacent home ranges of known social groups. All but the solo singing male immediately fled upon noticing a human observer.

The majority of social groups across census years were pair-living (average ± SD across years: 78.6 ± 10.7% of groups and solitary individuals; Table 17.1). However, more than two adults were found in 18.3% of groups ($n = 251$ groups; excluding solitary individuals). Most non-pair-living groups were multimale (average ± SD across years: 15.8 ± 10.4% of groups and solitary individuals, see Appendices 1, 2, 3, and 4), but maximum group size did not exceed six members. Multimale groups typically contained only two adult males except in one group where three adult males lived together with one adult female for several months (see Appendix 2). Other social arrangements were rare. For example, one-male multifemale groups were recorded only five times (average ± SD: 1.7 ± 2.5% of social groups and solitary individuals, see Appendix 3), and only one mixed-species multifemale multimale group was recorded; the same group was observed during two consecutive census years (average ± SD: 1.0 ± 2.4% of groups and solitary individuals, see Appendix 4).

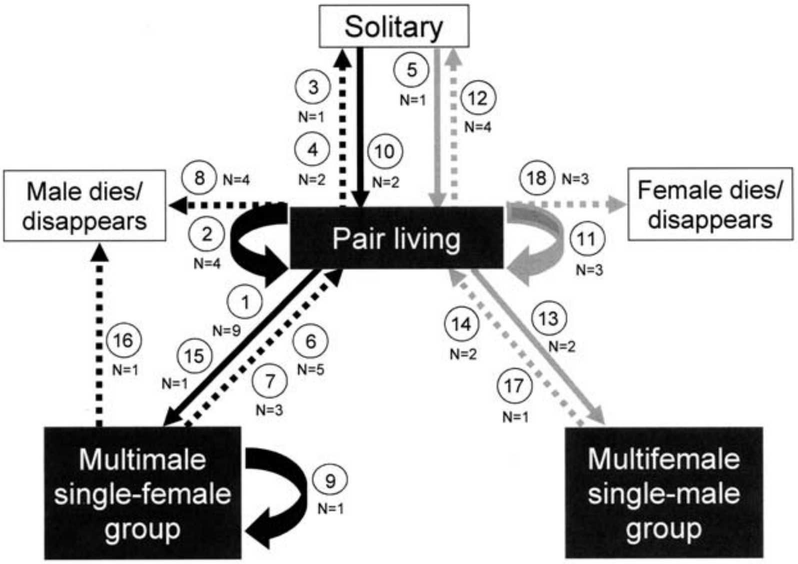
Pair-living and multimale grouping seemed to be alternative strategies in the Khao Yai population, because (1) only pairs and multimale groups were frequent (i.e., > 5% of groups) and consistently present throughout the entire 14-year study period. In contrast, other group types showed considerable interannual variation and were absent during most census years. (2) Group formation and dissolution was witnessed only for pairs and multimale groups, except for the formation of the exceptional mixed-species multimale multifemale group (Fig. 17.3). (3) Only pairs and multimale groups were stable over time and lasted several years. The longest known multimale group existed for 12 years; the longest known pair-living groups existed for 14 years. In contrast, the longest known multifemale group existed for about two years.

The Variable Mating System of Khao Yai Gibbons

Assessment of sexual activities of Khao Yai gibbons was limited to a subset of individuals included in annual censuses, because mating was infrequent and largely unpredictable. Documentation of sexual interactions required observing habituated individuals to avoid bias against observations of non-monogamous mating, as the chance to witness non-monogamous mating behavior in a dyad where only one member is habituated is negligible.

Sexual Behavior Data Collection

Data on sexual behavior presented here come from the Khao Yai long-term database accumulated by field assistants, students, and me, entered on daily observation check-sheets since October 1989. Mating behavior was recorded following standard instantaneous, continuous, or *ad libitum* sampling methods (Martin and Bateson 1993).



① Male immigration results in multimale single-female group (N=9)
② Male replacement results in pair-living group (N=4)
③ Male emigration leads to solitary female (N=1)
④ Male replacement leads to solitary male (N=2)
⑤ Male joins solitary female resulting in pair-living group (N=1)
⑥ Male emigration results in pair-living group (N=5)
⑦ Male death/disappearance results in pair-living group (N=3)
⑧ Male dies/disappears following male replacement in pair-living group (N=4)
⑨ Male emigration results in multimale single-female group (N=1)
⑩ Female joins solitary male resulting in pair-living group (N=2)
⑪ Female replacement results in pair-living group (N=3)
⑫ Female death/disappearance leads to solitary male (N=4)
⑬ Female immigration results in multifemale group (N=2)
⑭ Female disappearance results in pair-living group (N=2)
⑮ Male immigration into multifemale single-male group results in multifemale-multimale group (N=1)
⑯ Male death/disappearance results in multifemale single-male group (N=1)
⑰ Female emigration results in pair-living group (N=1)
⑱ Female disappears after female replacement in pair-living group (N=3)

Fig. 17.3 Membership transitions in social groups in white-handed gibbons. *Light gray* = change involving female; *black line* = change involving male; *broken line* = subtraction; *solid line* = addition; *bent arrow* = change in individual membership without change in social organization

Identification of mating strategies follows common classifications. Males seen to mate with only one female partner were categorized as sexually *monogamous*; males who mated with multiple females were considered sexually *polygynous*. Females seen to mate with a single male mating partner were identified as sexually *monandrous* and those with multiple partners as sexually *polyandrous*.

Individual contribution to the data set of sexual activities was heterogeneous, because adult individuals spent between <1 month and 14 years continuously in the population. This extreme individual variation occurred because individuals matured or disappeared at different times during the long data collection period. A detailed description of individual contributions to the overall observation period and social histories in relation to sexual activity is omitted, because high interindividual variation with regard to time of maturation or continuous presence in the study population would have required lengthy case-descriptions of many individuals. Varying individual contribution to the data set did not bias my analyses because I was primarily interested in gross patterns of mating strategies.

The Data Set of Adult, Sexually Active Gibbons in the Population

Between 1992 and 2006, fifty-four adults ($n = 25$ females, $n = 29$ males) were resident in fourteen habituated focal groups (A, B, C, D, E, H, J, M, N, NOS, R, S, T, and W). Thirty-three sub adults reached adulthood during the study ($n = 15$ females, $n = 18$ males). Of these matured subadults, seven males and six females disappeared with unknown fate after their natal dispersal, as did one female upon reaching maturity, which coincided with her secondary dispersal. These individuals were omitted from analyses, although they were technically adults in the population. Of the remaining matured subadults ($n = 8$ females, $n = 11$ males), two males and one female delayed dispersal, whereas nine males and five females remained in the study population after successful dispersal. Two females that reached adulthood were seen copulating for the first time with immigrant males prior to natal dispersal and were included in the analyses despite their dispersal/disappearance with unknown fate shortly thereafter.

In summary, data on sexual activities originate from 17 females ($n = 17$) and 20 males ($n = 20$) that were adult at the onset of observations and eight females ($n = 8$) and nine males ($n = 9$) that became adults over the course of data collection. The following analyses treat all 25 adult females and 29 adult males equally, independent of their maturation history.

No mating behavior was recorded for 12 females (48.0%; $n = 25$) and 10 males (34.5%; $n = 29$ males; Tables 17.2 and 17.3). Of this group, it is unlikely that sexual strategies were adequately documented for six females and five males, because (a) four individuals remained in their natal groups (three males, one female); (b) one male and one female were only very briefly seen after dispersal before their disappearance; (c) one female and one male disappeared shortly after the beginning of data collection, and (d) three females

Table 17.2 Sexual strategies of wild white-handed gibbon females, Khao Yai National Park 1992–2006

		Polyandrous					
	Monoandrous	Serial monogamous	Serial monandrous and EPCs	Serial monandrous and polyandrous	Polyandrous	Polyandrous and EPCs	Serial monoandrous and polyandrous and EPCs
Female	Akira[1]	Rung[3]	Bridget	Brenda	Cyrana	Jenna	Andromeda
	Eclipse[2]		Brit		Daow		
	Natasha		Cassandra		Hima		
Total	3	1	3	1	3	1	1

[1] young adult female first seen when still in the natal group; dispersed/disappeared shortly thereafter.
[2] female initially not followed systematically; left after 3 years.
[3] young adult female, matured and subsequently dispersed the year before data collection ceased.

Table 17.3 Mating strategies of wild white-handed gibbon males (Khao Yai National Park, Thailand 1992–2006)

		Polygynous				
	Monogamous	Serial monogamous	Serial monogamous and EPCs	Monogamous and EPCs	Monogamous and EPCs (attempt)	Polygynous
Males	Actionbaby[1]	Chikyu	Bard	Amadeus	David	Christopher[3]
	Chana[2]	Elias	Claude	Efendi		
	Diego	Fearless	Cassius II	Chet[5]		
	Frodo		Marlon			
	Joe					
	Nithat[3]					
	San[4]					
Total	7	3	4	3	1	1

[1] lived successively with two females, but sexual activity was only recorded for one mateship due to irregular observations during previous mateship.

[2] immigrated into the population < 3 years before data collection ceased.

[3] only lived with a female during last 1.5 years of data collection.

[4] delayed dispersal; resident in his natal group.

disappeared shortly after they were first noticed in the population. If I omit individuals from whom I was unlikely to record mating behavior even if it occurred, no mating behavior was recorded for six females and five males. In other words, the majority of adults in the population were sexually active and available for analyses of sexual strategies (68.4%, $n = 19$ females; 79.2%, $n = 24$ males). Two additional unhabituated males were involved in extrapair copulations (EPCs) with a habituated female, but they were not included in analyses of male sexual strategies.

Mating Strategies of Khao Yai Females and Males

Of females seen to copulate ($n = 13$), only three (23.1%) were seen to copulate with a single male, whereas 10 (76.9%) copulated with more than one male, usually two or three males and in one exceptional case (Andromeda) with eight different sexual partners (Table 17.2). Of females seen to copulate with a single sexual partner (i.e., monandrous females) one was a young adult female (Akira) still in her natal group, who dispersed/disappeared soon after her first copulations were noticed (Table 17.2). A second monandrous female (Eclipse) was initially not followed systematically when she lived with two males in a multimale group, and she left after two years. If these two females are set aside, because it is unlikely that their sexual strategies were described comprehensively, it becomes evident that with only one exception adult females at Khao Yai have more than one sexual partner (mean 2.3, SD ± 0.7 partner; excluding Andromeda, who seemed to have had unusually many sexual partners).

Of 10 females sexually active with more than one partner, only one, a young adult female, was observed only in successive partnerships, whereas nine females (90%) were involved in simultaneous mating relationships. Overall, the sexual strategies of Khao Yai females were flexible and diverse (Table 17.2). Of females that were sexually active, five (38.5%) were observed in at least one extrapair copulation, and six (46.2%) maintained simultaneous sexual relationships in multimale groups. Most females engaged in a combination of different sexual relationships during their reproductive careers, i.e., taking part in successive monandrous relationships in combination with extrapair copulations or periods of polyandrous mating in multimale groups or both (Table 17.2). Five of the six females (41.7%) that lived in multimale groups maintained long (>1 year) sexually polyandrous relationships.

Of sexually active males ($n = 19$), seven (36.8%) were monogamous (Table 17.3). However, one of the monogamous males, San, delayed dispersal and was still a resident in his natal group at the end of observations. Another male, Nithat, only lived with a female during the last 1.5 years of data collection. A third male, Chana, immigrated into the population less than three years before data collection ceased. Finally, a fourth monogamous male, Frodo, was known to have lived successively with two females; sexual activity was only recorded during one of these mateships because of irregular observations during his first pairing. After omitting those cases for which documentation of the full array of sexual strategies was unlikely, only 20% of sexually active males ($n = 15$) were monogamous (Table 17.3). Hence, as in females, the majority of adult males of the Khao Yai population engaged in polygamous mating strategies.

Of 12 males with multiple sexual partners, three (25%) were serially monogamous with successive partners. As already seen for females, males' sexual strategies were also variable (Table 17.3). For eight of 12 males (66.6%) their sexual strategy included documented EPCs or once an EPC attempt. Of the males living in multimale groups only one, Diego, was seen to attempt copulating with a neighboring female. Otherwise, all males who achieved extrapair copulations were pair-living at the time. Finally, only one male, Christopher, was seen to be involved in concurrent sexual relationships with two female group members after he had replaced a male and the group's subadult female, Akira, had matured to an adult. Interestingly, only weeks after sexual activity between Christopher and the Akira was noticed, this female disappeared with unknown fate.

For the males living in multimale groups "D" and "J," detailed information on sexual behavior was available for two periods of night-tree-to-night-tree follows (group "D": December 2003–August 2004; group "J": August 2003–December 2004). Copulation success was highly skewed in both groups. In group "D", one male was involved in 88.6% of copulations ($n = 79$) and likewise in group "J" one male achieved the majority of copulations (86.4%; $n = 88$), whereas copulation by the other two males was infrequent (Table 17.3). In both groups, both males had higher copulation rates during the same time periods (Fig. 17.4a,b), except at the end of 2004, when Frodo had a low copulation frequency while Joe copulated frequently (Fig. 17.4b). To attempt to discern which of the males was more likely to have fathered the female's subsequent offspring, I identified the month with the highest conception probability for the two females by back-counting 210 days – the average gestation length in white-handed gibbons – from the infants' births. During the presumed month of the group "D" female's conception, both males copulated with her. The pattern was less clear in group "J": male Frodo was seen to copulate during the month preceding and the month following the most likely period of conception, but during the conception month no copulation was recorded. Given the pattern of copulation around and during females' conception months, both males in multimale groups could have potentially fathered the females' offspring. Hence, a possibility for sperm competition may exist in gibbons. However, before conclusions about sperm competition can be drawn genetic paternity studies must be conducted.

Variable Social Organization and Mating System in Khao Yai Gibbons

The results of my long-term data confirm and extend earlier descriptions of multimale grouping and polyandrous mating at Khao Yai (Reichard 1995b; Sommer and Reichard 2000), and add to a growing body of evidence for a variable social organization and mating system of wild gibbon populations

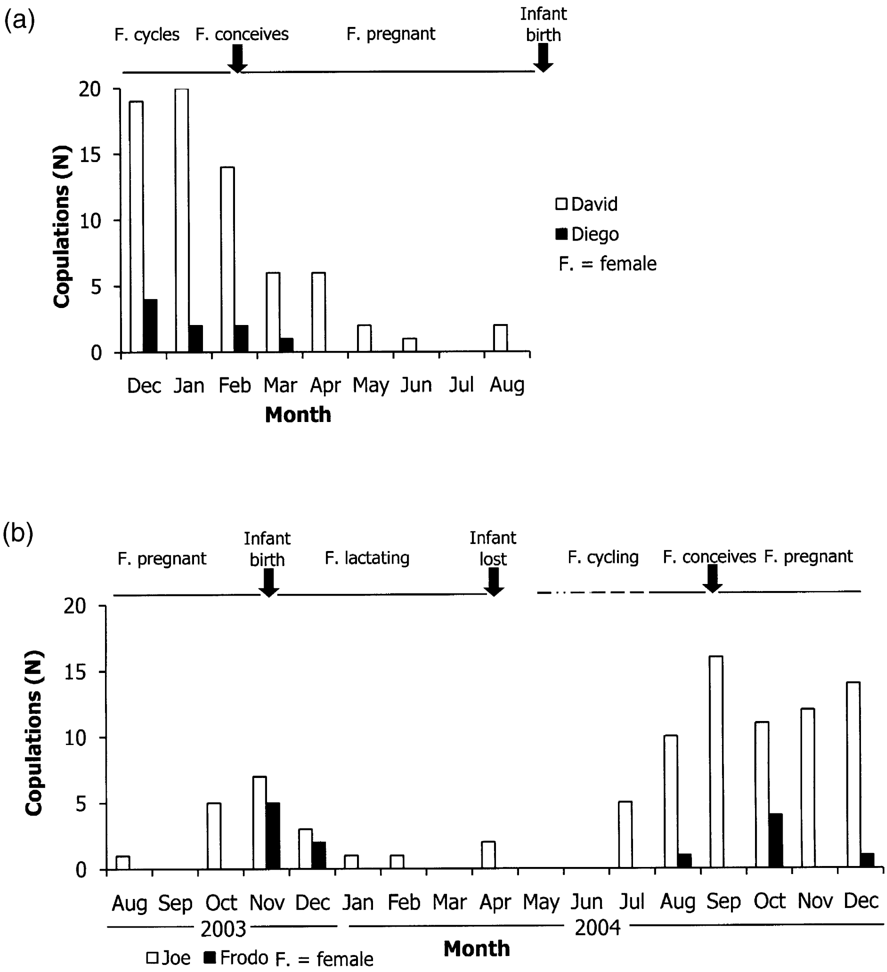


Fig. 17.4 Copulations and reproductive events in multimale groups (**a**) "D" and (**b**) "J", 2003–2004

(Palombit 1992; Fuentes 1999, 2000, 2002; Reichard 2003b; Lappan 2007a,b; Barelli et al. 2008; Malone and White 2008; Reichard and Barelli 2008). This study presents quantitative information on the magnitude of non-monogamous grouping and mating in a hylobatid community, which is important for an understanding of gibbon social dynamics and individual reproductive strategies.

Recognition of a variable social organization has important implications for a comprehensive understanding of gibbon social systems. It is becoming increasingly clearer that gibbon partnerships do not endure for lifetime nor are they terminated primarily by the death of one partner. In my sample, secondary dispersal occurred in males and females, indicating that intrasexual competition for partners and breeding positions does not end with natal dispersal and the formation of a close pair-relationship. Rather, competition continues to be important and permeates individuals' entire reproductive lives.

Four important points emerge from this study. First, the social organization of Khao Yai gibbons extends systematically beyond pair-living. Although pair-living dominated in frequency, and may therefore still be seen as the "modal social structure," a noticeable, stable fraction of about 15% of social groups were multimale, composed of two adult males living and mating for prolonged times with an unrelated adult female. With an adult male group size of two and rarely three, white-handed gibbons at Khao Yai exemplify the smallest possible multimale group structure.

Second, solitary individuals, who have frequently been noticed elsewhere (Mitani 1990a; Cowlishaw 1996), were rare or absent in the Khao Yai population in most census years, as were instances of multifemale grouping. A single, exceptional case of a mixed-species multimale multifemale group was observed. The dominant group types were pair-living and multimale groups. These groups did not reflect individual-specific strategies throughout reproductive careers, but rather flexible responses to changing social dynamics in the population resulting from phenomena such as individuals migrating, dying/disappearing, or aging, which leads individuals to become targets for replacement attempts. Group membership changes repeatedly led to multimale grouping, and many adults experienced periods of pair-living as well as periods of multimale grouping at different times in their reproductive years. These observations corroborate an early, commonly overlooked cautionary note by pioneer Carpenter (1940: 125) who wrote:

> It was found that the family pattern with limited variations characterized gibbon societies. The term 'monogamous mate-ship' might be used [...] but this description may be an overgeneralization [...]. It has also been shown that there are extra-group individuals which are described as being in a state of transition or as being old isolates.

Carpenter correctly noted that additional adults sometimes reside in gibbon groups and that these individuals were not always of old age. He also clearly and mistakenly thought deviation from the pair-living pattern generally represented a transitional stage. The long-term data from Khao Yai, at least, suggest that multimale units are an alternative grouping strategy to pair-living that potentially persist for periods of a decade or longer.

Third, in contrast to early descriptions of strict monogamy in gibbons (Brockelman and Gittins 1984; Leighton 1987), data on sexual activities of Khao Yai adults who spent sufficiently long periods of their reproductive lives in the population (>3 years) reveal that most adults were polygamous and established serial or simultaneous sexual relationships with more than a single partner (Barelli et al. 2007, 2008; Reichard and Barelli 2008). Additionally, for most sexually monogamous individuals in this study, the full sexual behavior repertoire could probably not be documented due to data limitations. The notion of polygamous sexual strategies in gibbons is consistent with previous records from Khao Yai (Reichard 1995b; Reichard and Sommer 1997; Sommer and Reichard 2000; Reichard 2003b) and recent observations from other gibbon populations (Palombit 1994b, 1996; Lappan 2005, 2007a,b; Malone and White 2008). The observation of an active female role in polyandrous mating behavior is also supported by the recently documented advertisement function of the moderate sexual swelling of white-handed gibbons (Barelli et al. 2007). Like many pair-living birds (Westneat et al. 1990; Griffith et al. 2002) and some mammals (Mason 1966; Hubrecht 1985; Richardson 1987; Sillero-Zubiri et al. 1996; Digby 1999; Fietz et al. 2000; Wolff and Dunlap 2002; Schülke et al. 2004; Morino this volume), Khao Yai gibbons of both sexes strive to maximize reproduction through mating with multiple partners.

Female sexual polyandry is a behavior that gibbons share with other primate females (Hrdy 1986, 2000) and a wide range of other organisms (Keller and Reeve 1995; Zeh and Zeh 1997; Hosken and Stockley 2003; Thom et al. 2004). The relatively high frequency of polyandrous mating in gibbon females is interesting. Since female gibbons cannot be forced to copulate, we must assume that they actively seek additional mating partners. Consequently, advantages that females gain from sexual polyandry should be expected to be substantial (Eberhard 1998) because mating can be costly and, other things being equal, is probably best avoided by females (Daly 1978; Gomendio et al. 1998; Johnstone and Keller 2000; Nunn et al. 2000; Nunn and Altizer 2004).

Fourth, in multimale gibbon groups two adult males are sexually active and copulate with the female. In two groups mating success was highly skewed toward one male, but both males of the group copulated during the same female cycle periods, including around or during the females' fertile phase. However, more data on multimale grouping and especially on female endocrinology and paternity are needed before conclusions can be drawn about the biological and evolutionary importance of female sexual polyandry and multimale grouping in gibbons.

In summary, Khao Yai gibbons were flexible along two axes: (1) social grouping patterns were variable and included pair-living and multimale grouping; and (2) mating relationships were variable with most adults mating polygamously with more than one partner at a time.

The important questions remaining include these: why is such extensive flexibility in grouping and mating observed at Khao Yai, and is the Khao Yai population perhaps exceptional? I believe that the Khao Yai population is not exceptional. What differs is that my data spans a longer period and involves more groups than at other sites. The presence of 14 habituated social groups with mostly adjacent home ranges and their neighbors (Fig. 17.1) allow the investigation of wild gibbon behavior at a community level that is not yet accessible at most other sites (but see Palombit 1992; Lappan 2007a). In gibbons, with their small group size, this type of investigation is a prerequisite to documenting non-pair-living group structures and non-monogamous mating, because otherwise dispersal and migration patterns as well as between-group contacts cannot be studied in detail.

Skeptics may still argue that the situation at Khao Yai is exceptional, because a “crowding effect” resulting from an unusually high population density could perhaps force otherwise pair-living, monogamous individuals to form larger, non-monogamous groups. Such an effect has been suggested for a small African antelope (Arcese et al. 1995) and some co-operatively breeding birds (Stacey and Koenig 1990). Crowding is, however, unlikely to explain the observed behavioral patterns at Khao Yai, because while population density at the site is high, it is within the range of comparable densities reported for other gibbon populations (Leighton 1987; Mitani 1990b; Borries et al. 2002; Yanuar this volume) where flexible grouping and mating has so far not been reported.

Non-monogamous group structures were likewise not attributable to aging of individuals leading to a rare influx of new individuals during periods of “social breakdowns” occurring only after long intervals of stability, as has been previously suggested (Chivers and Raemaekers 1980). Instead, shifts between pair-living monogamy and multimale polyandry occurred repeatedly in both directions during this study; multimale groups sometimes persisted for years, and social change was not primarily caused by deaths or disappearances of aged adults. Instead, immigration of young adult males into established pair-living groups was among the primary causes for the observed social dynamics in the population (Fig. 17.3).

Adaptive explanations for multimale polyandry by females appear straightforward. Generally, females may directly profit from this arrangement through additional food resources or increased paternal investment (Stacey 1982; Dunbar 1995; Põldmaa and Holder 1997; Soltis 1997; Heymann and Soini 1999). They may also profit indirectly through an increasing probability of conception in case of a social mate’s temporal or permanent sterility (Gromko et al. 1984), or by producing male offspring with an increased fertilization probability under conditions of sperm competition (Põldmaa and Holder 1997; Yasui 1997; Byers and Waits 2006). Decreased infanticide risk due to paternity confusion (Hrdy 1979; van Schaik and Janson 2000) and doubled infant-protection power from two potential sires are also the potential benefits for females (Borries et al. 1999). Future studies will have to address these possibilities and reveal which positive effects polyandry may have on gibbon females’ reproductive success, if any.

In contrast, explaining multimale polyandry from a male perspective appears more difficult because of the general reproductive advantages of polygyny for mammalian males (Williams 1966; Trivers 1972; Parker 1979). Multimale polyandry is rare in mammals and where it exists it often occurs in conjunction with pair-living monogamy. In tamarins for example (Goldizen 1987; Goldizen and Terborgh 1989), multimale polyandry derives from the need for direct paternal investment of more than one male to successfully raise sets of twins or triplets (Goldizen 2003). Such reasoning cannot explain multimale polyandry in white-handed gibbons or other hylobatids. Gibbon females produce a single offspring spaced at long three-year intervals, and direct paternal care in the form of infant carrying is absent in the hylobatid family, with the notable exception of occasional infant carrying by male siamangs (*Symphalangus syndactylus*). But even in siamangs male help may not explain the occurrence of polyandry (Lappan this volume).

Multimale Polyandry, Resource Distribution and Territorial/Female Defense

Multimale polyandry in the absence of direct paternal care may evolve via cooperative territory or female defense, or both. If female reproduction critically depends on the resources of a territory, male territorial behavior (advertisement and defense) may function to attract females and repel competitors (Carranza et al. 1990; Fischer and Fiedler 2001). Under such conditions, a single male may be capable of defending a female, her range, or both as long as female range size is small; when female range size increases, a pair or group of cooperating males may become more successful than a single male (Seddon et al. 2003).

In a recent socioecological study at Khao Yai (Savini et al. accepted), a negative relationship was found between the size and the productivity of gibbon females' home ranges. Across seven groups, larger home ranges were associated with lower productivity than were smaller ranges, and a positive relationship was detected between the time groups spent as polyandrous multimale units and home range size (Savini et al. accepted). On larger, poorer home ranges groups spent more time as multimale polyandrous units than on smaller, richer home ranges.

Perhaps variability in the social organization of Khao Yai gibbons is ultimately linked to the distribution of resources. Data from Khao Yai multimale groups are in agreement with the idea of cooperative male polyandry, because in such groups both males shared sociosexual access to the female. Male participation in social grooming and mating with the female was strongly skewed, allowing identification of a female's primary and secondary male partners (cf. Barelli et al. 2007, 2008). Secondary males were not entirely denied sexual access to the female by the primary males, and one secondary male was seen to copulate with the female during her conception month (Fig. 17.4a). Sexual access by secondary males was probably not a result of a primary male's inability to evict the other male, because replacement following male immigration was common on small home ranges (Fig. 17.3; Savini et al. accepted). Thus, the observations of multimale polyandry are more compatible with mutualism or cooperation, assuming that secondary males have leverage power (Lewis 2002), and that primary males perhaps make reproductive concessions rather than assuming incomplete control (Clutton-Brock 1998). Secondary males may provide a service to primary males such as participation in defending the territory/female against neighboring males, which may ultimately increase a primary male's tenure. Few systematic studies of multimale gibbon groups have yet tested such a hypothesis, but observations from Way Canguk (Lappan 2007a) and Khao Yai multimale groups show that secondary males either alternate or simultaneously engage with primary males in at least some intergroup encounters.

Intergroup encounters in white-handed gibbons are both frequent and potentially harmful (Palombit 1993; Reichard and Sommer 1997). Territorial/female defense may become more costly for a male with higher numbers of neighbors and longer shared borders, both of which may increase as female range size increases. Hence, males living on larger home ranges may experience higher costs for territorial/female defense. In particular, costs of female defense may increase drastically with increasing numbers of male neighbors when females mate polyandrously in the form of EPCs, as observed repeatedly in the Khao Yai population (Reichard 1995b, 2003, this study). Males living on a large home range surrounded by many neighbors may face a tradeoff between an increased need for mate guarding against EPCs and their own motivation to search for additional mating opportunities (Reichard 1995b; Lazaro-Perea 2001). In such a scenario, the benefits to a primary male of having a secondary male to help defend the female against neighboring males' EPC attempts may outweigh the cost of tolerating some copulations of a secondary male. Secondary males would likewise benefit from such arrangement – the low frequency of solitary individuals in this population and their shy behavior suggest that a solitary or "floating" lifestyle is associated with high costs and potentially the lowest reproductive potential. Becoming a secondary male in a polyandrous multimale unit may be a strategy that avoids potentially hazardous transfer, resembling the delayed dispersal of offspring (Brockelman et al. 1998), but with a greater than zero chance of reproduction, at least until a reproductive opening occurs in the neighborhood.

My model for the evolution of grouping and mating flexibility in Khao Yai gibbons is based on a number of assumptions that need to be tested empirically. Most importantly, the contributions of secondary males to intergroup encounters and the influence thereof on a primary male's tenure require critical evaluation. Also a number of basic questions still remain: (1) What are the costs of territory/female defense for gibbon males? (2) What is the relationship between home range size and cost of territory/female defense – does cost increase linearly or exponentially or not at all with moderate increases in range size or number of neighbors? Model calculations have pointed out that a single gibbon male theoretically is capable of defending an area as large as the combined ranges of 5–8 females (van Schaik and Dunbar 1990; Reichard 2003b; but see Bartlett this volume). This suggests that a single male should be capable of defending a territory/female living in a very large range. However, no quantitative study has yet measured actual costs of territorial defense in gibbons. (3) What is the cost of female extrapair copulations to primary males' reproductive success? These and other questions can only be addressed once more multimale gibbon groups are studied.

Sociosexual Flexibility and Advanced Cognitive Abilities

Flexible grouping and mating patterns observed in Khao Yai gibbons and elsewhere (Lappan 2007a; Malone and White 2008) may also be explained as a response to cognitive abilities that were already present in the last common ancestor of gibbons and other apes. In a recent model examining the evolution of great ape cognition, van Schaik et al. (2004) interpreted the flexible social systems and social structures of great apes as part of an evolutionary package associated with the development of a large brain. Van Schaik et al. (2004) argue that great ape sociality is more complex than that of other primates because it shows greater subtlety in dealing with social problems.

As van Schaik et al.'s (2004) model focused specifically on explaining cognitive abilities in great apes, gibbons were not included, perhaps because of the commonly applied simple, static monogamy concept of gibbon social organization that seemed not to fit into a framework of social flexibility and complexity. Gibbon cognition also appears modest at best compared to that of the great apes (Deaner et al. 2006), although interesting similarities in gibbon and great ape cognitive abilities exist (Ujhelyi 2000; Cunningham et al. 2006; Horton and Caldwell 2006). Nevertheless, gibbons and great apes share a recent common ancestry (Hacia 2001), which suggests that it is appropriate to test how gibbons fit into the framework of social commonalities described by van Schaik and colleagues (2004) as distinguishing great apes from other anthropoids. In the following paragraphs, I examine the data presented here in light of van Schaik et al.'s (2004) statements 1–4 highlighting social commonalities in great apes (italicized below).

1. *A tendency toward fission-fusion social organization (or at least toward impermanence of social units), with individuals out of contact with conspecifics for prolonged periods and with foraging females notably solitary*. Gibbons show no tendency toward fission-fusion organization, but neither do gorillas. Gibbons form cohesive groups, although male membership is flexible within limits as groups go through periods of multimale grouping and pair-living. Females clearly forage separately from each other, but they usually remain in the company of a male and flexible choice of association partners seems absent, so far. Thus, gibbon females differ from semisolitary orangutan females. However, the differences between gibbons and great apes may reflect an endpoint of a development along a scale of social flexibility, because not all great apes show a fission–fusion structure nor do females always live solitarily. Variation in female association patterns across chimpanzee populations, for example, is thought to at least partly reflect differences in ecological settings (cf. Boesch and Boesch-Achermann 2000; Wittig and Boesch 2003). The absence of flexible subgrouping in gibbons may be related to selection pressure for small group size and low levels of within-group contest competition rather than a qualitative difference between small and great apes.

2. *Relatively high subordinate leverage*. Observations of intergroup encounters (Reichard and Sommer 1997; Bartlett 2003) and same-sex relationships in

multimale gibbon groups suggest that clearly signaled decided ("formal") dominance relationships are absent in gibbons, despite the potential for clear-cut dominance at least among males in multimale groups. Instead, preliminary data on male–male interactions in multimale groups of Khao Yai gibbons and Way Canguk siamangs (Lappan 2007a) suggest rather cooperative relationships.

3. *Intrasexual bonds among nonrelatives are as common, or more so, than bonds among relatives*. Records of migration patterns in gibbons (Brockelman et al. 1998, this study) suggest that bonding among non-kin occurs in social groups of white-handed gibbons and siamangs (Lappan 2007a) between males but not between females, though again small group size may limit the options of non-kin bonding.

4. *Remarkably extensive intraspecific flexibility in social organization and affiliation*. This study clearly indicates the great potential for flexibility in gibbon social organization with the most prominent forms being pair-living and multimale groupings. Other social compositions were also observed despite their temporal limitations.

Considering the four features of great ape societies listed by van Schaik et al. (2004), gibbons share important social commonalities with other apes. Gibbons also share several other aspects of their biology with great apes (see Fig. 11.2 in van Schaik et al. 2004: 200) such as a slow life history, an arboreal life style, a relatively low vulnerability to predation despite a small body size (Reichard 1998; Uhde and Sommer 2002), a high-quality diet, a tendency toward solitary foraging, and vulnerability to lethal aggression from conspecifics (Palombit 1993; Reichard unpubl. data). The sociosexual flexibility that gibbons at Khao Yai (Sommer and Reichard 2000; Barelli et al. 2007, 2008; Savini et al. 2008) and other sites (Palombit 1994a; Lappan 2007a; Malone and White 2008) share, to some extent with the great apes, may reflect a specific set of cognitive abilities that arose at the time of the last common ancestor between gibbons and great apes, presumably in response to nonsocial selective pressures. That gibbons differ from great apes in specific features is not unexpected and may partly be explained by selective pressures that favored small group size, perhaps as an alternative means of coping with novel social pressures, or may also be interpreted as a reflection of gibbons' more limited cognitive abilities (Deaner et al. 2006). In conclusion, a basic cognitive capacity for solving nonsocial problems with social solutions may have been in place in the last common ancestor of gibbons and great apes, distinguishing them from cercopithecine primates.

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Because group structure variation has not yet been described in gibbons I provide short, descriptive Appendices describing the formation of and social relationships in representative multimale single-female groups (Appendices 1 and 2), a multifemale single-male group (Appendix 3), and the sole multimale multifemale group (Appendix 4). All "father–son" relationships mentioned in Appendices are based on observed *social* parentage of co-residence; genetic relationships were unknown.

Appendix 1: Multimale Single-Female Groups

Multimale groups developed when an adult male immigrated and joined an existing pair ($n = 11$), except once when a multimale unit formed by female-female replacement. In this case, a resident female was replaced by another female; a young adult male group member and his father subsequently both became the female's new partners. Although multimale groups usually formed through male immigration, not all male immigration events resulted in multimale groups because male immigration sometimes led to a rapid male replacement when the former resident male was ousted by the newcomer. Male immigration was competitive and usually accompanied by intense aggression between males, except when a father immigrated into the home range of his son.

With the notable exception of cases where social fathers migrated onto their sons' home ranges, successful immigrants all displaced the resident males from their close relationships with resident females. Male replacement had previously been noticed in this population (Treecuson and Raemaekers 1984; Brockelman et al. 1998), and the Khao Yai long-term monitoring suggests that it amounts to a common cause for group composition changes.

I have observed variable patterns of multimale group formation. Two males in this study, for example, delayed natal dispersal before immigrating into a neighboring group, and an additional observation that closely resembles these cases has been described in detail elsewhere (Brockelman et al. 1998). Another two immigrants were secondary dispersers (one secondary dispersal event occurred after a male was replaced by another immigrant and the other for unknown reasons). An unexpected new pattern observed in this study was males transferring into groups where their sons were the resident males ($n = 2$). In the first case, son Amadeus dispersed from group "A" in 1999 and founded group "T" with the previously solitary female Brenda (Fig. 1). The following year, a new male immigrated into Amadeus' father Fearless' group and replaced Fearless as the female's primary mate (see below). Fearless' group was multimale for about 6 months until Fearless briefly transferred into neighboring group "E" before moving again to join his son Amadeus on home range "T." Before and until shortly after his father's arrival, Amadeus had fiercely resisted immigration attempts by other males, whereas no aggression was observed against his social father. Initially, the female had duetted almost exclusively with Amadeus. Subsequently, however, during a time when Amadeus moved back and forth between his group and neighboring group “SD,” Fearless became the primary duet partner of the female, and remained so even after Amadeus’s permanent return. Social grooming between Fearless and Amadeus had been frequent when they were residents in group “A,” but no grooming was observed between them in group “T,” although both groomed with the female.

In the second case where a social father followed his son, mature son Christopher of group “C” dispersed into group “A” in 2000. About 4 years later, an unknown male immigrated into the group of his father, Cassius II. The immigrant male frequently provoked agonistic interactions with Cassius II. Within a week, Cassius II transferred to group “A” and was accepted by his son Christopher and female Andromeda without hostility. A nearly mature son of Cassius II and brother of Christopher, Chikyū, co-dispersed with Cassius II. Three months later another younger brother, Chuu, likewise transferred into group “A.” The duet pattern in the group remained unchanged after the arrival of the new males, and Christopher is still the regular duet partner of the female at the time of writing. By 2005, Chikyū had reached adulthood, which made the unit the only known multimale gibbon group at Khao Yai with three fully adult (although related) males living with one female. Social relations among the males appear relaxed, and no overt aggression has been noticed, perhaps due to their kinship. Christopher has been seen allogrooming with his younger brothers, who have likewise been groomed by Cassius II, but no allogrooming has been observed between Christopher and Cassius II. All males have been seen allogrooming with female Andromeda.

In multimale group “N” adult males Claude and Nithat were also presumed to be father and son, but unrelated to the immigrant female Hima. After Hima’s arrival in group “N,” she displayed continuous hostility towards resident female Natasha. Hima consistently interfered with Natasha’s foraging, threatened, and chased her. Even though Natasha began lagging behind the group soon after Hima’s appearance, and showed submissive behaviors toward Hima, the young immigrant female continued to dash back and chase Natasha out of fruiting trees. Multiple times Natasha escaped from Hima by descending to the forest floor, which is a very rare behavior in wild gibbons, where she remained cowering while Hima hovered above her. Twice, contact aggression was observed, but more fighting may have occurred, because a few weeks later Natasha disappeared with unknown fate.

Hima began duetting with Nithat, the adult son of the group, when she arrived in the group. During the first days after Hima’s immigration, duets were also still heard from the resident pair Natasha and Claude. However, Hima’s ongoing threats presumably forced Natasha to stop singing shortly thereafter. Hima and Nithat continued to duet, and Claude began to also add replies to Hima’s great calls (for a description of gibbon duet calls see Raemaekers et al. 1984). The males did not overlap with their singing; Nithat would reply first, followed by a less-vigorous response from Claude.

Appendix 2: Multimale Single-Female Group "A"

Male Amadeus of group "T" (described above) tried unsuccessfully to establish polyterritorial polygyny with two females. He was Brenda's pair mate from the summer of 1999. However, in the beginning of 2001, after young female Cyrana immigrated into group "E," joining pileated female Emanuelle and male Bard (see Appendix 3), Amadeus also began traveling with members of group "E." Male Bard was rarely seen with Cyrana and Emanuelle, and Amadeus copulated and sang duets with Cyrana, but also regularly traveled and interacted with Brenda. Repeatedly, Amadeus led Brenda toward the overlapping area between the home ranges of groups "T" and "E." Amadeus appeared to increase group "T's" share of the overlap zone as he foraged ever deeper into group "E's" range. He would then slowly depart from the overlap area and travel even further into group "E's" home range. He emitted contact calls and appeared to wait for Brenda to follow. Brenda rarely crossed deep into "E's" home range and would eventually stay behind when Amadeus proceeded further. Their calling and activity in the overlap area regularly resulted in contact with group "E," and Amadeus was then seen copulating and duetting with Cyrana. Although no quantitative data are available, Amadeus' frequent movement back and forth and simultaneous interactions with the two females gave the impression that he was trying to persuade one of the females to join him and follow onto the other female's home range. He also appeared to try to lead Cyrana toward Brenda and her home range. Cyrana followed him deeper into the group "T" home range than Brenda had followed onto the group "E" home range. However, Cyrana remained cautious and Brenda's constant hostility apparently prevented spatial proximity between the two females and the development of a multifemale group. Brenda frequently threatened Cyrana, and long chases were witnessed during which Brenda pursued Cyrana back onto the "E" home range. Intergroup encounters during this period often exceeded two hours. Eventually, however, Brenda would leave the encounter area and forage away toward the opposite side of her home range. Amadeus often remained, traveled, and spent the night with Cyrana, before he would return to Brenda the following morning or during the day, usually when he heard Brenda singing solo female great calls. One morning, Brenda began calling close to the overlap between her range and that of group "ST." After only a few minutes, a dark male rapidly approached her from the south. The pair copulated and started to duet when suddenly Amadeus brachiated at high speed down the slope and vigorously chased the intruder away. After about two months of changing location and trying to maintain simultaneous socio-sexual relationships with the two spatially separated females, Amadeus ceased traveling with Cyrana and returned to exclusively reside with Brenda. During all this time, Emanuelle had been with Cyrana and Amadeus on most days, but the group's resident male, Bard, was rarely seen with them. There was low-intensity hostility between

Emanuelle and Cyrana and soon after Amadeus ceased traveling with members of group “E,” Cyrana emigrated and Bard was seen back with Emanuelle again.

Appendix 3: Multifemale Single-Male Group “J”

Group “J” was identified as multifemale when it was first contacted in November 1998, because two females each carried approximately 2-month-old infants. The group composition remained stable for 26 months until January 2001, when one female and her now-juvenile offspring disappeared with unknown fate. Between November ‘98 and January ’01, the group was contacted on 25 days. Qualitative observations were available for $\sim$25 contact hours despite the females’ fear of humans because the adult male of the group, Frodo, was a known, habituated individual born in study group “A” (cf. Brockelman et al. 1998). Frodo dispersed from group “A” in 1990. Between 1991 and 1992 he was encountered a few times with a female of unknown origin (designated as group “K”). During the 1993 census, Frodo was in the company of a new female in the same area as before, but by the end of 1994 both individuals had disappeared. Frodo was rediscovered four years later in group “J.”

No hostility was noticed between the females in group “J”; instead, the females were repeatedly observed calmly feeding within 5 m of each other in the same tree crown. The females likewise both tolerated close spatial proximity with each other’s infants during feeding and travel as the infants became more independent from their mothers. The females traveled together and in the company of the male on a daily basis and coordinated their movements through contact vocalizations. Their travel pattern resembled those observed in units with other social organizations, e.g., pair-living gibbon groups. Interestingly, both females were heard to sing duets with the male. Neither interfered with the song of the other nor did they sing “in parallel” as typical for maturing daughters with their mothers (cf. Brockelman and Schilling 1984; Raemaekers et al. 1984). Instead, on some days the male first sang a duet with one female and later with the other; on other days, only one of the females duetted with the male during the contact time. Such duet pattern was unique to this group.

Observers did not witness the emigration or death of one of the females and her offspring and the females’ social histories were unknown. It is possible that the females were mother and daughter (or sisters) and that Frodo immigrated and displaced the resident male at around the time when the presumably nulliparous daughter reached sexual maturity. Both females may subsequently have copulated and conceived with Frodo and the group remained stable until the onset of a new reproductive cycle when the females’ offspring were independent. Female sexual competition is one possible explanation for the disappearance of one of the females. Such a theory of the origin of a multifemale group would parallel the familial polygyny described by Srikosamatara and Brockelman (1987), although in this case the multifemale structure lasted much longer.

Alternatively, two unrelated females may have formed a multifemale group with the male. The presence of two infants, an absence of overt feeding competition, and the females' unusual alternating duet singing with the male, which has never been observed in another gibbon group at Khao Yai or elsewhere, support such interpretation. Delayed female dispersal has in fact been rare in Khao Yai. Still, it remains unclear why one of the females then left after more than a year. Predation or another sudden death appears unlikely, because the female disappeared with her independent juvenile offspring, leaving voluntary emigration the most plausible explanation. Perhaps the benefits of multifemale grouping were outweighed by increasing costs of resource competition and increasing group size, or a better opportunity arose elsewhere?

A pressing question remains: why or how a female could join another female on her territory in the first place? So far, it has forcefully been argued that ecological constraints would not allow gibbons to jump over the poylgyny-threshold and form multifemale groups (Brockelman and Gittins 1984). However, in a recent study Savini et al. (2008) show that female reproduction is less food-limited then previously assumed, which suggests that under the right ecological conditions gibbons may be able to form multifemale groups. More research is needed on other multifemale gibbon groups to illuminate which specific ecological and social conditions allow for the development of socio-sexual multifemale grouping.

Appendix 4: Mixed-Species Multimale Multifemale Group "E"

The mixed-species multimale multifemale group "E" formed after a pair-living female disappeared and the adult male and two immature offspring were first joined by a pileated gibbon female (*H. pileatus*) and then within a few days by a white-handed gibbon female (*H. lar*). Khao Yai National Park marks the eastern distribution border of the subspecies *Hylobates lar entelloides*. The western part of Khao Yai National Park is inhabited by white-handed gibbons, whereas pileated gibbons live in the eastern part. A small hybrid zone exists ~30–40 km east of the Mo Singto – Klong E-Tau research site (Brockelman and Gittins 1984; Suwanvecho 2003). Central Mo Singto has traditionally been believed to be inhabited exclusively by lar gibbons (Brockelman 1975; Raemaekers et al. 1984), but over the years pileated gibbons have occasionally migrated into the Mo Singto – Klong E-Tau area where their species-specific calls are sometimes heard.

The pileated gibbon female was first observed in group "E" in spring 1997 and remains there at the time of writing. Both females of group "E" were adult at the time of their immigration into "E's" home range, but both appeared to be young, presumably nulliparous, judging from their small, nonpendulous nipples. By the end of 1997, the mixed-species trio was joined by a second adult male from the neighborhood, who emigrated after he was replaced by another male. The relationship between the males appeared relaxed and tolerant as no overt aggression – but also no allogrooming – was witnessed between the two. In contrast, relations between the females seemed tense. The pileated gibbon female repeatedly threatened and briefly chased the white-handed gibbon female. The males were not observed to intervene in situations of female hostility, and both females duetted with the males. The white-handed gibbon female emigrated in 1999 and was joined by a recently matured neighboring male. Both animals disappeared from the study site the following year. The pileated female remained with the two white-handed gibbon males until one of them likewise emigrated, changing the structure to pair-living. During the 2005 census, however, the latter pair was again found in the company of a white-handed gibbon female of unknown origin, now as a mixed-species multifemale group.

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Part VI
Conservation Biology

Chapter 18
Status and Conservation of Yellow-Cheeked Crested Gibbons (*Nomascus gabriellae*) in the Seima Biodiversity Conservation Area, Mondulkiri Province, Cambodia

Benjamin Miles Rawson, Tom Clements, and Nut Meng Hor

Introduction

The yellow-cheeked crested gibbon (*Nomascus gabriellae*) occurs east of the Mekong River in southern Vietnam, northeastern Cambodia, and possibly southernmost Lao PDR (2000, Nomad RSI unpubl. data). The northern distributional limit is unclear as it either borders or intergrades with the southern white-cheeked crested gibbon, *N. siki* (Duckworth et al. 1995, 1999; Geissmann et al. 2000; Konrad 2004). *N. gabriellae* is currently listed as Endangered in the IUCN Red List of Threatened Species (IUCN 2008).

Little behavioral or ecological work was conducted on the species until recent years; however, a picture of the species is beginning to emerge with current studies, particularly in the SBCA (Rawson 2004) and Ratanakiri province, Cambodia (Traeholt et al. 2006), and Cat Tien National Park (NP) in Vietnam (M. Kenyon pers. comm.). It appears that *N. gabriellae* generally prefers undisturbed evergreen forest with a reasonably high canopy (Nguyen Xuan Dang and Osborn 2004; Traeholt et al. 2006) although the species inhabits other habitat types such as semi-evergreen, mixed deciduous, and even bamboo forest (M. Kenyon pers. comm., this paper). The species can apparently survive a reasonably high degree of habitat and incidental disturbance, persisting in selectively logged habitats and close to human habitation when not hunted to extirpation (Duckworth et al. 1999; Polet et al. 2004, BMR and TC pers. obs.). It has wide altitudinal limits, occurring from 100 m above sea level (m asl) in Cat Tien NP (Eames and Robson 1993) to above 2000 m asl on the Da Lat plateau, Vietnam (Eames and Nguyen Cu 1994).

N. gabriellae, like other gibbon species, is territorial and monogamous (Traeholt et al. 2006), with mated individuals producing loud vocal duets

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(Geissmann et al. 2000; Rawson 2004). These songs are sexually dimorphic in that each sex provides its own unique contribution to the call (Geissmann et al. 2000). While gibbons make a large range of vocalizations, here we refer only to the duet, and hereafter the terms sing, call, vocalization, and duet are used synonymously. Home range sizes for the species in prime habitat are similar to those for other species of gibbon (Chivers 1984), at approximately 30 ha in evergreen forest, but may be up to 100 ha in bamboo forest (M. Kenyon pers. comm.). *N. gabriellae*'s diet consists of fruits, leaves, and flowers (Traeholt et al. 2006) as with most other gibbon species.

This paper describes a research, population estimation, and monitoring program for *N. gabriellae* conducted by the Wildlife Conservation Society (WCS) Cambodia Program in collaboration with the Australian National University in the Seima Biodiversity Conservation Area (SBCA), Mondulkiri Province, Cambodia. The program was established in response to the finding that a population of yellow-cheeked crested gibbons likely to be of global importance existed within the area (Walston et al. 2001).

Methods

Study Site

The SBCA was established in 2002 by decree of the Ministry of Agriculture, Forestry, and Fisheries of the Royal Government of Cambodia. The conservation area covers 3,034 km^2, comprising a core area of 1,550 km^2 in Mondulkiri province and a surrounding buffer zone of 1,484 km^2 in Mondulkiri and Kratie provinces. It is managed by the Forestry Administration with the support of WCS.

The area has a wide range of habitats, from dense evergreen hill forests along the Vietnamese border to extensive deciduous dipterocarp forests in the plains to the north and west. Altitude ranges from 100 m asl in the lowland deciduous dipterocarp forest to $>$700 m asl on the Sen Monorom plateau. Yearly rainfall averages 2,500–3,400 mm/year (Rawson 2004, Nomad RSI unpubl. data), with most falling during the wet season (May–November). Monthly temperatures average 25–32°C.

The complex mosaic of different forest types (Zimmerman and Clements 2002) at this juncture of two distinct biogeographical regions (the Annamite Mountains and the Indochinese Lowlands), containing many streams, wetlands, and mineral licks, supports a high diversity of species at globally significant densities. For example, eight species of primate and seven of cat have been recorded – among the highest figures for single sites anywhere in Asia. The two most notable features of the fauna are the high number of locally endemic species and the high numbers of Globally Threatened species. Many of the endemics are also threatened (Walston et al. 2001).

Endemic species are mostly restricted to the evergreen/semi-evergreen forests of the southern Annamite Mountains along the Vietnamese border. The SBCA represents one of the most important remaining areas of evergreen/semi-evergreen forest in this region, and so is central to the survival of these species. Key examples of such species include yellow-cheeked crested gibbon (*Nomascus gabriellae*), black-shanked douc langur (*Pygathrix nigripes*), Germain's peacock-pheasant (*Polyplectron germaini*), and orange-necked partridge (*Arborophilia davidi*).

The site is also a key refuge for many other species that are more widespread but are nonetheless threatened throughout their ranges. Examples from a long list include tiger (*Panthera tigris*), clouded leopard (*Pardofelis nebulosa*), marbled cat (*Pardofelis marmorata*), sun bear (*Ursus malayanus*), Asiatic black bear (*Ursus thibetanus*), Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), banteng (*Bos javanicus*), Eld's deer (*Cervus eldii*), green peafowl (*Pavo muticus*), giant ibis (*Pseudibis gigantea*), white-winged duck (*Cairina scutulata*), white-rumped vulture (*Gyps bengalensis*), and several turtle species (Walston et al. 2001).

The landscape is the traditional home of a large part of the Phnong ethnic minority group and, in the west, some Stieng communities. These people have a long connection to the area, detailed local knowledge, and complex cultural ties to the land as a result of family histories, traditional livelihoods, and beliefs. They mostly engage in low-impact shifting agriculture, chiefly in old fallow areas, together with paddy and cash crop cultivation where soils and markets permit. The collection of forest products is a central part of livelihoods. The most important forest activity is resin tapping, which supplies 40–50% of total livelihood needs in most villages (McKenny et al. 2004). Studies have shown that locally used techniques at the current level of intensity have little impact on the health of the forest (Evans et al. 2003), and so this is a good example of a product that can be harvested sustainably, linking human benefits to forest conservation. Other important resources include rattan, timber, bamboo, and fish.

Major threats to wildlife and their habitats include hunting with guns and snares, forest conversion, logging, land grabbing, immigration, and economic concessions. External pressures, such as commercial logging, immigration, and land grabbing, have increased considerably in recent years. These also threaten the livelihoods of the local indigenous Phnong and Stieng, principally through loss of the forest habitats that are essential for their livelihoods, and the denial of forest resources. The area has been the target for a joint project of the Forestry Administration and WCS since the declaration of the SBCA in 2002. This project includes research, law enforcement, and land-use planning in co-operation with both the authorities and the local communities. These activities have been broadly successful at mitigating many of the major threats to wildlife, habitats, and local livelihoods, principally through the maintenance of the forest cover and reduction in commercial hunting pressures. The deforestation rate, based on satellite image analysis, was only ~0.05%/year over the 4 years from 2001 to 2004 (WCS unpubl. data). With continuing government support, it is hoped that the initiative will build on these initial successes to establish a landscape vision for the SCBA.

The SBCA also forms part of a much larger complex of linked protected areas, including four in Cambodia (three Wildlife Sanctuaries and one Protected Forest) and two National Parks in Vietnam. The total area of this group of reserves is greater than 10,000 km^2, making it one of the largest and most important in southeast Asia. This conservation landscape offers one of the best opportunities in Indochina to preserve viable populations of the largest and rarest mammals.

Intensive Study Plots

Brockelman and Ali (1987) recommend that before a regional listening post system is implemented for gibbons several population parameters must be established from intensive study plots. These include the mean proportion of groups calling per day (p), the effect of weather, and the timing of calls. Two intensive study plots – ER (N 12° 11′ E 106° 59′) and SH (N 12° 9′ E 106° 57′) – were used to collect this information. The plots were non-overlapping and placed in areas typical of the SBCA. Further data were available from another intensive study plot – C6 (N 12° 15′ E 106° 55′) – described in Rawson (2004).

Based on long-term work on gibbon vocalizations in the area, it was known that *N. gabriellae* vocalizes more frequently in the dry season (November–April) than the wet (May–October), as rainfall suppresses vocal activity (Rawson 2004). Consequently, data collection was scheduled to coincide with the driest part of the year (December–February) to maximize the number of vocal bouts heard by surveyors. Each intensive study plot was monitored by the same individual over a period of 27 days: 13 consecutive days in December 2003 and 14 consecutive days in January 2004. Both surveyors had extensive previous experience collecting data on *N. gabriellae* vocalizations.

We took data on all duets and solos heard between half an hour before sunrise and 12:00 pm at SH and ER, while at C6 we took data throughout the day. We excluded data from male solo songs from all analyses as these may be made by unmated ‘floating’ males who may not be residents of the area. For each duet the following information was recorded: time of call, compass bearing to the group, estimated distance, and prevailing weather conditions. Data on weather conditions were also taken at sunrise and whenever conditions were judged to have changed. A subjective scale of 0–3 was used (0 = absent, 1 = low, 2 = medium, 3 = high) for both cloud cover and wind, and the presence or absence of prevailing rain or fog was recorded. Rain within the previous 12 h was also recorded. We analyzed the effect of weather on calling probability using Spearman Rank Correlation Coefficients, with ‘absent’ and ‘low’ conditions and ‘medium’ and ‘high’ conditions being lumped for cloud cover and wind.

We calculated the number of groups at ER and SH both from the maximum number of groups heard calling on any one morning and by mapping the calls, with groups differentiated based on the direction and timing of vocalizations. Both methods gave the same result. The number of groups from C6 was determined using triangulation and long-term observation.

The cumulative proportion of groups heard calling over survey periods of different length was mathematically determined by calculating the calling probability for a single day and applying the equation:

$$p(m) = 1 - [1 - p]^m$$

where $p =$ calling probability and $m =$ number of survey days at a site (Brockelman and Ali 1987). This assumes that vocal activity is independent between consecutive days, an assumption which is broadly supported by available data from a related genus in an adjacent country (Brockelman and Srikosamatara 1993).

Site Population Trends

Gibbon population estimates and trends were estimated from 28 listening posts situated across a study area of 1,140 km^2 within the SBCA. We defined the study area based upon a previous zonation of the SBCA (Clements 2003) that identified areas of highest importance for the conservation of globally threatened species. The posts were established in December 2002. They were placed randomly in pairs 4 km apart, with stratification by habitat (Evergreen or Deciduous Forest – the classification system used is described below) and location (approximately southern, central, and northern SBCA). This ensured that the posts were representative of the habitats and areas present within the SBCA. Posts were clearly marked, by painting the number on the nearest large tree, to allow them to be easily located in subsequent years. The posts were also re-marked every December before the survey season.

Counts were made from posts twice per year, once in January and once in February, in 2003, 2004, 2005, and 2006. Counts were conducted only in January and February in order to control for seasonal variation and to coincide with the peak calling time for *N. gabriellae*. The survey design was informed by the work at the intensive study plots. All listening posts were manned from 5:30 to 7:30 am. For every call, the observer recorded the time, compass bearing, estimated distance category (near, medium, far), and whether the call was from a lone male or a duet. We also took data on weather conditions following the same methodology as that used at the intensive study plots. These surveys were conducted simultaneously with fixed point counts of green peafowl (*Pavo muticus*), which also makes loud vocalizations in the early morning during the same months (Brickle 2002).

We estimated trends in calling frequencies based upon the number of groups calling on the first morning of each post survey. The number of groups calling from each post was calculated by mapping the calls as per the intensive study plots. This gave 56 possible data points from each year (two counts from 28 posts) except for 2003 when not all posts were surveyed due to logistical constraints. We removed data from days when there was rain or strong wind (2 or 3 on the scale) from the dataset for the purposes of analysis, based on the results of the intensive study plots. The effect of the year and posts on the number of gibbon groups calling was tested using Analysis of Variance, with the number of calling groups log-transformed to stabilize the variance.

Site Population Estimates

We made population estimates for SBCA based on data from 2004, when observers spent three days at each listening post. Four posts produced insufficient data, however, so these were excluded from the analysis, leaving 24 posts on which results were based.

As with the intensive study plots, a cumulative count of the number of gibbon groups at each of the 24 listening posts was determined by mapping vocalizations recorded over the three days. Cumulative counts were then divided by the calling probability (p), as determined from the intensive study plots, to give a total estimated number of gibbon groups for each post, using the formula:

$$x_i = \frac{c_i}{p(m)}$$

where $x =$ the number of gibbon groups, $c =$ number of gibbon groups heard in the three-day period, $p =$ calling probability, $m = 3$ (number of survey days at each post) and i is the number of the listening post, where $i = 1$ to $k = 24$.

The population density estimate depends upon the hearing distance from each post. Maximum hearing distances were estimated to be 1.5 km, based on triangulated data from C6 and another dataset from the SBCA (Traeholt et al. 2006). Other researchers have generally suggested that 1.5 km is a reasonable estimate for maximum carrying distance of *N. gabriellae* vocalizations (Duckworth et al. 1995; Traeholt et al. 2006, Y. Huang pers. comm.). Accordingly, population density estimates were calculated based upon a hearing distance of 1.5 km. However, to provide a more conservative population estimate, calculations were also performed using a hearing distance of 2 km. The maximum area surveyed was 7.1 km^2 for a hearing distance of 1.5 km and 12.6 km^2 for 2 km. This area was adjusted by excluding parts beyond high ridges, where an observer could not hear.

Forest cover was assessed based on the Japan International Cooperation Agency (JICA) digital data, which are the most accurate available for

Cambodia (JICA 2003). We grouped data to identify three habitat classes: Evergreen Forest, comprising all evergreen, semi-evergreen, mixed deciduous and riverine forest; Deciduous Forest, including natural grasslands and scrubland; and Non-Forest. The area of each type within the listening post area was calculated. Ground truthing indicated that the JICA (2003) digital data underestimated the availability of small fragments of evergreen, semi-evergreen, mixed deciduous, and riverine habitat, perhaps due to the relatively low resolution of the dataset and the classification system used. These fragments are associated either with small hills or the many rivers within the SBCA (Zimmerman and Clements 2002). Accordingly, the length of rivers within the listening post area was also calculated. We tested the effects of river length and evergreen forest area on the estimated number of gibbon groups using Analysis of Variance, with all variables log-transformed to stabilize the variance.

We obtained population estimates from the listening posts using a similar approach to that used by Brockelman and Srikosamatara (1993). The density of gibbon groups at a post is:

$$d_i = \frac{c_i}{p(m) \cdot a_i}$$

where d = the density at post i and a_i = the area of post i. The estimate of the total population of groups $\hat{X}$ is:

$$\hat{X} = \hat{D}S$$

where $\hat{D}$ = average density of gibbon groups and S is the total study area (1,140 km^2).

Calculating the variance of the total population is not as simple as extrapolating the variance in the estimated number of calling groups, as this estimate has its own variance: the variance in the calling probability. The normal Delta Method equation:

$$\hat{\text{var}}(\hat{X}) = S^2.\hat{\text{var}}(\hat{D}) = S^2.\hat{D}^2.\left\{\frac{\hat{\text{var}}(\hat{p})}{\hat{p}^2} + \frac{\hat{\text{var}}(x)}{x^2}\right\}$$

where S is the total study area (1,140 km^2), $\hat{p}$ is the estimated calling probability, and $x = \sum_i x_i$ is the estimated number of gibbon groups, is not appropriate because the variance components are correlated. Therefore, we adopted the approach used in Distance Sampling for when there is a common variance component (Section 3.7.1, Buckland et al. 2001). It should be noted that this method differs from that used by O'Brien et al. (2004) when calculating similar population estimates from listening posts. The variance equation is:

$$\hat{\text{var}}(\hat{X}) = S^2.\hat{\text{var}}(\hat{D}) = S^2.\hat{D}^2.\left\{\frac{\hat{\text{var}}(\hat{p})}{\hat{p}^2} + \frac{\hat{\text{var}}(c)}{c^2}\right\}$$

where $c = \sum_i c_i$ is the estimated total number of gibbon groups heard. The $\hat{\mathrm{var}}(c)$, taking into account the area of the listening post, is:

$$\hat{\mathrm{var}}(c) = \frac{A \sum_{i=1}^{k} a_i (c_i/a_i - c/A)^2}{k-1}$$

where$A = \sum {}_i a_i$ is the area sum, for listening posts $i = 1, \ldots, k$, where $k = 24$.

The confidence interval for $Var\ (\hat{X})$ is given by the Student's t-distribution (Krebs 1999).

We were also able to generate an independent estimate of gibbon population density from line transect distance-sampling. Twenty-eight 2 km transects were established across the SBCA in December 2004 using a random sampling procedure. Sampling was stratified in the same manner as the listening posts – by habitat (Evergreen or Deciduous Forest) and location (approximately southern, central, and northern SBCA). This ensured that transects were representative of the habitats present within the SBCA. Transects were clearly marked using paint, and cut to allow observers to walk quietly, but minimally so, so as to restrain any influence of the transect itself on animal distribution. We conducted two surveys of each transect during January–April 2005 (56 samples) and a further two of most transects during January–March 2006 (42 samples).

Results

Intensive Study Plots

Timing of Duets

Gibbons showed a clear predisposition to sing during the early hours of the morning. Of 219 recorded bouts, the earliest recorded duet started at 6:04 am and the latest started at 9:51 am. However, given that gibbons' diurnal activity is guided by circadian rhythms, which are affected by light-dark cycles, data might better be analyzed with reference to sunrise. When duet times were corrected for the time of sunrise, 90% of loud calls were made in the space of 1 hour, starting 10 min before sunrise (Fig. 18.1). The earliest duet occurred 11 min before sunrise (6:04 am) and the latest at 3 h and 45 min after sunrise (9:51 am), giving a range of 3 h and 56 min. At C6 observations were taken throughout the day and the latest recorded vocalization was at 9:51 am. Based on these data, times for area wide survey were set for 5.30 until 7:30 am, which captured 96% of all duets from the C6 data set.

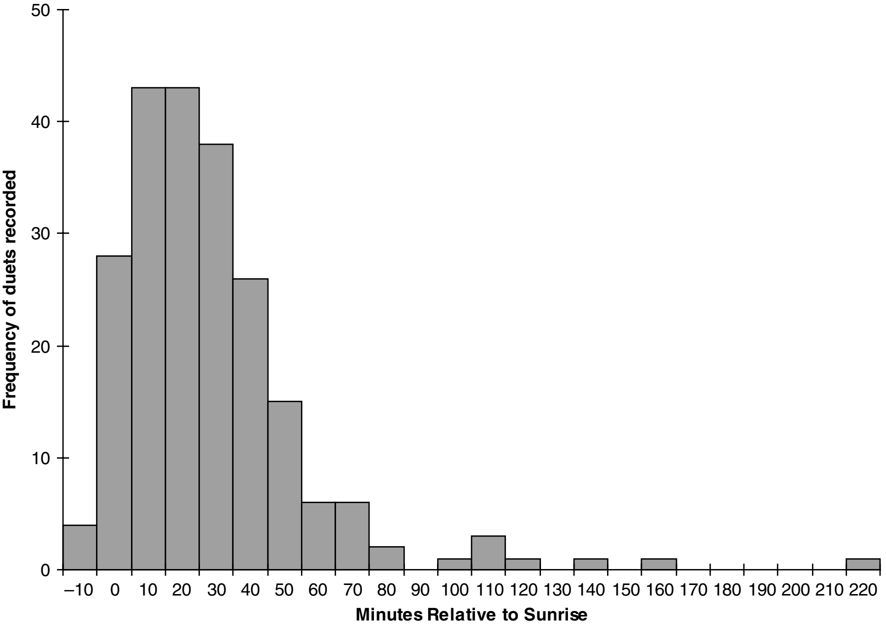

Fig. 18.1 Timing of *N. gabriellae* duets relative to sunrise

Seasonality and Weather Conditions

Previous work had suggested that seasonality and weather conditions, especially rainfall, affect calling probabilities of *N. gabriellae* (Rawson 2004). Rawson (2004) showed that the mean number of groups calling was lower in the wet season than in the dry season but did not give calling probabilities by season. Reanalysis of these data from C6 found that median calling probabilities were significantly lower during the wet season than the dry ($U = 591$, $p = 0.001$, $n_{\text{wet}} = 45$, $n_{\text{dry}} = 44$, Mann-Whitney U-test), with respective mean calling probability values of 0.28 and 0.52 (Fig. 18.2).

Rawson (2004) also showed that rain the previous night reduced calling probability, but lacked sufficient data to test for the effects of several other weather variables. The datasets from all three intensive study plots were combined to test for the effect of rain, wind, cloud, and fog on calling probability. Strong wind and heavy cloud were defined as days when the effect was medium (2) or high (3), rather than absent (0) or low (1). Figure 18.3 shows the calling probability for each major weather condition in comparison with clement mornings with no adverse weather conditions. Heavy cloud showed limited suppressing effect, while days with rain, strong wind, and rain the previous night returned much lower calling probabilities. Calling probability was significantly negatively correlated with rain the previous night ($r_s = -0.328$, $p < 0.001$, $n = 140$), cloudiness ($r_s = -0.247$, $p < 0.01$, $n = 139$), and windiness

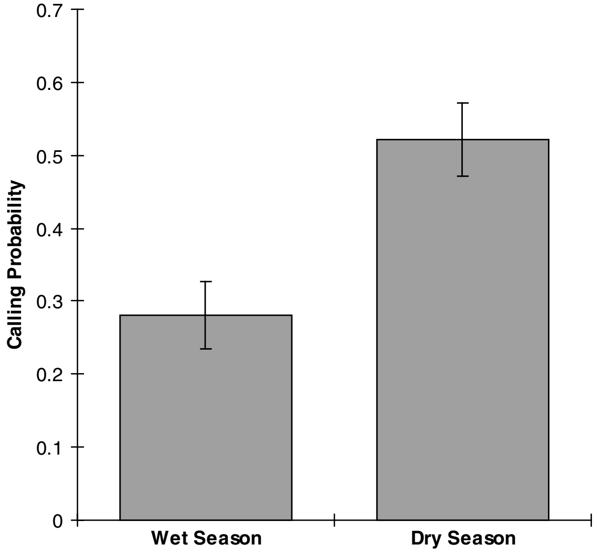

Fig. 18.2 Calling probability of *N. gabriellae* by season from C6. Standard error bars are shown

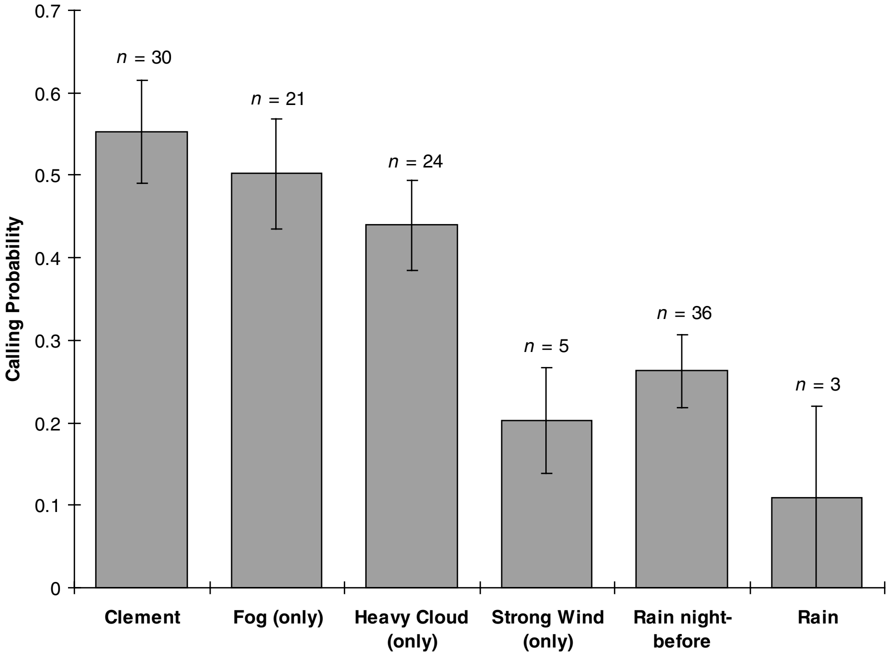

Fig. 18.3 Effect of weather on calling probability of *N. gabriellae*. Standard error bars and sample sizes (*n*) are shown

($r_s = -0.202$, $p < 0.05$, $n = 140$). Presence of fog did not significantly affect calling probability. Due to the effect of weather, days with strong wind, rain, or rain the night before were removed from further analysis.

Calling Probability

Both the vocalization mapping and the maximum number of groups heard across all days indicated that at least eight groups were present at SH and ER. The mean number of groups calling by site were 4.96 (±0.36) groups/day at SH, and 3.40 (±0.47) groups/day at ER, when days with rain or strong wind (2 or 3 on the scale) were removed from the dataset. This corresponds to calling probabilities of 0.620 (±0.045) and 0.425 (±0.058). Only three groups were present at C6, where the calling probability was 0.600 (±0.054). The mean value for calling probability across all intensive study plots during clement weather was therefore 0.560 (±0.032). When used in the equation $p(m) = 1 - [1 - p(1)]^m$, this showed that the proportion of groups heard at any survey site on clement days in the dry season would be 56.0% for one survey day, 80.6% for two survey days, 91.5% for three survey days, 96.3% for four survey days, and 98.4% for five survey days. Brockelman and Ali (1987) suggest that only survey periods where $p(m) = 0.90$ or above be used, therefore only the 24 posts that had three survey days spent at them were included when calculating population estimates.

Site Population Estimates and Trends

Population Trends

Two listening post surveys were completed annually, one each in January and February 2003, 2004, 2005 and 2006. Fewer posts were surveyed in 2003 as they were just being established; otherwise the reduction in data points (from $n = 56$) is indicative of the days lost due to poor weather.

The average number of gibbon groups heard from the posts increased significantly from 2003 to 2006 ($F_{1,141} = 7.81, p < 0.01$, Fig. 18.4), by an average of 8.5% each year. There were significant differences between the numbers of groups heard between different posts ($F_{27,141} = 3.81$, $p < 0.001$). The effect of posts was used as a blocking term in the Analysis of Variance, indicating that the significant increase from 2003 to 2006 was not due to surveying fewer posts in 2003.

Population Estimates from Listening Posts

The cumulative number of groups heard from the 24 posts totaled 93 over 72 survey mornings and ranged from one to nine groups per post, with a mean of 3.9 (± 0.49). The length of river within the listening post area had a

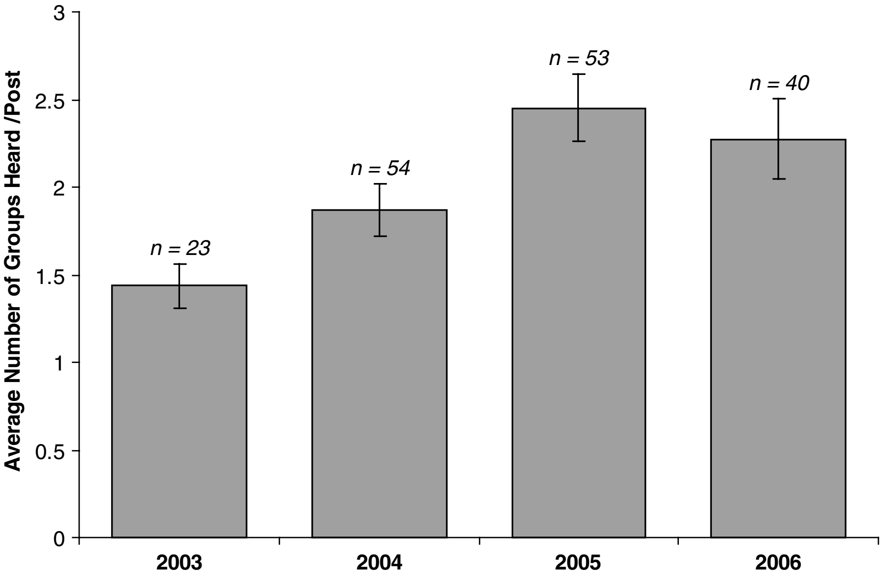

Fig. 18.4 Trends in calling frequency of *N. gabriellae*. Standard error bars and sample sizes (*n*) are shown

highly significant positive effect on the estimated number of gibbon groups ($F_{1,21} = 9.69$, $p < 0.01$); however, effect of the area of evergreen forest was not significant ($F_{1,21} = 0.40$, $p = 0.534$).

The yellow-cheeked crested gibbon population estimate from the listening posts is given in Table 18.1. The average density of groups based on a 1.5 km listening radius was 0.71±0.07 groups/km^2. Based on a total forest area of 1,140 km^2 (JICA 2003) the total number of groups inside the SBCA is estimated to be 809±83 with a 95% confidence interval of 646–972. Using a 2.0 km listening radius returns a mean density of 0.48±0.05 groups/km^2, with a population estimate of 543±56 and a 95% confidence interval of 433–653.

Table 18.1 Yellow-cheeked Crested Gibbon density and population estimates for the Seima Biodiversity Conservation Area (SBCA), based on listening post counts and line transect distance-sampling. Standard errors are given in brackets

Parameter	Listening posts	Line transects
Effective strip width (m)		37.69 (4.32)
Density of groups ($\hat{D}$)/km^2	0.710 (0.070)	0.736 (0.224)
Number of groups ($\hat{X}$)	809.0 (83.0)	828.0 (255.0)
95% Confidence interval	646–972 groups	508–1, 349 groups
Coefficient of variance	10.26%	30.8%

Population Estimates from Line Transects

Only eleven gibbon observations were obtained from the line transects, a total which was insufficient to estimate the detection function. This was instead estimated by combining all large-bodied, strictly arboreal primate observations from the SBCA – black-shanked douc langur *Pygathrix nigripes*, silvered langur *Trachypithecus germaini* and *N. gabriellae*. The observed effective strip width was 37.69±4.32 m. This is considerably larger than most other published estimates for gibbons, e.g., Nijman and Menken (2001) found a strip width of 26.0 m for *Hylobates muelleri* in Borneo (but see Yanuar this volume). The forests in the SBCA are on average more open than dense evergreen forests in Borneo, suggesting that the effective strip width should be larger; however, gibbons are likely to be less detectable than the other arboreal primate species, which exist in larger groups. Based on the observed strip width and a mean encounter rate of 0.055±0.016 groups/km (in 2005 and 2006 data pooled), the mean gibbon density is 0.73±0.22 groups/km^2. This equals 828 gibbon groups, with a 95% confidence interval of 508–1349 groups (Table 18.1). The variance of the density and group number estimates was calculated using the delta method (Buckland et al. 2001).

Discussion

Vocal Behavior

Accurate information about *N. gabriellae* calling probabilities and the effect of weather and season on calling probabilities was essential in order to design the area-wide listening post survey and to analyze the data obtained. *N. gabriellae* duets were found to be made within a small time frame around sunrise, with 90% of calls during the first hour of daylight. The early calling time for this species contrasts with Cambodia's other gibbon species, *Hylobates pileatus*, which shows a clear predisposition to duet between 9:30 and 11:00 am (Brockelman and Srikosamatara 1993; Rawson and Senior 2005).

Recorded calling probabilities were significantly higher for *N. gabriellae* during the dry season, and were heavily reduced during periods of rainfall and strong wind. The reasons for this probably relate to actual suppression in calling frequency as opposed to inability of observers to hear during these weather conditions. Wind and rainfall have been found to reduce gibbon vocalizations in other species, including *N. concolor* (Johnson et al. 2005), *H. pileatus* (Brockelman and Srikosamatara 1993), *H. agilis* (O'Brien et al. 2004), *H. muelleri* (Nijman and Menken 2001), *Hoolock hoolock* (Ahsan 2001), and *Symphalangus syndactylus* (O'Brien et al. 2004). A probable explanation for this is that if gibbons use duets for territorial defense (Goustard 1984; Raemaekers and Raemaekers 1985), and loud vocalizations are energetically expensive (Cowlishaw 1996; Wich and Nunn 2002), then it is likely that the reduced hearing distance and increased difficulty in determining calling direction during windy and rainy periods reduces the benefits of territorial advertisement relative to the energy costs of vocalizing. Accordingly, gibbons would be expected to reduce their vocal activity during adverse weather conditions. Indeed, Rawson (2004) showed that, for *N. gabriellae*, calling frequency was positively correlated with fruit abundance, as has been shown in some other gibbon species (Cowlishaw 1996), suggesting energy availability is a limiting factor for vocal behavior.

The calling probability for *N. gabriellae* in the SBCA is within the (large) range of published estimates for other hylobatid species (Brockelman and Ali 1987). Probabilities from C6 and SH were very similar despite being located in quite different habitats, the former a mosaic of semi-evergreen and mixed deciduous forest and the latter in evergreen forest. Calling frequency at ER was lower than either of the other two though it was also situated in evergreen forest. This variability is not unusual in gibbon studies, with calling probability varying by species, by site, and also by individual group (Brockelman and Srikosamatara 1993). The latter, variation in vocalization frequency between groups, has already been shown for *N. gabriellae* (Rawson 2004). The large number of groups (19) and days (140) surveyed over only the driest time of the year, however, provides a robust calling probability from the SBCA.

Habitat Requirements

Gibbons are generally typified as being restricted to aseasonal evergreen forests, being unsuited to riverine or more deciduous forest types (Leighton 1987; Brockelman and Srikosamatara 1993; Bartlett 1999; Fleagle 1999), probably due to the fact that the majority of gibbon ecological work to date has occurred in equatorial aseasonal forests. There is, however, a growing body of work on those species inhabiting more northerly seasonal areas, and with it an appreciation of how gibbons interact with these forests (Chivers 2001).

Results presented here demonstrate no significant difference in group density across evergreen, semi-evergreen, and deciduous forest types, suggesting that *N. gabriellae* is quite flexible in its habitat usage. The classification system used by the digital habitat data layer (JICA 2003) and the layer's resolution were, however, insufficient to illustrate the heterogeneous nature of the deciduous forests found in the SBCA. Within the deciduous areas, small patches of evergreen or semi-evergreen forest are commonly found along rivers and on hills (Zimmerman and Clements 2002), but are absent from the JICA (2003) digital habitat data. Analysis of projected calling locations from the areas supposedly dominated by deciduous forest suggests that many gibbon groups in these areas were found along rivers or on hills. This probably explains the finding that although the number of calling gibbon groups was not significantly affected by the area of evergreen forest (from the JICA, 2003 data), it was strongly associated with the area of rivers within the listening post area.

This suggests that gibbons are utilizing deciduous forest where it coincides with patches of evergreen forest, such as that found on rivers and hills. Anecdotal evidence from other areas in eastern Cambodia suggests that gibbons appear to have lower densities or to be totally absent where patches of evergreen forest are not present. An example is the northwestern SBCA, which is dominated by an area of extensive deciduous forest with only minor river systems (Fig. 18.5), where surveys failed to record gibbons (WCS unpubl. data), although the degree of hunting pressure is unknown here and may be a confounding factor. Also, gibbon densities in Phnom Prich Wildlife Sanctuary (WS), which is predominantly deciduous forest, appear to be very low, although only two posts were surveyed (Traeholt et al. 2006).

Gibbons' use of deciduous forest where it intergrades with evergreen forest was also recorded through the observations at C6. One gibbon group (SL2) was commonly seen feeding in and traveling through *Lagerstroemia* spp.-dominated deciduous forest, although their home range included evergreen forest also

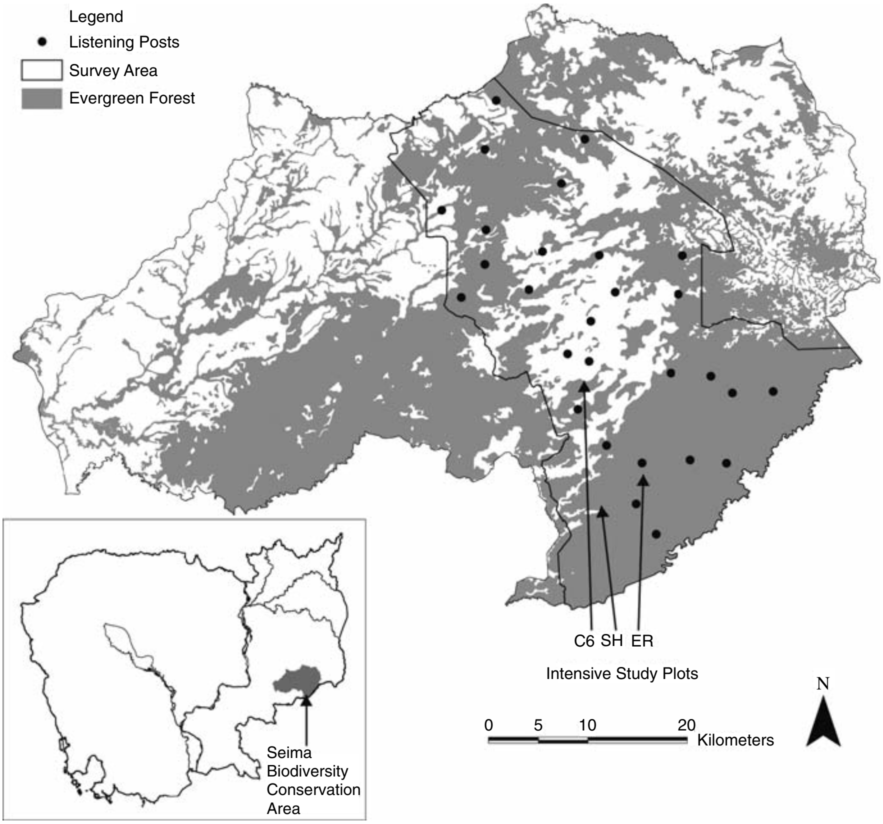

Fig. 18.5 Map

(BMR pers. obs.). In Cat Tien NP, the only other area where extensive surveys of the species have been conducted, gibbons are found across the majority of the park, including areas dominated by evergreen, semi-evergreen, mixed deciduous, and even bamboo forest (M. Kenyon pers comm.; Yiwen pers. comm.). Both the SBCA and Cat Tien NP have large amounts of semi-evergreen/mixed deciduous forests dominated by *Lagerstroemia* spp. (Blanc et al. 2000; Zimmerman and Clements 2002; Polet 2003), suggesting that these areas can be used by *N. gabriellae*, at least when in association with more evergreen forest.

Therefore, it appears that patches of evergreen forest in the deciduous areas in the central SBCA may be integral components of gibbon home ranges possibly acting as refuges during periods of low resource availability or high resource demand. Gibbons may be unable to survive in habitat completely lacking patches of evergreen forest. More research is required to demonstrate whether this is the case and, if so, exactly how different habitats are utilized seasonally.

Site Population Trends

Based upon 4 years of observations from the same listening posts between 2003 and 2006, the number of calling gibbon groups increased by 8.5% annually. Although this suggests an increasing population, it is not conclusive. Calling frequencies may have increased in response to lower hunting pressure (i.e., less disturbance and persecution) or small increases in the number of gibbon groups may have led to increases in calling frequency due to mutual stimulation (Raemaekers and Raemaekers 1985). Nevertheless, at least some of the increase in vocalizations is likely to be due to an increasing population, which is related to the reduction of hunting and stabilization of habitat loss in the area over recent years.

While the degree of hunting pressure on gibbon populations in the SBCA in the past is unknown, it is likely that at least some gibbons currently found in the trade in southern Vietnam have been sourced from across the border in Cambodia (Traeholt et al. 2004; Traeholt et al. 2006). Hunting of gibbons has probably declined since 1998 when a national gun confiscation program was initiated. The European Union Assistance on Curbing Small Arms and Light Weapons in Cambodia (EU-ASAC) and other gun confiscation programs removed 138,154 guns between 1999 and 2004 (EU-ASAC 2004). Most hunting in the SBCA is now conducted using ground snares while hunting with guns is generally conducted at night, both of which methods place little pressure on arboreal, diurnal primates. Since 2002, only a couple of instances of wildlife trade involving gibbons have been recorded in the area around the SBCA.

Forest cover loss has also been stabilized, initially by the concession (1997–2002), which employed guards to limit encroachment, and more recently by the conservation program of the Forestry Administration with the support of WCS. The concessionaire's logging activity may have depressed gibbon numbers in parts of the SBCA, although there are no data available to test this hypothesis. Since the withdrawal of Samling International Ltd in 2002, the Forestry Administration has been responsible for direct management of the area.

Site Population Estimates

This study is the first to calculate a site population estimate for a *Nomascus* species using standard techniques from any of the countries where this genus is found. Previous published estimates have relied either upon expert opinion (e.g., Eames and Robson 1993; Ruggeri and Timmins 1995/1996) or extrapolation from densities obtained from a small number of listening posts over entire sites (Duckworth et al. 1995; Traeholt et al. 2006).

The population estimates obtained from the two methods were very similar: 809±83 groups from the listening posts and 828±255.0 groups from line-transect distance-sampling. Assumptions were made both about the maximum hearing distance for the listening posts and the effective strip width for the line transects; however, the fact that both population estimates are very similar (and easily within confidence intervals) suggests that the estimate obtained is relatively robust. Further research both on hearing distances from listening posts and effective strip width of transects is required for *N. gabriellae*.

The status of the species in other areas is largely unknown, but current knowledge suggests that most other protected populations may be smaller than that in SBCA. If this is true, the SBCA is of global significance.

In Vietnam the total number of white-cheeked gibbons (i.e., of *N. leucogenys*, *N. siki* and *N. gabriellae* combined) in the country's protected areas was estimated to be in the range of 450–600 individuals (Eames and Robson 1993), although this estimate was certainly far too low. Probably, the largest effectively protected population of the species in the country is in Cat Tien NP and may only number several hundred groups in two separate populations (Y. Huang pers. comm., M. Kenyon pers. comm.). No robust population estimates, however, are available from any site in the country.

Further, the species faces serious persecution in Vietnam through hunting for pets, meat, and traditional medicine, and because suitable habitat is being reduced due to the conversion for agriculture, illegal logging, and fragmentation. From the limited data available, it appears that many populations are decreasing under these threats [e.g., on the Da Lat Plateau and in Nghia Trung State Forest Enterprise (Nguyen Xuan Dang and Osborn 2004)] with some being extirpated in recent years, [e.g., Lo Go-Sa Mat National Park (Tordoff et al. 2002) and possibly A Yun Pa Nature Reserve (Tran Quang Ngoc et al. 2001)]. However, considerably more work is required to ascertain the status of the species in Vietnam.

The status of populations in Lao PDR is also uncertain both due to the lack of information over the taxonomic affinity of populations in southern Lao PDR and the absence of data from the area over the past decade. Morphological and vocal phenotypes are somewhat contradictory in these southern Laotian populations, and it is not clear whether they are *N. gabriellae*, part of an intergrade zone between *N. siki* and *N. gabriellae*, or represent an undescribed taxon (Duckworth et al. 1995, 1999; Geissmann et al. 2000). Regardless of the taxonomic issues, combined populations of *N. gabriellae*, *N. leucogenys*, and *N. siki* have been estimated at anywhere between 400 and 6,000 groups in the country (Ruggeri and Timmins 1995/1996), based mainly on expert opinion in the absence of population estimates.

If indeed the southerly populations are representatives of *N. gabriellae*, the most important protected areas for the species in Lao PDR would be Dong Amphan National Protected Area (NPA) and Xe Pian NPA, although population estimates are lacking and no information is available from less than a decade ago (Timmins et al. 1993; Duckworth et al. 1995; Davidson et al. 1997). In both of these areas, the species is commonly hunted and is also, to a lesser extent, under threat from habitat loss (Duckworth et al. 1995; Davidson et al. 1997). Nowhere in southern Lao PDR has effective landscape-level protection from hunting been implemented (Duckworth pers. comm.) and so, as the situation now stands, Lao PDR may not be able to provide long-term protection for the species.

In Cambodia, *Nomascus* gibbons are widespread east of the Mekong River, ranging from Snoul WS in Kratie north to Virachey NP in Steung Traeng and Ratanakiri provinces. Recent population surveys have suggested that Virachey NP, which is contiguous with gibbon habitat in southern Lao PDR, contains one of the largest populations of gibbons in eastern Cambodia (Traeholt et al. 2006). Based on song analysis, the Virachey NP population has been tentatively assigned to the same ambiguous taxon as that found in southern Lao PDR (Konrad 2004). Vocally, gibbons in this area appear to be more closely related to those from Bach Ma National Park in Vietnam, close to the collection location for the type specimen for *Nomascus siki* than to the more southerly Mondulkiri population described in this study (Konrad 2004).

Based on this, Konrad and Geissmann (2006) divide Cambodia's *Nomascus* gibbons into a southerly "typical" population of *N. gabriellae*, situated in Mondulkiri and Kratie Provinces, and a northerly population, in Ratanakiri and Steung Traeng Provinces, of questionable taxonomic affinity. They suggest these populations may have been genetically isolated by either the Srepok River or the Central Indochina Dry Forests. The area between the two populations is dominated by deciduous dipterocarp forest (JICA 2003), which has also been suggested as a barrier to gibbon dispersal in northeast Thailand (Brockelman and Srikosamatara 1993). The current study suggests that deciduous dipterocarp forest could be a barrier to dispersal if evergreen or semi-evergreen forest fragments were much reduced or absent.

If these populations are indeed differentiated, the population in SBCA is of critical conservation value. It represents the largest population confirmed to be of the southern, or “typical”, form, and additionally occurs within an area with an effective protection management structure. The area is contiguous with the smaller Snoul WS, an area confirmed to contain *Nomascus* gibbons, but known to be under heavy threat due to illegal logging and land-grabbing with very little effective protection (Traeholt et al. 2006). Additionally, while the current study was conducted in the core area of the SBCA, the total area of suitable habitat in the conservation area is 2,061 km^2 (study area and all remaining evergreen forest combined), indicating that the true population present may be considerably larger than the estimates given here.

In summary, the population of *N. gabriellae* within SBCA is globally one of the most robust protected populations of the species. Hunting pressure is low, and forest protection effective, which has apparently resulted in real increases in population numbers since monitoring work began. If populations of gibbons in northernmost Cambodia and southern Lao PDR do indeed represent a different taxon, as has been suggested, then the population within SBCA is the most globally important protected population of *N. gabriellae*.

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Chapter 19
The Distribution and Abundance of Hoolock Gibbons in India

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Introduction

A clear understanding of the distribution of organisms in time and space is central to the evaluation of the conservation status of threatened species and critical for the formulation of appropriate conservation strategies. The hoolock gibbon has a broad geographic distribution across tropical and subtropical regions of Bangladesh, China, India, and Myanmar. Groves (1967) distinguished two subspecies of hoolocks based on the variation in pelage coloration on opposite banks of the river Chindwin in Myanmar: *Hoolock hoolock hoolock* (the western hoolock gibbon) and *Hoolock hoolock leuconedys* (the eastern hoolock gibbon). Subsequently, Mootnick and Groves (2005) described these taxa as distinct species.

Distribution of the Western Species (H. hoolock)

The eastern limit of the western species is believed to be the river Chindwin of Myanmar (Groves 1967, 1972). *H. hoolock* is found as far west as the forests of Sylhet, Chittagong (Gittins 1980; Gittins and Akonda 1982), and Mymensingh (Khan 1984, 1985) in Bangladesh. Its northern limit is the Dibang – Brahmaputra river system of India (Tilson 1979) (Fig. 19.1), while the southern limit to the range of the western hoolock has not been precisely determined (Groves 1972). Groves (1972) reported that western hoolocks range from 152 m to 1372 m asl.

Specimens assigned to the western species have been collected in the following localities in Assam: Margherita (27°17′ N, 95°40′ E), Bara Hapjan, Zubya, Sadya (27°51′ N 95°41′ E), Hatikhali (25°40′ N, 93°06′ E), Chang-chang Pani, Nagaland : Mokokchung (26°19′ N, 94°31′); and in Myanmar: Kabaw valley,

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Fig. 19.1 Approximate distribution of hoolock gibbons in India

Mt. Victoria (21°30′ N, 93°30′ E), Hkamti (26°00′ N, 93°35′ E), Ka way (25°00′ N, 95°00′ E), Linhpa West, Hahti (26°08′ N, 95°35′ E), Kawai (26°04′ N, 95°38′ E), Haibum (26°03′ N, 95°56′ E), Chenga Hka (26°10′ N, 95°58′ E), Dagung Hka (26°12′ N, 95°59′ E) (Groves 1972).

Distribution of the Eastern Species, H. leuconedys

The eastern species of hoolock gibbons is distributed in Myanmar east of the Chindwin River and in southwestern Yunnan Province, China, at altitudes of 1067–1219 m (Groves 1972). Prior to this study, there was no record of the eastern species in India.

Specimens identified as eastern hoolocks have been collected in the following localities in Myanmar: Sumprabum (26°35′ N, 97°42′ E), Gokteik (22°21′ N, 96°55′ E), Htingnan (26°36′ N, 97°52′ E), Goletu (27°37′ N, 97°54′ E), Homalin (24°55′ N, 95°01′ E), 25 miles west of Myitkying (25°20′ N, 96°25′ E), Maungkau (25°08′ N, 95°01′ E), Phawzaw (25°33′ N, 95°23′ E), Kaunghein (25°41′ N, 95°26′ E), Linhpa East, Htawgaw, Tasubum (26°00′ N, 96°09′ E), Tapa Hka (26°40′ N, 96°12′ E), N′bunghka (25°57′ N, 96°09′ E), Taulep Ga, Nanyaseik (25°40′ N, 96°44′ E), Lonkin (25°42′ N, 96°22′ E), Mansum (25°48′ N, 96°15′ E), Tawmaw (25°44′ N, 96°19′ E), Pyepat, Pumsin (25°59′ N, 96°09′ E) (Groves 1972); and in the following localities in Yunnan : Homushu Pass (25°00′ N, 98°50′ E), Hotha, West Yunnan, and Teng-yue-chow (25°02′ N, 98°28′ E) (Anderson 1881). They have also been recorded in the Kakhyen Hills on the frontier of Yunnan and Burma (presently Myanmar) and the defile of the Irrawaddy (or Ayeyarwady) below Bhamo (Anderson 1879).

Status of Hoolock Gibbons

As canopy-dependent animals, gibbons are particularly vulnerable to habitat loss and disturbance due to human activities. The hoolock's area of occupancy has declined by more than 30% in the past decade due to habitat loss, habitat fragmentation, and human encroachment. There has also been a reduction in the quality of remaining habitat fragments due to loss of fruiting trees and sleeping trees and the creation of gaps in the canopy (Das et al. this volume).

Reports of the status of hoolocks (the eastern and western taxa together) describe them as highly endangered (restricted isolates) in India and Bangladesh, and probably endangered in Myanmar (Brockelman and Chivers 1984). Hoolocks were identified as a high-priority species in the IUCN Action Plan for Asian Primate Conservation in 1987 (Eudey 1987). More recently, the hoolock was listed as endangered based on reduction in the extent of occupation and habitat disturbance [criteria A2abcd + 3bcd; C1 + 2a(i)] in a CAMP assessment in 2002 (Molur et al. 2003). The hoolock is currently included on Appendix I of CITES, and is listed as Endangered (criteria A2acd+3cd+4acd) on the IUCN Red List (IUCN 2008). The western hoolock species (*Hoolock hoolock*) is among the most endangered primate taxa and is critically endangered in Bangladesh (Molur et al. 2003).

Hoolocks in India are geographically isolated from the populations in Bangladesh and Myanmar, and the Indian hoolock population is fragmented into many small remnant populations (Choudhury 1991, 1996, 2000; Das 2002; Das et al. 2002, 2003; Molur et al. 2005). All of these populations are threatened, and many are too small to be considered viable in the long term. Accordingly, hoolocks were been placed on Schedule I of the Indian Wildlife Protection Act of 1972: the highest legal protection available in India.

Detailed surveys of the species distribution are required to formulate appropriate area-specific conservation plans. This chapter summarizes the results of surveys of hoolock gibbon populations of both the eastern and the western species in all seven states in northeastern India (Assam, Arunachal Pradesh, Nagaland, Meghalaya, Manipur, Mizoram, and Tripura). During the surveys, animals resembling the eastern species of hoolock gibbons were found in India for the first time. This chapter will therefore also describe what is known about the distribution range for eastern species-type gibbons in India.

Methods

We collected distribution records from the existing literature to assess the distribution of hoolocks in India. We then used both direct and indirect methods to survey hoolock populations across their distribution range in India. Detailed surveys were carried out in Assam as well as in parts of Arunachal Pradesh, Mizoram, and Meghalaya.

Direct Sightings

We used a modified line transect method (NRC 1981; Mohnot et al. 1995; Struhsaker 1997) to census gibbon populations. Prior to initiating a census, we modified pre-existing forest trails at each site to lay line transects in a stratified random manner, covering representative areas of the forest (Mueller-Dombois and Ellenberg 1974; Kent and Coker 1994). The transects covered at least 10–15% of the total forest area in each region. The width of the area surveyed along the transects was visually estimated every 500 m of the transect walk. Some of the widths in long-term monitoring sites were verified later using a range finder. Surveys were carried out from 0600 h to 1800 h with a break of 1 h at mid-day. On each day we walked 10–18 km (mean = 15 km) along the transects at a speed of approximately 1.5 km/h (depending on weather conditions and habitat type), with occasional stops of 1 min to search for gibbons. When gibbons were located, group size and composition were recorded. During our surveys, we stopped every 500 m along the transect and visually estimated the percentage of canopy cover in a circular area of 10 m radius above as 1–20%, 21–50%, 51–75%, or 76–100%.

Indirect Methods

All gibbon vocalizations detected while walking along the trails were recorded. When vocalizations were detected, additional efforts were made to contact the groups to obtain accurate estimates of group size and composition. Where captive gibbons were identified in villages and towns, we collected information about the circumstances of collection from the home owner. Trophies of primates (skulls) in households in the villages were also noted.

Survey Area

Surveys were conducted from January 1997 to January 2006. The northeastern region of India includes sections of the Himalaya and Indo-Burma biodiversity hot spots. About two thirds (170,035 km^2) of this area is forested, but only about 38% of the area (97,823 km^2) has the dense forest cover, which is essential for the canopy-dependent hoolock gibbon (Table 19.1), and part of this dense forest is outside of the distribution range of the species. All of the protected areas (National Parks and Wildlife Sanctuaries) within the known distribution range of northeast India (Assam, Arunachal Pradesh, Nagaland, Meghalaya, Manipur, Mizoram, Tripura) were surveyed during this period. We also surveyed all the Reserved Forests (RF), District Council Reserved Forests (DCRF), Proposed Reserved Forests (PRF) in Assam and parts of Arunachal Pradesh, Meghalaya, and Mizoram. Additional intensive surveys were conducted in Anchal Reserved Forests (ARF) and Village Reserved Forests (VRF) in Lohit district of Arunachal Pradesh.

Estimation of Population Size

To estimate the number of individuals in a particular forest and the actual composition of each group, we surveyed each transect on six consecutive days, plotting each group and the number of individuals in that group on the map and then compiling all the data for that particular area. Each group was identified with specific descriptions such as size of the infant (if any), marks

Table 19.1 Forest cover in the seven northeast states of India, in km^2 (FSI 2003)

State	Area (km^2)	Forested area (% total area)	Dense forest (% total area)
Arunachal Pradesh	83,743	68,019 (81.2)	53,511 (63.9)
Assam	78,438	27,826 (35.5)	13,042 (16.6)
Manipur	22,327	17,219 (77.1)	6,538 (29.3)
Meghalaya	22,429	16,839 (75.1)	6,491 (28.9)
Mizoram	21,081	18,430 (87.4)	7,488 (35.5)
Nagaland	16,579	13,609 (82.1)	5,707 (34.4)
Tripura	10,486	8,093 (77.2)	5,046 (48.1)
Total	255,083	170,035 (66.7)	97,823 (38.4)

on the body, etc. Records of groups contacted repeatedly were consolidated on the map daily. We believe we were able to accurately estimate the number of groups and individuals in each transect.

To estimate the total number of individuals in Assam, we first estimated the mean density from the compiled survey data. Statewide data on the percentage of forest cover were provided by the Indian Institute of Remote Sensing (IIRS). The data were classified into the following types: dense, moderately degraded, and highly degraded forest cover. As gibbons are canopy-dependent species and we have not found them in highly degraded forests, we defined suitable gibbon habitat as areas with dense cover and moderately degraded cover. We then multiplied the estimated density by the area of suitable habitat to arrive at the estimated total number of individuals. Finally, we followed the methods outlined in ‘Conservation Priorities in the Eastern Himalayas’ (WWF and ICIMOD 2001) to identify conservation priority areas. The diversity of diurnal primates and landscape integrity indices of each of the surveyed areas were analyzed to define candidate priority areas (CPA). An integration matrix (Fig. 19.2) was then used to rank them from I to V, as follows: level I = highest priority area, level II = highest priority area for restoration, level III = high priority area, level IV = priority area, level V = important area.

Landscape integrity score

Primate diversity score	1 (high)	2 (med)	3 (low)
1 (high)	I	I	II
2 (med)	III	IV	IV
3 (low)	IV	V	V

Fig. 19.2 Matrix for the calculation of priority levels for candidate priority areas (CPAs). Landscape integrity scores are as follows: 1 = >500 km^2 of intact forest, 2 = 101–500 km^2 of intact forest, 3 = 1–100 km^2 of intact forest. Primate diversity scores are as follows: 1 = $\geq$5 diurnal primate species, 2 = 4 diurnal primate species, 3 = 1–3 diurnal primate species

Results

The Distribution of Hoolock Gibbons in Protected Areas

There are 72 PAs in Northeast India, and 55 are within the distribution range of hoolock gibbons. However, gibbons were only found in 39 of these PAs, which cover a total of 8,573 km^2 (Table 19.2), and only a portion of this area was actually occupied by gibbons. Hoolocks are restricted to tropical wet evergreen forest, tropical semi-evergreen forest, tropical moist deciduous forest, and subtropical broad-leaved hill forest, and occur only in forests with dense cover or moderately degraded cover. For example, less than 10 km^2 of the area in the 860 km^2 Kaziranga NP is actually occupied by hoolock gibbons. Individuals tentatively identified as belonging to the eastern hoolock gibbons (*H. leuconedys*) were found only in one protected area, Kamlang WLS.

Table 19.2 Protected Areas (NP = National Park, WLS = Wildlife Sanctuary) in India containing hoolock gibbons. * = areas possibly containing the eastern hoolocks

State	Protected Area	Area (km^2)
Arunachal Pradesh	Namdapha NP	1,985.2
	Kamlang WLS*	783.0
	Mehao WLS	281.0
	Total	**3,049.2**
Assam	Dibru-Saikhowa NP	340.0
	Kaziranga NP	860.0
	Garampani WLS	6.1
	Nambor WLS	37.0
	Gibbon WLS	21.0
	Bherjan-Borajan-Padumani WLS	7.2
	East Karbi-Anglong WLS	222.0
	North Karbi-Anglong WLS	96.0
	Nambar-Doigrung WLS	97.2
	Marat Longri WLS	451.0
	Dhing Patkai WLS	111.2
	Amchang WLS	78.6
	Barail WLS	326.3
	Total	**2,653.5**
Manipur	Yangoupoki-Lakchao WLS	184.8
	Bunning WLS (data from Choudhury 2006)	115.8
	Jiri Maku WLS (data from Choudhury 2006)	198.0
	Kailam WLS (data from Choudhury 2006)	157.8
	Zeilad WLS (data from Choudhury 2006)	21.0
	Total	**677.4**

Table 19.2 (continued)

State	Protected Area	Area (km^2)
Mizoram	Murlen NP	150.0
	Phawngpui Blue Mountain NP	50.0
	Dampa WLS	500.0
	Nengpui WLS	110.0
	Khawnglung WLS	41.0
	Lengteng WLS	80.0
	Tawi WLS	35.8
	Total	**966.8**
Meghalaya	Nokrek NP	68.0
	Balpakram NP	312.0
	Siju WLS	5.2
	Nongkhyllem WLS	35.0
	Baghmara Pitcher Plant WLS	0.02
	Total	**420.2**
Nagaland	Intanki NP	202.0
	Fakim WLS	6.4
	Pulie Badge WLS	9.2
	Rangapahar WLS	4.7
	Total	**222.4**
Tripura	Gumti WLS	389.5
	Trishna WLS	194.0
	Total	**583.5**
	Total PA area in Northeast India with gibbons	**8,573.0**

Distribution of the Western Species Outside the PAs

Detailed surveys were conducted outside of the PAs in the states of Arunachal Pradesh and Assam and in parts of Mizoram, Meghalaya, and Tripura (Table 19.3). Gibbons were found in 20 of 34 forest divisions in Assam (Appendix, Fig. 19.3). The westernmost locality in which hoolock gibbons were recorded in Assam is the Goalpara Forest Division, which represents the northwest boundary of the western hoolock gibbon's global distribution range. We also detected gibbons outside of the PA's in 20 forests in Arunachal Pradesh, 7 forests in Meghalaya, 1 forest in Mizoram, and 13 forests in Tripura (Table 19.3).

First Possible Record of the Eastern Species in India

While conducting surveys in the Lohit district of Arunachal Pradesh, we observed groups of gibbons with a distinctly different coat color from the

Table 19.3 Distribution of western hoolock gibbons in forests outside of the protected areas in Arunachal Pradesh, Meghalaya, Mizoram, and Tripura. ARF = Anchal Reserved Forest, VRF = Village Reserved Forest, RF = Reserved Forest, P = gibbons present; A = gibbons absent; NS = not surveyed. Data from Gupta (2005) are indicated with an asterisk (*) and data from Choudhury (2006) are indicated with a double asterisk (**). All other data are from this study

State	Forest Division	Forest	Area (km^2)	Gibbon status
Arunachal Pradesh	Khonsa	Longding ARF	1.9	A
		Longding Bania VRF	0.6	A
		Tinfa VRF	8	A
		Khelapathar Protected Forest	1.0	A
	Deomali	Russa-chopsa VRF	7.5	A
		Rujen VRF	20.3	P
		Chopnu VRF	5.1	A
		Chattong VRF	3.0	A
		Mopaya	26.0	P
	Khonsa Project	Namsang VRF	108.9	P
		Borduria	38.5	P
	Nampong	Namphai ARF	14.1	P
		Deipan ARF	119.1	P
	Changlang	Rangran Ranglom VRF	13.5	P
		Namdapha RF	177.4	P
	Jairampur Project	Kathang RF	17.5	P
		Koriapani	6.1	A
		Honkap RF	73.4	NS
		Pangsan RF	69.1	NS
		Namgo RF	18.3	P
		Rima RF	67.6	P
		Namdang RF	42.8	NS
	Miao Project	Diyun RF	173.2	P
		Miao RF	125.8	P
		Namphuk RF	57.3	P
		Namchik RF	49.8	P
	Namsai	Namsai RF	23.7	P
		Noa Dihing RF	11.2	P
		Khamti-Singphoo-Punkar ARF	28.2	NS
		Kharen VRF	20.8	NS
	Lohit	Paya RF	66.0	P
		Denuing RF	256.4	A
		Udiomanjum RF	256.4	A
		Ditcher RF	1,792	P
		Tezu RF	646.0	A
		Tebang RF	55.4	P
		Digaru RF	184.0	P
Meghalaya		Songsek RF		P
		Baghmara RF		P

Table 19.3 (continued)

State	Forest Division	Forest	Area (km^2)	Gibbon status
		Songsek Tasek RF		P
		West Garo Hills		P
		Narpuh RF Part-I		P
		Narpuh RF Part-II		P
		Saiphang RF		P
		Angratoli RF**		P
		Chimabongshi RF**		P
		Dambu RF**		P
		Darugiri RF**		P
		Dhima RF**		P
		Dibru Hill RF**		P
		Dilma RF**		P
		Emangiri RF**		P
		Ildek RF**		P
		Rajasimla RF**		P
		Rongrenggiri RF**		P
		Rewak RF**		P
		Nongkhyllem RF**		P*
		Unclassed forests near Lumshnong**.		P
Mizoram		Nengpui RF		P
		Inner Line RF**		P
		Palak Dil**		P
Manipur		Anko range**		P
		Ch-as-ad PRF**		P
		Cheklaphai RF**		P
		Dampi RF**		P
		Irangmukh RF**		P
		Kangbung RF**		P
		Longya RF**		P
		Moreh PRF**		P
		Shiroi proposed NP**		P
		Tolbung RF**		P
		Vangai Bongmukh RF**		P
		Yangenching RF**		P
Nagaland		Ghosu **		P
		Saramati-Noklak areas **		P
		Singphan FR**		P
		Satoi area**		P
Tripura		Dewachera RF		P
		Harinchere RF		P
		Phuldansai RF		P
		Betlingship RF *		P
		Sabul RF *		P

Table 19.3 (continued)

State	Forest Division	Forest	Area (km^2)	Gibbon status
		Conzai RF *		P
		Vangmung RF *		P
		Kanchanchera RF *		P
		Manu Nepal Tills RF *		P
		Laxman Joypara RF *		P
		Thalchere RF *		P
		Ganganagar RF *		P
		Khowichere RF *		P

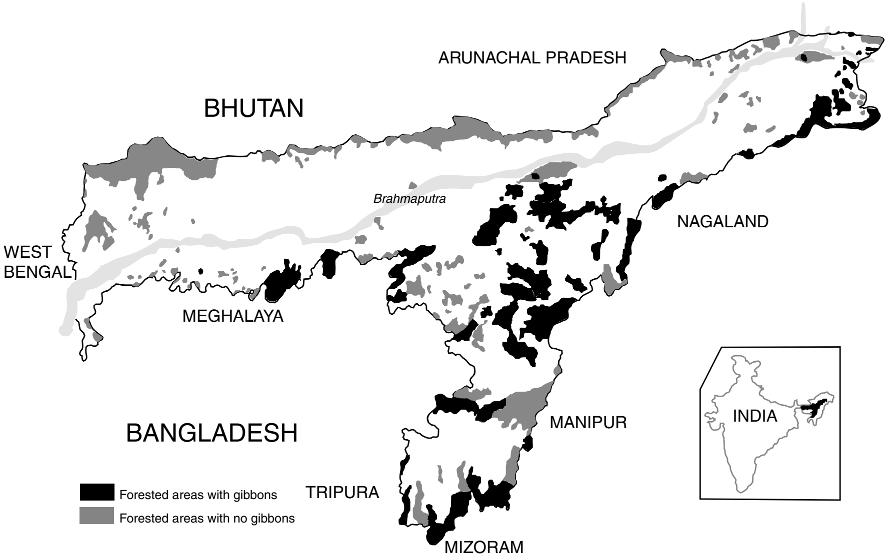

Fig. 19.3 Distribution of hoolock gibbons in Assam

western species. The adult males were black with a brown overlay, the preputial tuft was white, and the brow streaks were well separated with no white hairs between. Adult females had somewhat lighter hands and feet. Most of these characters are typical of the eastern species of hoolock gibbon (*H. leuconedys*), suggesting that the distribution of the eastern species of hoolock gibbon extends into India (Das et al. 2006).

Individuals resembling the eastern species were found between the river Lohit in the north and the high-altitude mountainous area of the Dafa Bum in the south, between 27° 25′ and 27° 48′ N and between 95° 55′ and 96° 25′ E. Subtropical evergreen and semi-evergreen forests dominate the vegetation at

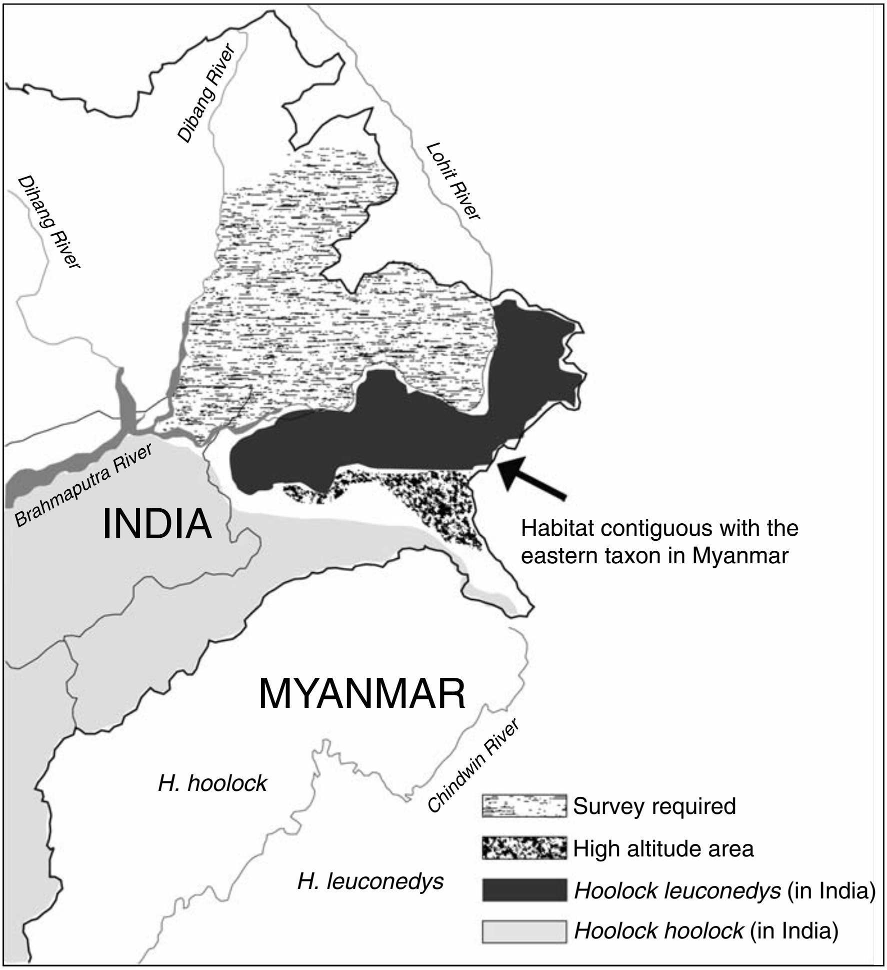

Fig. 19.4 Distribution of the eastern and western hoolock gibbon taxa in eastern India

this elevation with much of this area under cultivation. Figure 19.4 indicates the approximate distribution range of the eastern species based on our surveys. In the lower elevations (122–100 m asl) in the Barrang Nao-Dehing River complex, forms intermediate between the eastern and western species were recorded.

The area of distribution of eastern-type hoolocks in India lies mostly in the Namsai Forest Division and parts of the Miao Wildlife Division of Arunachal Pradesh, and the distribution range of the two species seems to overlap in the lower portion of the Namsai Division. The eastern species was recorded in all of the forested areas under these divisions (Table 19.4), which together comprise an area of more than 2500 km^2, including the Kamlang Wildlife Sanctuary.

Table 19.4 Distribution of *H. leuconedys*-type gibbons in the Lohit district of Arunachal Pradesh (WLS = Wildlife Sanctuary, RF = Reserve Forest, ARF = Anchal Reserve Forest)

Forest	Area (km^2)	Forest Division	Status of eastern hoolocks
Kamlang WLS	783.0	Miao	present
Turung RF	143.5	Namsai	present
Kamlang RF	978.2	Namsai	present
Manbhum RF	136.1	Namsai	present
Piyeng RF	12.3	Namsai	present
Lohit RF	47.6	Namsai	present
Tengapani RF	443.9	Namsai	present
Kamphai ARF	13.5	Namsai	present
Lai ARF	38.9	Namsai	present

Altitudinal Distribution

In Assam, western hoolock gibbons (*H. hoolock*) were located at altitudes from 50 m asl in the forests of Digboi and Doom Dooma Forest Divisions to 1,400 m asl in the Hamren Forest Division. In the high altitude (~1000 m) areas of Hyuliang and other areas, gibbons were not spotted and secondary information does not indicate their presence. Across the Lohit River to the north the vegetation drastically changes and the area most likely does not support gibbons. However, gibbons have also been recorded from altitudes of less than 50 m in Meghalaya to above 2,600 m in Nagaland (Choudhury 2006). Eastern-type hoolocks were recorded at altitudes from 165 to 1075 m.

Group Size and Composition

Hoolock gibbons live in small family groups. The groups usually consist of adult mated pairs and 1–2 immatures. Solitary individuals are also occasionally recorded. Group size and group composition parameters were calculated from line transect data, and solitary individuals were excluded from estimates of mean group sizes. A total of 196 individuals in 62 groups were observed in Assam, with a mean group size of 3.16 individuals (Table 19.5). The largest

Table 19.5 Average group sizes for hoolock gibbons

Area	Mean group size	N	Reference
Meghalaya, Assam	3.2	24	Tilson (1979)
Eastern Bangladesh	3.5	6	Gittins (1980; 1984)
Tripura	3.2	5	Mukherjee (1984)
West Banugach RF, Bangladesh	4.0	6	Siddiqi (1986)
Assam, Arunachal Pradesh	3.0	14	Choudhury (1989; 1990)
Assam	3.2	130	this study
Arunachal Pradesh	3.1	46	this study
Mizoram	3.0	3	Gupta (2005)
Meghalaya	4.0	22	Gupta (2005)
Tripura	3.1	8	Gupta (2005)

group, consisting of 6 individuals, was observed in Chandubi USF in the Kamrup West Forest Division. In the 62 groups contacted, 72% of the individuals were adults, 16% were juveniles and 12% were infants. There was one infant recorded for approximately every 2.6 adult mated females, and there were 1.18 adult males per adult female.

A total of 46 groups of hoolock gibbons with an average group size of 3.1 individuals were sighted in Arunachal Pradesh during surveys in 2005–2006 (Table 19.5). In Meghalaya, 13 groups were sighted in 1997–1998, with an average group size of 2.69. However, in a more recent survey, 22 groups were recorded, with an average group size of 4 individuals (Gupta 2005).

A total of 168 individuals of the eastern species were found, including 49 groups (containing 165 individuals) and 3 lone individuals. The average group size was 3.37 ± 0.98 individuals, but 44% of groups contained ≥ 4 individuals.

Population Estimates for the Western Hoolock Gibbon in the State of Assam

The total forested area in Assam on the south bank of the river Brahmaputra (i.e., the area within the distribution range of hoolocks) is 15,063 km^2. We conducted surveys in areas that comprised 12,772 km^2, or 84.8% of this total forested area, and found gibbons in forests that covered a total area of 9,261 km^2 within the surveyed area. However, only about 67% of the forest in Assam is the relatively intact forest preferred by gibbons (IIRS 2003). Accordingly, we estimated that 7,369 km^2 of forests in Assam actually constituted gibbon habitat (A_h).

We used our survey data to estimate hoolock group density (D_g), individual density (D_i), and total population sizes in Assam. Densities were calculated as:

$$D_g = N_g A^{-1}$$
$$D_i = N_i A^{-1}$$

where N_g = number of groups recorded along the line transect, N_i = number of individuals recorded along the line transect, and A = estimated area sampled along the transects (in km^2). Given an estimated transect area of 306.43 km^2, N_g of 62, and N_i of 216, we estimated that the mean density of hoolock gibbons in Assam is approximately 0.2 groups/km^2 and 0.7 individuals/km^2 in forests containing gibbons.

The estimated numbers of gibbon groups (N_g) and individuals (N_i) in Assam were then calculated as

$$N_g = D_g A_h$$
$$N_i = D_i A_h$$

The resulting estimate was approximately 5,194 individuals (excluding solitary individuals and village populations) in 1,491 groups, or 5,435 individuals (including solitary individuals).

Priority Conservation Landscapes in Assam

We identified sixty CPAs in Assam on the basis of high primate diversity and landscape integrity. These areas support not only hoolock gibbons but also other primates. The spatial relationships between the candidate priority areas, the area of remaining forest, conservation gaps based on the viability and representation analysis, and remaining habitat blocks were then used to identify larger conservation landscapes using the methods described by WWF and ICIMOD (2001). We identified eight highest priority conservation landscapes (Levels I and II) in Assam (Table 19.6). These larger landscapes have the greatest potential in terms of supporting populations in the long term. Similar analyses are required for the identification of priority conservation landscapes in other states.

Table 19.6 Conservation landscapes for primate conservation in Assam. HH = *Hoolock hoolock*; MA = *Macaca arctoides*; MS = *M. assamensis*; MM = *M. mulatta*; MN = *M. nemestrina*; NC = *Nycticebus coucang*; TP = *Trachypithecus phayrei;* TI = *T. pileatus*

Conservation landscape	Area (km^2)	Primate species
Innerline-Kathakhal-Singhla complex	1,291	HH, MA, MS, MM, MN, NC, TP, TI
Langlakso-Mikir Hills-Kalioni complex	1,044	HH, MM, MS, MN, NC, TI
Joypur-Dirak-Upper Dehing-Dilli-Abhayapuri complex	580	HH, MM, MS, MN, NC, TI
Barail-North Cachar complex	300	HH, MA, MS, MM, MN, NC, TI
Borjuri-Junthung-Western Mikir Hills complex	287	HH, MM, MS, MN, NC, TI
Rani-Garbhanga complex	281	HH, MS, MM, NC, TI
Khurimming-Panimur-Amreng complex	186	HH, MM, MS, MN, NC, TI
Dhansiri-Borlanfer complex	105	HH, MM, MS, MN, NC, TI

Discussion

We estimate the population of hoolock gibbons in Assam to be around 4,500–5,500 individuals (excluding solitary individuals), and the total area of gibbon habitat as 7,369 km^2. Choudhury (2006) estimated that the total population in other states in India is between 1,700 and 2,200 individuals (in all populations, regardless of long-term viability), including 350–500 gibbons in Manipur, 500–600 in Meghalaya, 500–600 in Mizoram, and 350–500 in Nagaland. Therefore, we estimate that the total number of individuals in India is in the range of 6,200–7,700. However, the actual area of occupancy and number of individuals might be less than estimated, for several reasons. Gaps in the forest canopy more than 10 m wide restrict the movement of hoolocks. Therefore, small isolated forest patches not connected by canopy corridors cannot be used by hoolocks, even when the habitat type is appropriate. Also, our calculations assumed that gibbon densities are equal across all areas of appropriate habitat while, in fact, hoolock densities are higher in some forest types than others. In this study, most (80%) of the groups were observed in areas with 51–75% canopy cover. In areas with >75% canopy cover no hoolock gibbons were found. Density may also vary with altitude. Heavy hunting for the pet trade in infant gibbons has apparently eliminated hoolocks from most of the forested areas of Hill Circle, so the area of intact forest is not a good predictor of hoolock numbers in this region. Therefore, these population estimates should be used cautiously when setting priorities for the conservation of hoolock gibbons. Moreover, the patterns of threats to hoolock gibbon populations in different areas of northeast India are different. Area-specific conservation efforts should be initiated where possible.

Although gibbons are found in many locations in Assam, most of the populations are small and isolated (Fig. 19.3). There are no contiguous forest patches left that could support a population of more than 300 individuals, and many forest patches contain only a single pair of gibbons. Furthermore, the gibbon populations that formerly inhabited the Reserved Forests (Pophanga RF, Gendabari RF, Kashumari, Khongkhal PRF) in the Lakhipur and Goalpara areas have been lost to extinction due to forest destruction and human encroachment, thus reducing the extent of occurrence of this species. The forests near the western boundary of the hoolock's range should be the focus of special conservation effort, so that further reduction in the extent of occurrence can be prevented.

In this study, the presence of the eastern species of hoolock gibbon (*Hoolock leuconedys*) in India was recorded for the first time. From our preliminary survey, we estimate that their distribution range in India lies between the river Lohit in the north and west and high altitude mountains including Dafa Bum (>4,500 m asl) in the south (Fig. 19.4). This area is contiguous with the distribution range of the eastern species in Myanmar, although the existing literature suggests that the Chindwin River divides the eastern and western species. There is no record of hoolock gibbons north of Sumprabum (26°35′ N, 97° 42′ E) in Myanmar. The Chindwin River starts south of the Chukan Pass in Myanmar. North of the Chukan Pass there is no permanent barrier to the movement of gibbons, and the habitat in this area is contiguous with the eastern species' distribution range (Fig. 19.4). Further surveys will be required to determine the status of populations between the Dibang River and the Lohit River (Miao Wildlife Sanctuary).

Prior to this study, all gibbons in India were considered to belong to the western species, and Namdapha NP, Kamlang WLS, and Kamlang RF were considered to be the largest continuous forest patches left for conservation of western hoolock gibbons in India. But the present findings, if supported by further taxonomic study, segregate the Kamlang populations (RF and WLS) of hoolock gibbons from the Namdapha population as members of the eastern species and hence the conservation scenario for both species in India is changed substantially. Detailed study is required to evaluate the population status and phylogeography of the eastern species in India.

Groves (1972) suggested that the altitudinal range of the eastern species is between 1066.8 m and 1219.2 m asl. However, the eastern species was found at much lower elevations (165–1075 m asl) in India. Further surveys of the eastern species including a broader range of altitudes are clearly required.

Although the 'Mishmi' tribes who inhabit the region occupied by eastern hoolocks do not kill gibbons, there are several problems facing eastern hoolocks in India, including rapid habitat loss, fragmentation, and degradation. Except for Kamlang WLS, the areas inhabited by eastern hoolocks are unprotected, and traditional as well as commercial practices affect conservation efforts. Clearly, sincere efforts for conservation with long-term vision will be required to protect the eastern hoolock gibbon in India. Fortunately, most areas at high elevations are inaccessible and healthy hoolock population may persist in these forests.

Gibbons are dependent on the forest canopy for food and locomotion. As a result, many populations of hoolock gibbon have become isolated from one another due to habitat disturbance, even when the gaps created are relatively small. There are several threats to the persistence of small populations of both hoolock species, but habitat loss, degradation, and fragmentation are the largest factors. Habitat destruction causes a cascade of effects through the loss of important feeding and sleeping trees and breakage in canopy highways, which can lead to population fragmentation, increased mortality, reduced reproductive output, increased risk of diseases transmitted from domestic animals, and demographic instability. Population simulation models using VORTEX with current information about western hoolock gibbon biology predicted a very high probability of extinction within 20 years for populations of less than 15 individuals (Molur et al. 2005). Therefore, most populations of hoolock gibbons in India are likely to become extinct due to deterministic events like demographic stochasticity, even without considering factors such as inbreeding, disease outbreaks, or other environmental phenomena. In the future, inbreeding depression may also pose a threat, as these populations are totally cut off from each other, preventing gene flow between populations. Some populations may require special integrated management to assure their survival. A number of goals must be addressed in conservation planning, including the maintenance of viable population sizes, reduction in habitat fragmentation, protection of existing habitat, and management of the population as a whole. As maintenance of populations of adequate size is crucial in the prevention of local extinction, conservation and management of larger landscapes are essential to ensure the long-term persistence of hoolock gibbons.

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Appendix

The distribution of gibbons outside of protected areas in Assam. RF = Reserved Forest, PRF = proposed Reserved Forest, DCRF = District Council Reserved Forest, P = hoolock gibbons present, NS = not surveyed, A = hoolock gibbons absent. (?) = secondary information from local villagers suggests the presence of gibbons, but this could not be confirmed from direct sightings or calling records.

Division	District		RF/ PRF	Area (km^2)	Gibbon status
Digboi	Tinsukia	1	Digboi E/B	0.70	P
		2	Digboi W/B	9.29	P
		3	Kotha	10.48	P
		4	Tingkupani	35.52	P
		5	Tipong	4.45	P
		6	Tirap (1st Addn.)	30.25	P
		7	Tirap	14.55	P
		8	Upper Dehing (EB)	131.68	P
		9	Upper Dehing (WB)	274.85	P
		10	Dirak	30.42	P
		11	Makumpani	4.83	P (?)
		12	Bagapani	0.96	A
		13	Namphai	20.48	A
		14	Lekhapani	13.96	A
		15	Paharpur	1.66	A
Sibsagar	Sibsagar	1	Dilli	30.30	P
		2	Abhayapuri	67.36	P
		3	Sapekhati	7.45	A
		4	Solah (Addn)	6.83	A
		5	Dirai	48.32	A
		6	Geleki	59.25	A
Dibrugarh	Dibrugarh	1	Dihingmukh	47.27	A
		2	Jakai	18.27	A
		3	Jeypore	108.68	P

(continued)

Division	District		RF/ PRF	Area (km^2)	Gibbon status
		4	Namdang	18.57	A
		5	Telpani	13.31	A
Jorhat	Jorhat	1	Dessai	27.97	A
		2	Dessai Valley	174.48	P
		3	Tiru Hills	58.59	A
Nagaon South	Nagaon	1	Doboka	117.41	P
		2	Lumding	224.03	P
		3	Hawainpur	18.92	A
		4	Jamunamoudanga	14.71	A
		5	Kaki (Pt.)	111.46	A
Doom Dooma	Tinsukia	1	Kakajan	23.46	P
		2	Philobari	3.18	P
		3	Takowani	5.03	P
		4	Pengri	3.17	P
		5	Doom Dooma	28.81	P
		6	Buridihing N/B	15.17	P
		7	Buridihing S/B	7.78	P
		8	Tarani	20.39	P
		9	Kundilkalia	72.84	P
		10	Debang Valley PRF	35.64	P
		11	Hahkhati	6.72	P
		12	Kumsang	22.53	P
		13	Mesaki	13.66	P
		14	Holonghabi	5.20	A
		15	Nalini	3.74	A
		16	Dangori	9.19	A
		17	Talpathar	1.80	A
		18	Duarmara	6.53	A
		19	Lakhipathar	1.05	A
		20	Mohongpathar	4.66	A
		21	Deopani	16.18	A
		22	Halongaon	3.71	A
		23	Kukurmara	3.65	A
		24	Sadia Stn. N/B	23.31	A
		25	Sadia Stn. S/B	4.51	A
K.A. West	Karbi Anglong	1	Dhansiri RF	70.39	P
		2	Daldali RF	123.33	P
		3	Disama RF	11.26	P
		4	Englonggiri DCRF		P
		5	Miyungdisa DCRF		P
		6	Borlanfer DCRF		P
		7	Hafjan PRF		P
		8	Kaki RF	121.49	A
		9	Hidipi DCRF	20.08	A
		10	Jamuna DCRF	1.13	A

(continued)

Division	District		RF/ PRF	Area (km^2)	Gibbon status
E.A.W.L.	Golaghat	1	Panbari RF	7.66	P
Assam State Zoo	Kamrup	1	Hengrabari RF	1.18	A
N.C. Hills	N.C. Hills	1	Barail RF	15.90	P
		2	Khurimming RF	108.41	P
		3	Lanting Mupa RF	493.35	P
		4	Panimur PRF		P
		5	Barail PRF	17.60	P
		6	Doyong Plantation		A
Hamren	Karbi Anglong	1	Amsolong PRF		P
		2	Balasore PRF		P
		3	Umjakini PRF		P
		4	Amreng RF	56.95	P
		5	Rongkhong	33.79	A
		6	Jokota	14.64	A
K.A. East	Karbi Anglong	1	Mikir Hills RF	299.79	P
		2	Kalioni RF	209.79	P
		3	Khonbamon DCRF	165.49	P
		4	Nambor N/B RF	53.09	P
		5	Nambor W/B RF	166.33	P
		6	Jungthung RF	32.57	P
		7	Patradisa DCRF	67.34	P
		8	Longit DCRF	117.62	P
		9	Haithapahar DCRF	54.39	P
		10	Mahamaya DCRF	5.58	P
		11	Borjuri PRF	214.88	P
		12	Western Mikir Hills PRF	39.36	P
		13	Langlakso PRF	534.68	P
		14	Kaziranga PRF	33.88	P
		15	Dolamora PRF	5.53	P
		16	Kalapahar PRF	9.77	P
		17	Bokajan PRF	9.81	P
		18	Tikok PRF	25.89	P
		19	Balasore PRF		A
		20	Selabar	335.40	A
		21	Sildharampur	21.58	A
		22	Hidipi DCRF	20.08	A
		23	Jamuna DCRF	1.13	A
		24	Lahorijan PRF	36.08	A
Hailakandi	Hailakandi	1	Innerline RF	502.08	P
		2	Katakhal RF	134.53	P
Goalpara	Dhubri	1	Bamundanga	2.29	A
		2	Bandarmatha		A
		3	Bordal	0.86	A
		4	Dipalsang	2.77	A

(continued)

Division	District		RF/ PRF	Area (km^2)	Gibbon status
		5	Dhamar	1.61	A
		6	Dipkai	1.93	A
		7	Kumrakhali	8.85	A
		8	Nakkati	2.00	A
		9	Nalbari	1.66	A
		10	Mogho	3.73	A
		11	Saikiabhaga	1.68	A
		12	Dashikata	16.85	A
		13	Dewlee	1.90	A
		14	Dwaraka	1.85	A
		15	Gonbina	1.17	A
		16	Matia	7.67	A
		17	Nalanga	8.39	A
		18	Randu	2.45	A
		19	Rokhapara	1.96	A
		20	Segunbari	2.38	A
		21	Pancharatna	9.76	A
		22	Ajajoar Hill	45.39	A
		23	Barjhar	8.07	A
		24	Chikebim	0.21	A
		25	Dabli Hill	1.40	A
		30	Pophanga	2.77	P
		26	Gendabari	5.29	P (?)
		27	Geradubi	0.78	A
		28	Guriajhar	12.63	A
		29	Paikan	7.11	A
		31	Salpara	1.06	A
		32	Zangrajansa	15.39	A
	Goalpara	1	Kashumari (Pt-I) PRF	0.85	P
		2	Kashumari (Pt-II) PRF	0.22	P
		3	Khongkhal PRF	2.51	P
Nagaon	Nagaon Marigaon	1	Bagser RF	33.67	P
		2	Deosur RF	5.87	P
		3	Kamakhya RF	5.18	P
		4	Kafitoli RF	2.92	P
		5	Suang RF	26.45	P
		6	Bamuni RF	1.55	A
		7	Borpani RF	31.73	A
		8	Hirapunja RF	2.28	A
		9	Kukrakata RF	15.93	A
		10	Lutumai RF	20.40	A
		11	Pilkhana RF	1.64	A
		12	South Diju RF	13.06	P

(continued)

Division	District		RF/ PRF	Area (km^2)	Gibbon status
		13	North Diju RF	10.02	P
		14	Daboka (part) RF	43.82	NS
		15	Jakota (1st addition) RF	1.39	NS
		16	Kondil PRF	6.8	A
		17	Deosur Hill PRF	0.68	P
		18	Kholahat RF	61.64	P
		19	Killing RF	4.45	P
		20	Barbari RF	0.55	A
		21	Dhuadoloni RF	0.05	A
		22	Sonaikachi RF	53.03	A
		23	Tetelia Boghra RF	18.07	A
Karimganj	Karimganj Cachar	1	Innerline RF	1136.96	P
		2	Longai RF	21.20	P
		3	Singla RF	19.20	P
		4	Patharia RF	10.70	P
		5	Badsahitila RF	75.13	A
		6	Dohaliia RF	38.74	A
		7	Tilbhum RF	17.95	A
		8	North Cachar RF	37.90	P
Silchar	Cachar	1	Innerline RF	135.20	P
		2	Barail RF	10.40	P
		3	Katakhal RF	19.70	P
		4	Upper Jiri RF	63.26	P
		5	Sonai RF	35.95	A
		6	Lower Jiri RF	36.43	NS
Golaghat	Golaghat	1	Diphu N/B	183.66	NS
		2	Dayang	246.36	NS
		3	Lower Doigrung	20.73	NS
		4	Nambar (Pt.)	426.5	NS
		5	Rengma	139.22	NS
		6	Upper Doigrung	21.50	NS
		7	Koko donga	44.41	NS
Kamrup East	Kamrup	1	Gorbhanga	114.61	P
		2	Jorsal RF	12.56	P
		3	Kuwasingh	9.98	P
		4	Rani	43.69	P
		5	Amchang	53.18	A
		6	Aprichola	60.75	A
		7	Chamata	0.27	A
		8	Dhaniangaon	0.36	A
		9	Fatasil	6.70	A
		10	Gotanagar	1.71	A
		11	Hengrabari (Pt)	4.98	A
		12	Jalukbari	0.98	A

(continued)

Division	District		RF/ PRF	Area (km^2)	Gibbon status
		13	Morakdoal	14.27	A
		14	Sarania Hills	0.08	A
		15	Sildhar	0.51	A
		16	Sonpara	2.21	A
		17	South Kalaphar	0.70	A
		18	Teteliguri	1.20	A
		19	South Amchang	15.50	P
		20	Khanapara	9.96	NS
		21	Maliata	3.26	NS
Kamrup West	Kamrup South	1	Chandubi USF	2.00	P
		2	Chaygaon RF	12.94	P
		3	Kulsi RF	18.55	P
		4	Pantan RF	112.85	P
		5	Bogaikhas RF	246.69	P
		6	Barodobha RF	4.34	P (?)
		7	Barduar RF	72.39	P (?)
		8	Gizang RF	34.74	P (?)
		9	Luki RF	9.05	P (?)
		10	Mtaikhar RF	16.86	P (?)
		11	Barjuli RF	11.28	A
		12	Dhuniagaon RF	0.37	A
		13	Dimali RF	0.53	A
		14	Dudhkhuri RF	0.93	A
		15	Dampara Hill RF	1.93	A
		16	Garubaldha RF	1.10	A
		17	Ghoraputa RF	0.48	A
		18	Gohaigurung RF	1.26	A
		19	Jaipur RF	3.26	A
		20	Jharikhuri RF	12.47	A
		21	Khaksi Sikrabura RF	10.20	A
		22	Khatajuli RF	1.10	A
		23	Khatkhati Hill RF	2.49	A
		24	Khurkhuri RF	0.66	A
		25	Mayang Hills RF	21.39	A
		26	Melghat RF	3.63	A
		27	Milmilia RF	19.63	A
		28	Moman RF	32.11	A
		29	Mugakhal RF	1.29	A
		30	Silmla Hills RF	1.26	A
		31	Singra RF	3.78	A
		32	Sursuria	3.90	A
		33	Taraibari	3.19	A
		34	Uttar Nampathar	13.78	A
		35	Dakhin Nampathar		A

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Chapter 20

Census of Eastern Hoolock Gibbons (*Hoolock leuconedys*) in Mahamyaing Wildlife Sanctuary, Sagaing Division, Myanmar

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Introduction

The hoolock gibbons are now ranked one of four genera of the family Hylobatidae (Roos and Geissmann 2001; Brandon-Jones et al. 2004). They occur in closed canopy forest areas between the Salween River in the east and the Brahmaputra River in the west (Groves 1967; Marshall and Sugardjito 1986), including eastern India and Bangladesh, most of Myanmar, and a small part of Yunnan, China, that occurs west of the Salween River. Groves (1967) considered the hoolock to have two subspecies, *Hylobates hoolock hoolock*, the western Hoolock gibbon, and *H. h. leuconedys*, the eastern hoolock gibbon, separated by the Chindwin River system. This separation was supported by pelage differences in specimens in the American Museum of Natural History and the British Museum. More recently, Mootnick and Groves (2005) replaced the previous generic name proposed for the genus, *Bunopithecus* (Prouty et al. 1983), with *Hoolock*, and proposed elevating the two subspecies to species level. This convention has been accepted in the present volume.

While considerable survey work has been carried out on the western hoolock gibbon in India and Bangladesh (Gittins 1984; Gittins and Tilson 1984; Choudhury 1990; Islam and Feeroz 1992; Choudhury 1996; Das and Bhattacherjee 2002; Das et al. 2003, 2005, this volume; Molur et al. 2005), almost nothing has been known about the current distribution and population sizes of the eastern hoolock apart from information on the labels on museum specimens. Large forest areas of Myanmar have not been visited by collectors or primate researchers, and many wildlife and conservation personnel are still unaware that the hoolock gibbon can be easily distinguished from geographic neighbors such as *Hylobates lar* by its loud vocalizations.

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The total population of the western hoolock in India and Bangladesh is in the low thousands and is highly fragmented (Molur et al. 2005; Das et al. this volume). Is the eastern hoolock in a similar situation or are there still viable populations in the extensive forest tracts of Myanmar? To begin answering this pressing question, we have undertaken a survey of an area recently established as a wildlife sanctuary east of the Chindwin River.

This survey was part of a project that had four main objectives: (1) estimate hoolock gibbon population density in the newly established Mahamyaing Wildlife Sanctuary in western Myanmar, (2) conduct a detailed assessment of threats to the sanctuary, (3) promote education and public awareness, and (4) assist in management of Mahamyaing Wildlife Sanctuary. The project was a collaborative effort between the Wildlife Conservation Society–Myanmar Program, and the Nature and Wildlife Conservation Division (NWCD), Forest Department of Myanmar, with support from the US Fish and Wildlife Service. The first objective above, the subject of this chapter, was achieved through the following activities: (1) a training workshop conducted at the census site on census methods, habitat evaluation, and threat assessment; (2) gibbon population surveys carried out over a period of nearly 1 year; and (3) final meetings in Yangon with the survey team to finish the analysis of the gibbon census and habitat assessment data.

Hoolock Gibbons and Protected Areas in Myanmar

The current protected area system on Myanmar is based on the wildlife law of 1994. Protected areas (PAs) that lie west of the Salween River and contain closed-canopy mixed deciduous, semideciduous, or evergreen forest are potential habitat for hoolock gibbons. We identified at least seven significant PAs (larger than 100 km^2: Fig. 20.1), one of which, the Rakhine Yoma Elephant Range (1,755 km^2), lies west of the Ayeyarwady (or Irrawaddy) River and therefore probably contains a population of the western hoolock, *H. hoolock*. The Rakhine Yoma area is about 18° north latitude and probably is, or is near, the southernmost occurrence of hoolock gibbons. Wildlife officials report that gibbons occur there, but no information is available about population sizes. There is at least 50,000 km^2 of forest area (much of it degraded) in the Rakhine Yoma mountain range in Myanmar west of the Ayeyarwady–Chindwin Rivers (BirdLife International 2005), which potentially contains western hoolocks. An additional 23,000 km^2 lies to the north in the Chin Hills complex, but it is clear from satellite imagery that more than half of this forest is now degraded or destroyed. A couple of small PAs lie in this area. To our knowledge there have been no surveys of primates in any of the areas that are believed to harbor the western hoolock gibbon.

J.T. Marshall Jr. reported hearing eastern hoolock gibbons (*H. leuconedys*) along the Salween River from the Thai side in 1974 and 1981 (Marshall and

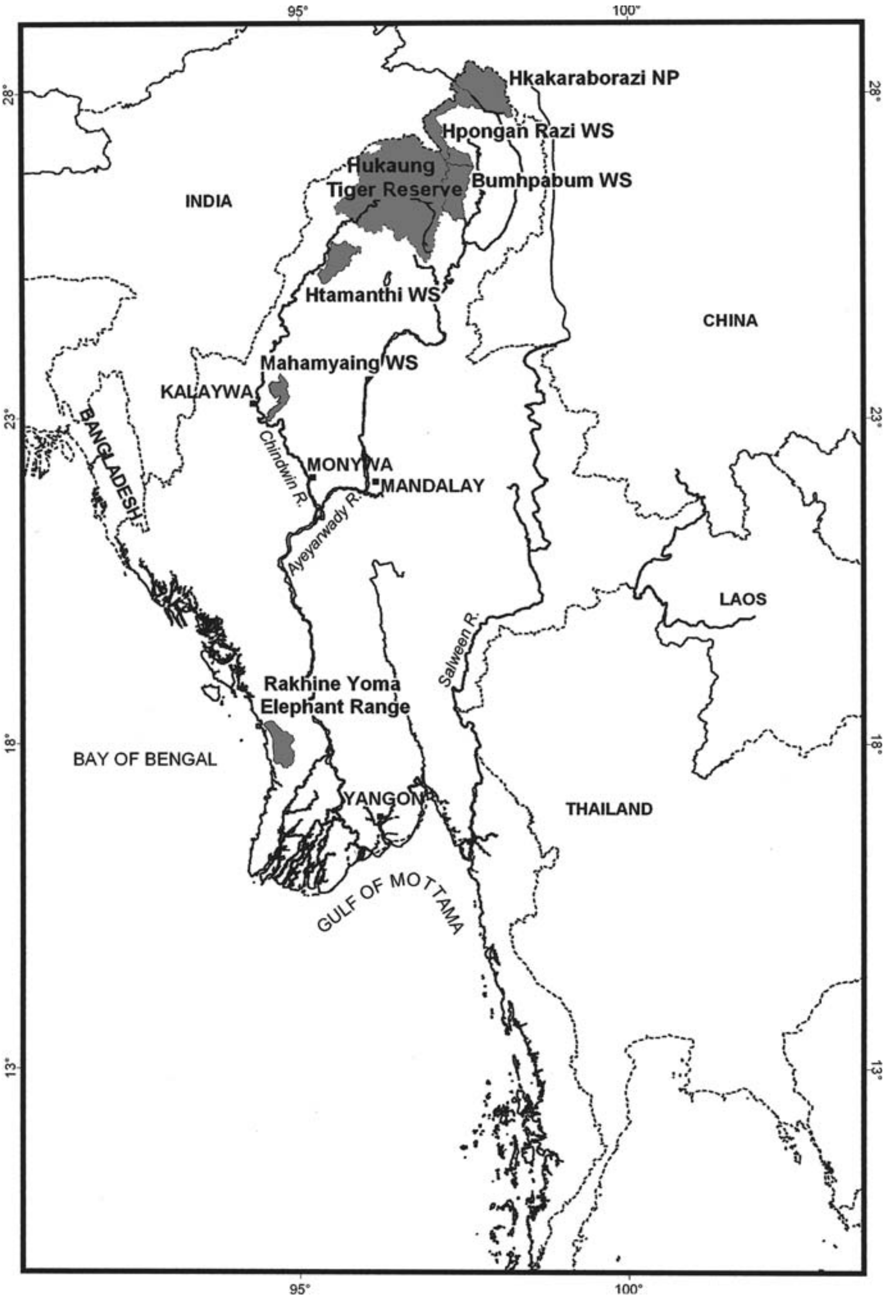

Fig. 20.1 Protected areas in Myanmar in the range of the hoolock gibbon, showing location of Mahamyaing Wildlife Sanctuary

Sugardjito 1986), but it is unclear if any viable population still exists there. There appear to be no conservation areas along the Salween River in the eastern parts of Myanmar.

Between 23° and 28° north latitude there are six other protected areas, mostly east and north of the Chindwin River (Fig. 20.1). These are (from south to north) Mahamyaing Wildlife Sanctuary (WS) (1,180 km^2), Htamanthi WS (1,320 km^2), the extended Hukaung WS or Tiger Reserve (about 21,802 km^2), Bumhpabum WS (1,854 km^2), Hpongan Razi WS (2,704 km^2) and Hkakaraborazi National Park (3,812 km^2). The last area is the northernmost part of Myanmar and gibbons are reported only in the park's southern parts. The northern limit of gibbons in the area, which is now in the center of Hkakaraborazi Park, was reported by naturalist-explorer Frank Kingdon-Ward (1937: 337) to be the Seinghku confluence of the Nam Tamai River, which is slightly north of 28° north latitude.

Many mountains in northern Myanmar exceed 4,000 m in altitude, and hoolock gibbons have been reported to occur at or above 8,000 ft (2,438 m: Kingdon-Ward 1949; Tun Yin 1967). There are some suggestions that they may move up and down mountains seasonally, although this has not been substantiated to our knowledge. For example, Kingdon-Ward (1949: 244) reported: "[Gibbons] ascend even in winter to 4,000 ft and perhaps higher. In the rainy season one hears them at 8,000 ft" At high elevations gibbons occur in forest "where the pine is a dominant forest tree" (Anthony 1941; cited in Tun Yin 1967).

The Hukaung–Bumhpabum reserves are broadly contiguous and from satellite images about 75% of the whole area is covered with closed forest, the remainder being agricultural area in the center of the valley, degraded swiddens, and bamboo forest. Hence, these reserves contain roughly 20,000 km^2 of suitable forest habitat for gibbons—effectively the largest intact evergreen forest of mainland Southeast Asia. Actual protection and management of this forest complex will be a difficult and complex problem requiring considerable local education and extension work, particularly as more than 50,000 people already reside in the Hukaung Valley (Rabinowitz 2008 is a rich source of information and history). As manpower of the NWCD of the Forest Department is nowhere near sufficient to enforce conservation laws over such a vast area, it is clear that effective conservation measures must be incorporated into the development goals of all government agencies active in the region, as well as the programs of local political minority groups.

The upper Chindwin River is fed by the Tanai River, which drains areas in the eastern part of the Hukaung Valley. Most of the watershed lies within the putative area of hybridization or intergradation between the eastern and the western hoolock gibbons (Groves 1967). The gibbons in the areas in the mountains north and west of the Hukaung Valley are especially unstudied and call for much more research on their genetics, phenotypes, and vocalizations to understand the relationship between the two forms now recognized as species.

Das et al. (this volume) report that there may be eastern hoolocks west of the Chindwin in India. More complete surveys of this area are needed.

In 2006 the NWCD and WCS–Myanmar sponsored another workshop on census methods for gibbons at Tanai in the Hukaung Valley, and gibbon census work has begun in the valley.

Study Area

Mahamyaing Wildlife Sanctuary, located about 220 km northwest of Mandalay in Sagaing Division (Fig. 20.1), was created out of five reserved forests or timber concessions, and contains 1,181 km^2 of area covered mostly with deciduous and moist evergreen forest. It consists of a core area of 577 km^2 and a buffer zone of 604 km^2 (Fig. 20.2). The core area in the north is nearly all (93%) moist mixed deciduous forest (which actually is mixed with evergreen species, and typically has *Dipterocarpus turbinatus* as a dominant emergent species) and evergreen forest, all of which is relatively closed canopy forest and therefore suitable for gibbons. The amount of closed canopy forest in the whole sanctuary and within each listening area was evaluated using ArcView software with Landsat 7 images taken in 2000, using bands 4 (red), 5 (green), and 6 (blue). The buffer zone, which lies to the south of the core area, consists of 42% closed canopy forest, and 58% open dry dipterocarp (indaing) forest or highly degraded logged habitat, which is generally unsuitable for gibbons. The sanctuary is drier in the southern, more lowland areas. The soil in the sanctuary is very sandy and in the dry season running water is nearly absent. The topography of the sanctuary is rather level in the south and hilly with numerous steep ridges in the north, and ranges in altitude from about 200 to 500 m above sea level. Other large wildlife species in the sanctuary include Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), banteng (*Bos javanicus*), wild pig (*Sus scrofa*), sambar (*Cervus unicolor*), common muntjac (*Muntiacus muntjak*), rhesus monkey (*Macaca mulatta*) (seen by authors), and langurs (probably *Semnopithecus phayrei*).

Methods

Workshop and Training Exercises

We conducted a week-long workshop on gibbon census methods, habitat evaluation, and conservation at Thetkegyin (Fig. 20.2), the main village near the sanctuary, from February 17–23, 2004. It was attended by 14 trainees from the Forest Department and from local universities. Trainees spent 4 days carrying out field exercises in the forest.

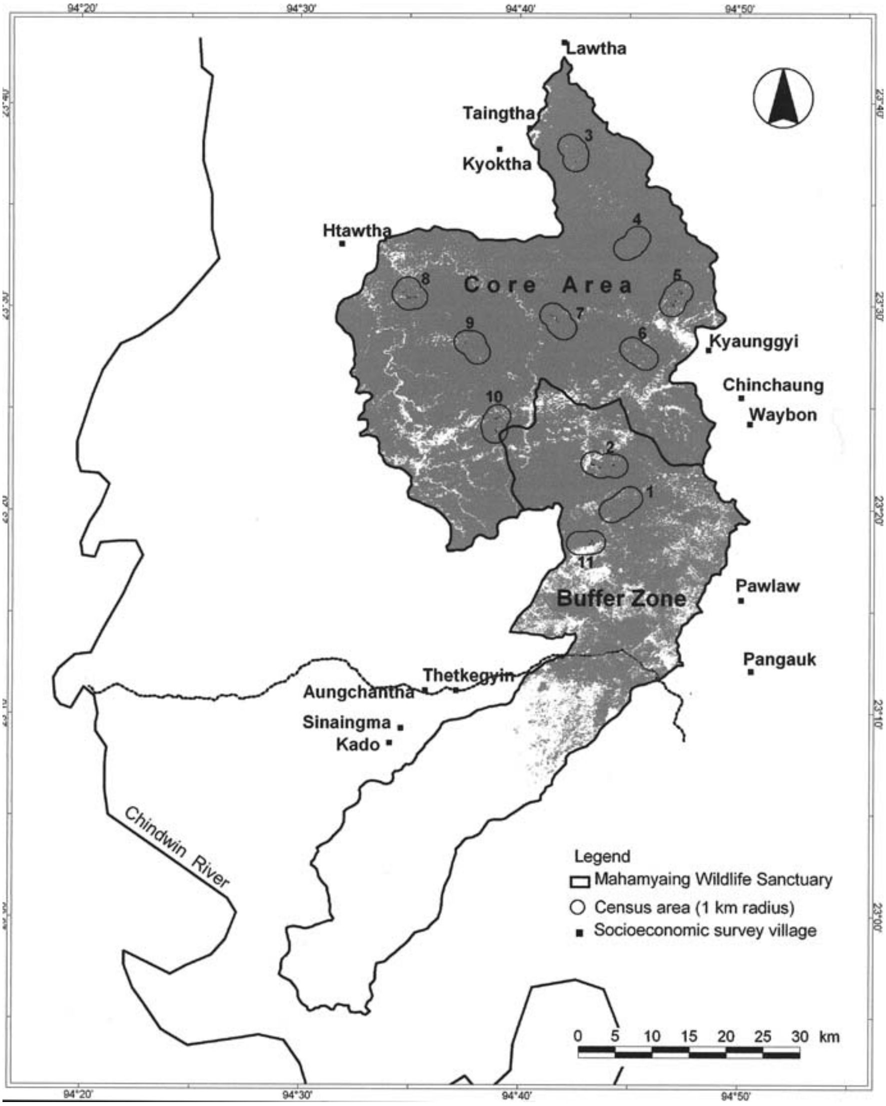

Fig. 20.2 Landsat 7 image of Mahamyaing Wildlife Sanctuary showing closed canopy forest (*shaded area*) and census areas with 1-km radius listening area boundaries. The *dotted line* passing through the village of Thetkegyin is a dirt road leading from the town of Kalaywa in the west to Monywa in the east

The following year a five-person survey team was selected from among the workshop participants to carry out a gibbon census at 11 sites in the wildlife sanctuary. The survey team finished the field census in early 2005. A five-day meeting was then held in March of 2005 in Yangon to complete the analysis of data on vocalizations and finish the mapping of gibbon groups and density estimation.

Census Methods

The survey used auditory methods for estimating group density within defined census areas (Brockelman and Ali 1987; Brockelman and Srikosamatara 1993; Phoonjampa and Brockelman 2008). The census areas were then treated as samples of the total area of interest, in this case the total amount of closed forest area within the sanctuary. The survey team selected 11 census areas from all parts of the sanctuary (Fig. 20.2). Eight of the census areas were placed in reasonably accessible parts of the core area, and three sites were placed in the more moist northern part of the buffer zone. Although the sites were not randomly selected, they were well scattered throughout the sanctuary and we do not believe that selection bias is a serious problem.

The auditory census method requires some knowledge of the duetting behavior of the species (Brockelman and Srikosamatara 1993). We assumed that the singing behavior of the eastern hoolock would not be much different from that of the western hoolock, summarized by Gittins and Tilson (1984). These authors reported that western hoolock gibbons in eastern India and Bangladesh gave duets in which males and females had recognizably different parts, that they duetted on most days (except during heavy rains) between about 0700 h and noon, and that they sometimes duetted more than once per day. The hoolock gibbon duet, however, has a complex structure in which male and female parts are not as distinguishable as in the duets of other species (Gittins and Tilson 1984; Haimoff 1984). Given these facts, we realized that although duets could probably be used to determine the number of breeding groups, the number of groups could not be assumed to equal the number of duet bouts heard, and we might have difficulty in distinguishing the groups singing around us. Indeed, we found that groups often duetted more than once per morning and usually moved within the territory between bouts.

At each census area four listening posts (LPs) were established 400–500 m apart, often along former logging tracks, on ridges or hill tops. One or two persons sat at each LP from about 0700 h until noon and on a field form noted the time, compass direction, and estimated distance of each duet bout. LPs were manned for 5 days, usually consecutive, to insure that all groups were heard. This proved to be ample time as the frequency of singing of hoolock groups was rather high.

Mapping and Density Determination

We plotted the group singing data on maps (1 inch = 500 m) showing the four listening areas at each census site by drawing arrows in the appropriate compass directions with the length equal to the estimated distance from each LP. One map was used to show all the groups heard on a single day; this resulted in five maps per census area. Groups heard from more than one

LP were plotted on each map by triangulation. Group bouts heard by only one LP could be plotted with less precision and were usually not used for density calculation (as they were usually more than 1 km away from any LP). When mapping was completed for all five days, the maps were laid out and compared. All group locations were then transferred onto a single map, with different symbols for different days. We then started the process of determining which calling locations shown on the map were from the same group and which were from different groups. This process was complicated by the fact that hoolock groups often have several duet bouts per day as they range through their territories, and by the sheer quantity of auditory data. The duet locations did not tend to cluster; they were spread out rather evenly throughout their ranges. Several rules of thumb were used to help determine the number of groups: (1) singing bouts that mapped more than 500 m apart were assumed to be by different groups; (2) singing bouts that were believed to be given by the same group, as suggested by timing and location, were identified and connected on the final map; and (3) singing bouts that were deemed to be from different groups on the day of listening, based on acoustical and timing cues, were also identified as such on the final map. This last information provided the critical evidence needed for determining the approximate location of territorial boundaries. Lines were drawn around mapped bout locations judged to be of the same group to indicate the approximate range of each group.

The final part of the mapping exercise involved determining the "listening area," which would allow us to determine the density of groups. "Listening area" is that region within which it may be assumed that all groups can be heard (Brockelman and Ali 1987). Listening area can sometimes be determined from topographic maps in hilly or mountainous terrain, by assuming that all gibbons can be heard within a valley where there are no hills to block the sound. Unfortunately, no suitable topographic maps of Mahamyaing were available to the team, so a different method had to be used. We arbitrarily assumed that all groups could be heard within a distance of 1 km from each listening post, and the total area within 1 km of any LP was taken as the listening area. Groups that were behind hills for one LP were assumed to be audible from other LPs. All groups that mapped within 1 km of an LP were used for density calculations. All groups that mapped on the boundary of the listening area were counted as a fraction equal to the proportion of bouts that mapped inside the listening area.

To provide a check on the reliability of these assumptions, we performed another density calculation using a listening area radius of 600 m, and all groups within 600 m of any LP were used in density determination. Both density estimates are presented; they do not differ greatly, although the estimate using the smaller radius usually gave a slightly higher estimate of density. The size of the listening area in km^2 was determined from ArcView GIS software, both for the area within 1 km from any LP and for the area within 0.6 km of any LP.

Assessment of Forest Condition

In the afternoons of census days, the survey team measured forest canopy cover and height in a 100 m × 100 m 1-ha plot (Brockelman 1998). Plots were placed in relatively level areas containing representative forest near the centers of the census areas. A total of 100 points regularly spaced 10 m apart in a grid were used to make vertical point-intercept readings of the highest canopy height. We used these readings to determine quantitatively (1) the frequency distribution of forest canopy height, and (2) the percent cover over the ground above each height. The latter was illustrated as a height vs. percent cover diagram. The diameter (dbh) of all trees larger than 10 cm dbh was measured for the whole hectare plot. We attempted to correlate gibbon density with habitat characteristics such as mean canopy height, percent canopy cover, number of trees over 40 cm in dbh per ha, and total basal area of trees $\geq$10 cm in dbh.

Results

Density of Groups

The 11 sites are listed in Table 20.1 along with mean altitude, percentage of closed canopy forest (determined from GIS analysis), date of census, 1-km radius area and density of groups, and 0.6-km radius area and density of groups. Gibbon group densities were based on the amount of closed canopy forest within each listening area. These densities (with standard errors of the mean) ranged from 0.84 to 3.26 groups km^{-2} (mean ± SE = 1.812 ± 0.263 groups km^{-2}) for the larger 1-km radius listening area, and from 0.71 to 5.15 groups km^{-2} (mean ± SE = 2.255 ± 0.410 groups) for the 0.6-km listening radius. Thus, the smaller 600-m listening radius yielded a mean density of groups 24% higher than the 1-km listening radius. This was because some of the groups beyond 600 m from the listeners were not heard well enough to record or because different groups nearer the listening posts could be distinguished more easily than groups farther away. Nearby groups can be located through triangulation more easily than distant groups. Groups behind hills sound more distant and many such groups 600–1000 m away may have been considered to be farther than 1 km away, and therefore not included in the listening area. For these reasons, the densities derived from the 0.6-km listening radius data are regarded as more reliable than those derived from the 1-km radius data.

We placed confidence limits on the mean density after applying a square root transformation on the raw data. The densities for both listening area sizes are somewhat skewed to the right, as is expected with population sampling data, and the square root transformation makes the distributions nearly symmetrical. The standard errors of the mean were calculated on the transformed data, and

Table 20.1 List of census sites with listening areas and gibbon group densities for listening radii of 1 km and 0.6 km from the listening posts. G = number of groups

Site	Date	Alt. asl (m)	Closed canopy (%)	Forest area <1 km radius	G < 1 km	Density (G/km^2) <1 km	Forest area <0.6 km radius	G <0.6 km	Density (G/ km^2) <0.6 km
1	16 June 04	474	95	6.14	20	3.26	2.66	13.66	5.14
2	25 June 04	352	83	5.41	14	2.59	2.42	8.75	3.61
3	15 July 04	297	99	5.70	16.42	2.88	2.64	8.47	3.20
4	6 July 04	359	100	5.78	14.68	2.54	2.74	8.60	3.14
5	23 Oct. 04	396	92	5.26	6.67	1.27	2.47	3.50	1.42
6	7 Nov. 04	357	97	5.51	5.83	1.06	2.57	2.51	0.98
7	31 Oct. 04	283	98	5.86	6.75	1.15	2.75	4.83	1.75
8	1 Dec. 04	258	94	5.39	6	1.11	2.59	3.00	1.16
9	25 Dec. 04	397	98	5.64	11.83	2.10	3.13	6.62	2.12
10	14 Dec. 04	394	93	5.40	6.17	1.14	2.59	1.83	0.71
11	2 Jan. 05	402	73	3.78	3.17	0.84	1.74	2.75	1.58
Mean				5.44		**1.812**	2.57		**2.255**

95% confidence limits (2 SE) were determined for the number of groups by untransforming the limits. This resulted in the lower limit being slightly closer to the mean than the upper limit; however, the transformation procedure is probably not essential because means always tend to be more normally distributed than the original variates.

Mean Group Size

To estimate gibbon population sizes from the number of groups, it is necessary to know mean social group size, as this is the unit that is estimated by auditory methods. Seven groups counted during the censuses had a mean size of 3.0 individuals (range 2–4), but most were seen while fleeing, which can sometimes lead to some individuals being missed. We lack any other published estimates for the eastern hoolock, but there is no reason to believe that it differs in this regard from the western hoolock. Das and Bhattacherjee (2002) state that the average western hoolock gibbon group size is three individuals. This number seems somewhat low, and is probably based heavily on surveys in highly disturbed and fragmented habitats in which reproduction is below normal. Estimates for both Indian and Bangladesh populations are given by Gittins and Tilson (1984). They report mean group size for 24 groups in Assam as 3.2, and for 7 groups in Bangladesh as 3.5. A mean of these estimates would be approximately 3.3 individuals (cf. Das et al. this volume), which will be assumed in the analysis that follows.

Gibbon Population Size

Total population sizes have been calculated for both the core area and the buffer zone, although confidence limits have been calculated only for the total area (Table 20.2). The population sizes are based on the area of closed canopy

Table 20.2 Final population estimates of gibbons in Mahamyaing Wildlife Sanctuary, including core area and buffer zone, based on a total area of 791 km^2 of closed deciduous and evergreen forest. Bottom line shows 95% confidence limits on the mean, based on square-root transformed densities of the 11 census sites. Total population estimates have been rounded off to the nearest 100 to avoid the impression of unwarranted precision

	Total area	Closed	1-km listening radius		0.6-km listening radius	
Area	(km^2)	forest (%)	Groups	Population	Groups	Population
Core	577	537 (93)	974	3200	1211	4000
Buffer	604	254 (42)	460	1500	572	1900
Total	1181	791 (67)	1433	4700	1783	5900
95% conf.			1051–1876	3500–6200	1210–2468	4000–8100

forest within each area as determined by the GIS, which is approximately 67% of the total area.

We estimated the total number of groups in the sanctuary, including the buffer zone, as 1,783. If group size averages 3.3 individuals, this yields a population size of about 5,900 individuals (rounded off to two significant figures). The minimum population estimate is 4,000 individuals, which represents the lower 2.5% 1-tailed confidence interval for mean density. Thus, Mahamyaing Wildlife Sanctuary contains roughly 4,000–8,000 gibbons, with the mean number predicted at approximately 6,000. The various assumptions made during the analysis (randomly selected census areas, accurate estimation of distances and separation of groups, normality, validity of the group size assumption, valid identification of gibbon habitat from satellite and GIS data) do not warrant a more precise statement.

The gibbon population in the northern core area of the sanctuary is estimated at 974 groups or about 3,200 individuals. This represents the most important component of the population because the forest in the core area is denser, moister, and less fragmented than the forest farther south in the buffer zone.

Forest Canopy in 1-ha Plots

Most of the plots had mean upper canopy heights of greater than 20 m, and five plots had mean canopy heights of 25 m or more (with some trees reaching 50 m), which is regarded as excellent forest in this region (Table 20.3). Two plots, however (nos. 3 and 9), had mean canopy heights below 15 m, and three others (nos. 5, 6, and 8) had heights below 20 m. These five forest patches were deemed not very suitable for gibbons. Sites 3 and 9 contained dense bamboo thickets. Plots 2, 5, 6, and 7 had relatively few large trees (defined as over 80 cm in dbh), and these plots were in suboptimal habitat.

In terms of forest canopy cover (Fig. 20.3), the plots cluster into two groups. Six areas have cover of close to 50% or more above a height of 25 m, and five areas have percent cover of less than 20% at this height. The 50% cover level is below 20 m for the latter group.

Relationship Between Density and Forest Condition

The gibbon densities for both 1 km and 0.6 km listening areas were plotted against several forest characteristics (graphs not shown), including mean canopy height, percent canopy cover at 20 m height, basal area of trees, and number of trees over 40 cm dbh. We predicted that density would be positively related to these forest characteristics, but in no case was the relationship significant.

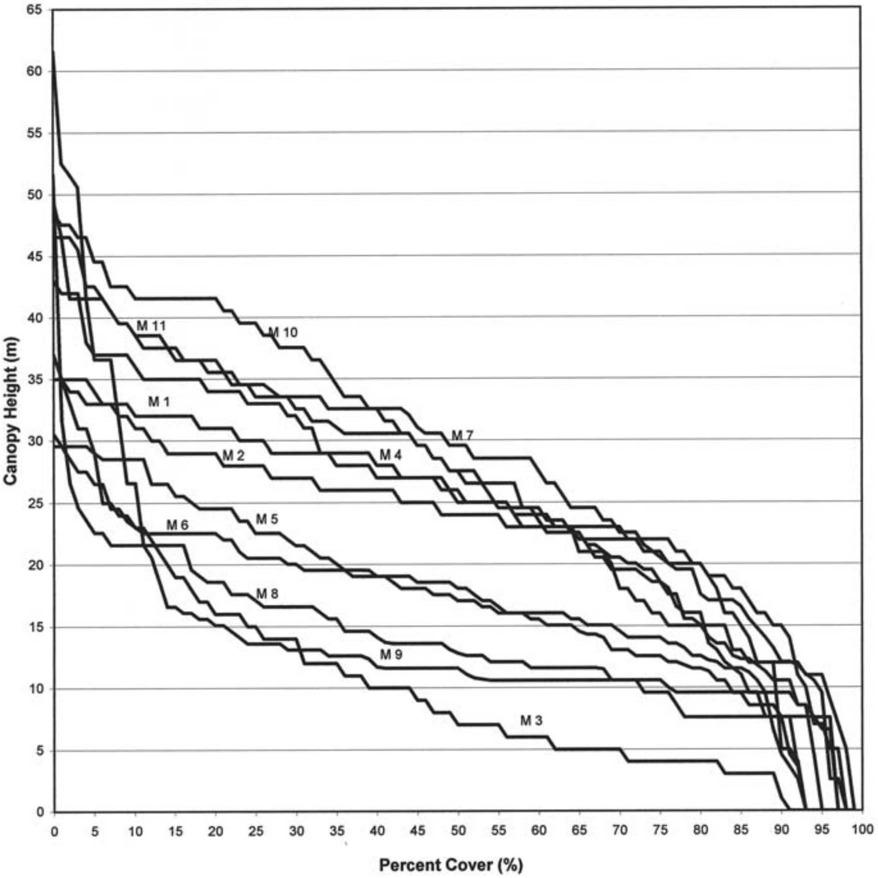

Fig. 20.3 Percent cover in relation to canopy height for the 11 1-ha plots

Table 20.3 Forest canopy characteristics and tree densities in 1-ha forest plots within listening areas (*h* = height in meters)

Site	Mean *h* (m)	% cover at *h* = 20 m	No. trees > 10 cm dbh	No. trees > 40 cm dbh	No. trees > 80 cm dbh	Tree basal area (m^2)
1	25	81	270	56	13	27.15
2	23	81	220	67	3	26.09
3	11	15	123	43	7	19.33
4	25	70	340	54	11	29.65
5	17	40	320	38	3	21.59
6	17	37	318	42	0	20.38
7	28	80	344	45	3	24.69
8	16	18	282	53	11	29.89
9	13	13	451	28	8	22.85
10	27	73	342	40	10	23.78
11	26	75	336	54	8	27.96

There are at least two reasons why the forest condition in the plots did not correlate with the density of gibbons. The first and most likely is that the 1-ha plots were sometimes placed in areas that were not representative of the whole listening areas. In some areas they were placed in a swampy areas or bamboo-choked valleys with poor forest structure. Gibbons often live on the steep slopes that usually have good canopy cover, but plots were preferentially placed in level areas for ease of measurement. Most of the terrain in the more northern, high-relief area was extremely steep. Of course, it is also possible that some of the plots selected had better forest canopy than most of the surrounding listening area, which was out of sight. Alternatively, areas with good forest but low gibbon density could also be areas with significant poaching.

Discussion

Mahamyaing Wildlife Sanctuary has about 800 km^2 of relatively closed canopy, moist mixed deciduous and evergreen forest that is suitable for gibbons. This forest contains an average of about 2.2 groups, or 8–9 individuals, per km^2. If we assume an average group size of 3.3 individuals, this gives a total figure of about 5,900 gibbons, of which about 4,000 are in the core area. The minimum population estimate for the whole sanctuary is about 4,000 gibbons in 1,200 groups. The core area is the most important refuge for gibbons because it has more moist forest than the southern areas in the buffer zone, and the forest is less fragmented and more continuous in the north. Moreover, the drier southern area is most likely to be affected by the warming associated with global climate change.

Although densities derived from the smaller 0.6 km listening radius averaged higher than those for a 1-km radius, use of the smaller listening area results in greater variability and larger confidence limits. For this reason, in areas of low density the larger listening area is recommended because otherwise some areas may not contain any gibbons.

The density of hoolock gibbons appears to be below carrying capacity in most listening areas, but it is close to the maximum in areas 1–4. For most gibbon species, a density of approximately 4 groups per km^2 appears to be the maximum a forest can support. This is true for gibbons in central Thailand, which is nearly the same latitude as Mahamyaing (e.g., Phoonjampa and Brockelman 2008).

The forest in the best habitat has a mean canopy height of over 25 m on average, with some trees reaching 50 m. Even the moist deciduous forest is excellent gibbon habitat as it is leafless for only a short period during January or February, and is virtually never completely leafless. Deciduous trees often carry flowers or fruits that gibbons can eat. However, the forest in this sanctuary is at the dry extreme of its distribution in the buffer zone. Forests to the south do not have any gibbons until the mountains of the Rakhine Yoma Range much farther south and the mountains to the west. The relatively low elevations of Mahamyaing will make it very susceptible to droughts and, if climate change brings rising temperatures, some of the drier mixed deciduous forest may become degraded and lose its gibbons. A study of the diet, foraging behavior, and reproductive rates of gibbons in different parts of Mahamyaing would be of great value in understanding their ecological limits and susceptibility to climate change. During the initial visit and survey of Area 1, groups encountered in the drier open forest were smaller than those seen in the more moist closed forest. The hypothesis that reproduction and group size in the more open deciduous forest are lower than those in the more optimal, moister forest should be further tested. O'Brien et al. (2003) found that habitat quality can affect infant and juvenile survival in gibbons (siamangs) as well.

Forest canopy characteristics as measured on the plot did not correlate with gibbon densities. This is probably mainly because the plots are not typical of the forest throughout the listening areas. Nevertheless, it is important to measure the forest characteristics in the census areas, and alternative (more dispersed) methods of sampling should be explored. In subsequent surveys, canopy measurements have been taken on long transects through the listening areas and forest characteristics measured on circular plots along these transects.

Listening areas nearest to the edge of the sanctuary or near populated areas tend to have on average lower gibbon densities; for example, areas 5, 6, 8, and perhaps 10 are located near the edge of sanctuary. Surprisingly, however, the two areas with the highest density are in the buffer zone, and near areas that have been selectively logged. Although the relatively recent selective logging (past 5 years) in the concession areas has not noticeably depressed gibbon densities, the logging damage is not uniform and areas with appreciable reduction of canopy cover restrict the movements of gibbons. There is also the danger that logging tracks will allow easier access by poachers.

Conclusions and Recommendations

Despite the promise of Mahamyaing WS as a gibbon conservation area, we believe that poaching by villagers may be the main reason that gibbon density appears to be below carrying capacity in some areas that have retained excellent forest cover, a situation very common for populations of the endangered pileated gibbon in Thailand and Cambodia (Phoonjampa and Brockelman 2008). It seems evident that the selective logging carried out in the concessions was not associated with significant gibbon poaching at Mahamyaing prior to the establishment of the sanctuary in 2004. More data need to be collected on the effects of forest disturbance, especially logging, on gibbons.

Village education projects have been carried out around Mahamyaing WS, and enforcement personnel are establishing a presence. Although local people rely heavily on game and other products from the forest for subsistence, they do not appear to have as many firearms as rural people in Thailand, Laos, and Cambodia. (However, this may not hold true for other areas of Myanmar where insurgent minority groups operate.) A crackdown on all use of game for subsistence is not possible, but villagers are being urged to respect the prohibition of capture of primates and large ungulates such as gaur and banteng. On the positive side, relations between villagers and conservation officials and other personnel are friendly, and village children have shown great enthusiasm about nature education and conservation programs.

Mahamyaing WS is an excellent site for ecological and behavioral research on hoolock gibbons. Much needs to be learned about their behavior and reproduction in relation to habitat type and quality. The population is at the edge of its ecological tolerance in the buffer zone area, and important information could be gained about its possible responses to a warming and drying climate. A research presence would also allow continued monitoring of local conservation problems and the population itself at its range limit in central Myanmar.

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Chapter 21
The Population Distribution and Abundance of Siamangs (*Symphalangus syndactylus*) and Agile Gibbons (*Hylobates agilis*) in West Central Sumatra, Indonesia

Achmad Yanuar

Introduction

Sumatran gibbons are presently experiencing serious population declines, due largely to habitat loss (from illegal and legal logging, traditional and modern crop plantations, land clearance for agriculture and new settlements/transmigration, forest fires, and droughts), as well as hunting for illegal trade as medicines and pets. In Sumatra, primary tropical rain forests, especially in the lowlands, have disappeared rapidly, with most of the land being converted for commercial timber concessions, crop plantations, or agricultural and human settlements (FAO 1981; Jepson et al. 2001).

Three gibbon species occur in the tropical rain forests of Sumatra: siamangs (*Symphalangus syndactylus*), white-handed gibbons (*Hylobates lar*), and agile gibbons (*H. agilis*: Groves 1972; Wilson and Wilson 1976; Rijksen 1978). The white-handed gibbon is sympatric with the siamang in northern Sumatra, while the agile gibbon occurs sympatrically with the siamang in central and south Sumatra (Wilson and Wilson 1976).

Gibbons usually live in small groups consisting of one adult pair and one to three dependent offspring, with small or medium-sized territories (Chivers 1973; Chivers 1974; Whitten 1980; Geissmann and Tranh 2001). These characteristics result in relatively low population densities. Gibbons also have long generation times, due to late sexual maturity (Geissmann and Tranh 2001) and relatively long interbirth intervals, resulting in low rates of reproduction in the wild.

To effectively conserve and manage gibbon populations and their habitats, the status of gibbon populations in critical and protected areas must be evaluated continuously (Struhsaker et al. 1975; Wilson and Wilson 1975). Unfortunately, there has been little effort to date to intensively survey or census many primate species, including gibbons, langurs, macaques, slow lorises, and western tarsiers,

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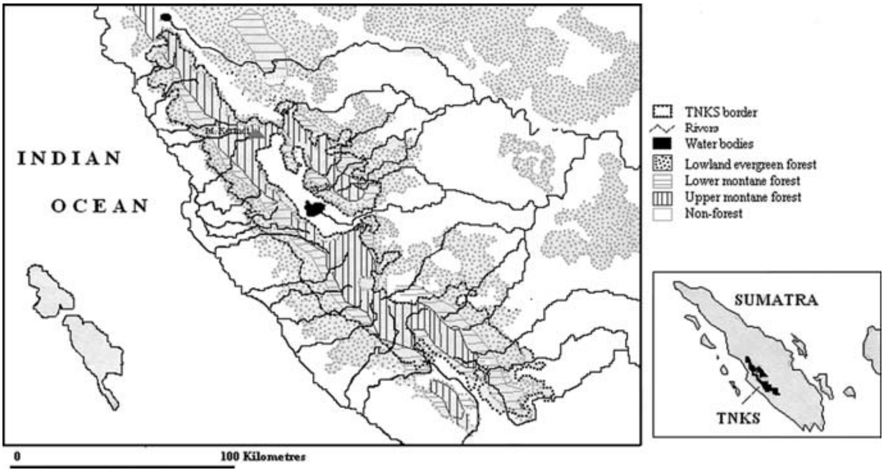

Fig. 21.1 Map of Kerinci-Sablat National Park, Sumatra, Indonesia, showing the habitat types surveyed

either within or outside of protected areas in Sumatra. The Kerinci-Seblat National Park/*Taman Nasional Kerinci-Seblat* (KSNP), in the extreme west-central region of Sumatra (Fig. 21.1), is one of the Indonesian “treasure houses” of faunal and floral diversity (MacKinnon and Suwelo 1984). It covers about 1.3 million hectares (Mha) and is the largest national park on the island of Sumatra, and among the largest protected areas in Southeast Asia (MacKinnon 1986). This park spans four administrative provinces: West Sumatra, Jambi, Bengkulu, and South Sumatra. Primary and secondary rain forests in the national park are occupied by two species of gibbons (agile gibbons and siamangs) and six other arboreal primate species, in addition to being an important habitat for many other endangered species.

I examined the population status and distribution of gibbons in KSNP by direct observations and line transect methods in four different habitat types (lowland, hill dipterocarp, submontane, and montane forests) that varied in altitude. The results of these surveys are presented and discussed in this chapter.

Study Sites and Methods

Study Sites

Survey routes were designed to cover a variety of habitat types within and outside of the 1.3 Mha National Park. A total of 25 sites were surveyed (Fig. 21.2, Table 21.1), most which have never been visited by other researchers. Only 20% of the total area of KSNP is lowland forest <600 m asl. Nonetheless, most survey sites were within KSNP and in lowland evergreen forests, because lowland forest is currently believed to be the habitat type most seriously threatened by a variety of human activities. Several sites close to

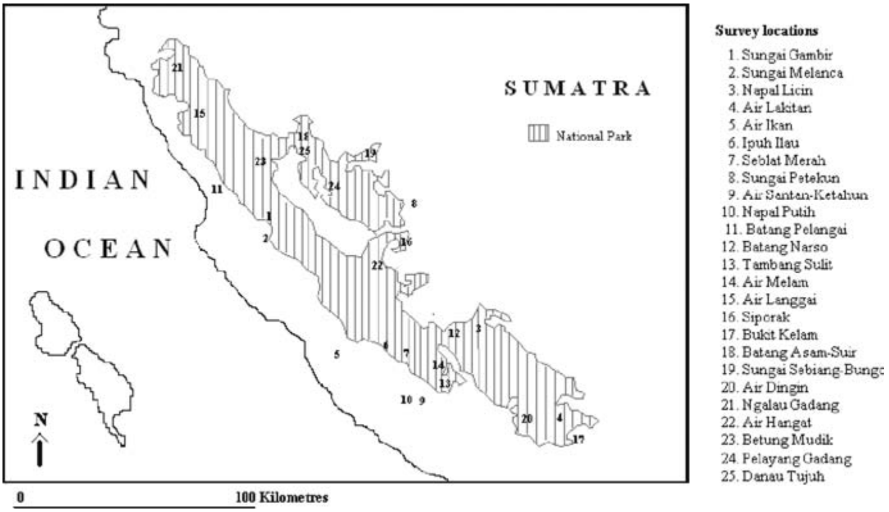

Fig. 21.2 Map of Kerinci-Sablat National Park showing survey sites

Table 21.1 Site, altitude, and habitat type for the 25 survey routes

Site/habitat type	Province	Altitude (m)	Forest	Forest status
Lowland		<450		
Sungai Gambir	West Sumatra	250 medium	Disturbed	National Park
Sungai Melanca	West Sumatra	250 medium	Primary	Conversion
Napal Licin	South Sumatra	300 steep	Primary	National Park
Air Lakitan	South Sumatra	350 steep	Primary	National Park
Air Ikan	Bengkulu	250 medium	Disturbed	Production
Ipuh Ilau	Bengkulu	350 medium	Primary	National Park
Seblat Merah	Bengkulu	350 flat	Primary	National Park
Sungai Petekun	Jambi	250 steep	Primary	Protection
Air SantanKetahun	Bengkulu	250 medium	Disturbed	Production
Napal Putih	Bengkulu	250 medium	Disturbed	Protection
Batang Pelangai	West Sumatra	250 medium	Disturbed	Protection
Hill		450–900		
B. Narso	Jambi	450 medium	Primary	Protection
Air Sulit	Bengkulu	450 steep	Primary	National Park
Air Melam	Bengkulu	450 steep	Primary	National Park
Air Langgai	West Sumatra	400 steep	Primary	National Park
Sungai Siporak	Jambi	450 medium	Primary	National Park
Bukit Kelam	South Sumatra	500 steep	Primary	National Park
B. Asam-Suir	West Sumatra	500 steep	Primary	National Park
Sungai Sebiang Bungo	Jambi	450 steep	Primary	National Park
Submontane		900–1400		
Air Dingin	Bengkulu	900 medium	Primary	National Park
Ngalau Gadang	West Sumatra	1100 steep	Primary	National Park
Air Hangat	Jambi	900 steep	Primary	National Park
Montane		1400–2400		
Betung Mudik	Jambi	1600 steep	Primary	National Park
Pelayang Gedang	Jambi	1500 steep	Primary	National Park
Danau Tujuh	Jambi	2100 steep	Primary	National Park

areas recently cleared for traditional and modern crop plantation as well as sites in selectively logged forests within or near to the KSNP were also chosen as survey priorities.

Methods

I employed the line transect method to estimate the density and population status of each gibbon species through direct visual observation. I conducted these censuses from 1996 to 1999, while also surveying other nonhuman primates and searching for new primate species.

I derived my methods for censusing gibbons from published methods (Southwick and Cadigan 1972; Wilson and Wilson 1975; Marsh and Wilson 1981; NRC 1981; Brockelman and Ali 1987; Barnett 1995), and adapted them to the field situation. Transects were constructed along established trails on hill ridges, slopes, and valleys in deep forest (85.9%) and old logged forest (8.4%) and along river banks (5.6%). Normally, existing human or animal trails/paths were used; new trails were made occasionally by trimming small trees. I usually avoided steeper terrains due to difficulty in detecting animals. After the transect system was cleared, trail lengths were measured by pacing or using a pedometer calibrated to the observer's stride. Trails were an average of 0.5–1.0 m wide in dense forest or 1.0–1.5 m wide in secondary forest, but trails were wider in recently logged forests as they followed old logging roads.

The average trail length surveyed on a given day was 2.57 km (range = 1.6–4.8 km). I walked slowly (average speed <1 km/h) with a local field assistant familiar with the terrain and wildlife. We frequently stopped for several seconds or minutes to listen for animal sounds, or, when we encountered primates, to determine the group size and group spread. We started the census walks in the morning between 0630 h and 0730 h and finished by the middle of the day. Gibbons were normally observed by eye (with binoculars), as well as being detected by auditory cues.

To estimate primate densities, it is first necessary to estimate the width of the strip surveyed (estimated strip width, or ESW) (Marsh and Wilson 1981). I estimated the maximum reliable detection distance (1/2 ESW) for density calculations for each species and habitat type using two methods: King's method, based on the "animal-to-observer," or direct distance, and Kelker's method, based on the "animal-to-nearest trail," or perpendicular distance. In either method, the maximum reliable distance is determined from the frequency-distribution curve of sightings, which generally shows an obvious plateau, followed by a marked drop in frequency (Marsh and Wilson 1981; NRC 1981; Garcia 1993; Brugiere and Fleury 2000). I estimated the maximum reliable detection distance as the last distance category before a drop of at least 50% in sighting frequency (NRC 1981). Maximum reliable perpendicular and direct distances were then used to estimate the ESW.

Results

Detection Distance and Estimated Strip Width (ESW)

Maximum Reliable Animal-to-Trail or Perpendicular Distance

S. syndactylus was detected up to 45 m from the trail in montane forests (mean = 17.8; SD = 10.4; *n* = 20) and hill dipterocarp forests (mean = 16.4; SD = 9.8; *n* = 18), and up to 40 m from the trail in submontane (mean = 17.1; SD = 9.9; *n* = 7), and lowland forests (mean = 15.4; SD = 10.7; *n* = 42). *H. agilis* was found in only three habitat types: submontane (range = 0–40 m; mean = 16.5; SD = 8.7; *n* = 9), hill dipterocarp (range = 0–50 m; mean = 18.3; SD = 12.9; *n* = 36), and lowland (range = 0–40 m; mean = 16.4; SD = 10.7; *n* = 17) forests.). Maximum reliable animal-to-trail distances for both species were estimated as the highest value in the distance class prior to the marked drop in frequency of detection (Fig. 21.3), and are presented in Table 21.2.

Maximum Reliable Animal-to-Observer or Direct Distance

S. syndactylus was detected (mean ± SD) 24.9 ± 12.3 m from the observer in lowland forest, 27.7; ± 13.6 m from the observer in montane forest, 23.3 ± 9.4 m from the observer in hill dipterocarp forests, and 25.7 ± 7.3 m from the observer in submontane forest. *H. agilis* were observed (mean ± SD) 27.9 ± 14.5 m from

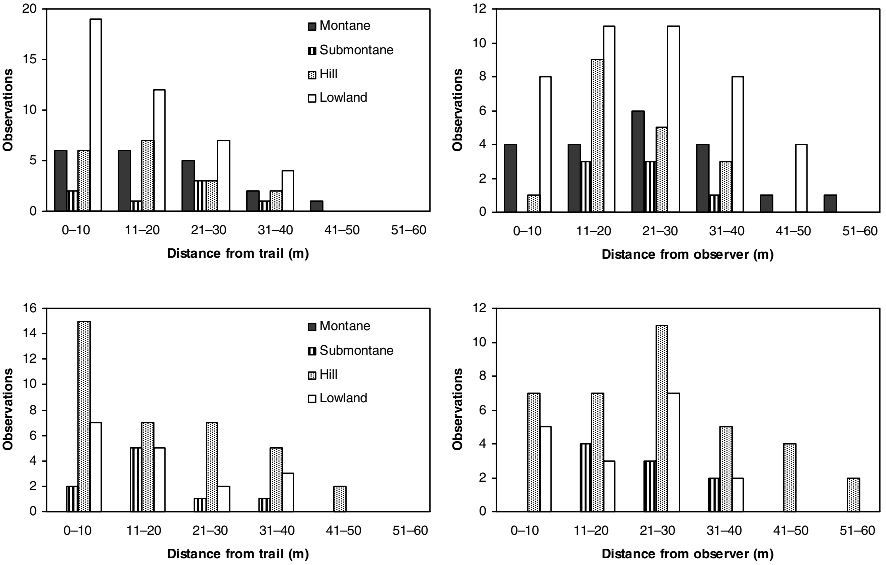

Fig. 21.3 Observed perpendicular and animal-to-observer distances for *Symphalangus syndactylus* (*top*) and *Hylobates agilis* (*bottom*)

Table 21.2 Estimated strip width (ESW) used for mean density calculations

	Species	
ESW (m)	Symphalangus syndactylus	Hylobates agilis
Perpendicular distance		
MF	60	–
SF	60	60
HDF	80	80
LF	60	80
Direct distance		
MF	80	
SF	60	80
HDF	80	100
LF	100	80

the observer in hill dipterocarp forest, 25.5 ± 8.8 m from the observer in submontane forest, and 30.9 ± 9.5 m from the observer in lowland forests Maximum reliable animal-to-observer distances for both species were estimated as the highest value in the distance class prior to the marked drop in frequency of detection (Fig. 21.3), and are presented in Table 21.2.

Siamang and Agile Gibbon Densities

Group density estimates for each species were calculated from data collected from a total of 311.2 km of line transects in four habitat types: lowland forest (eleven locations), hill dipterocarp forest (eight locations), submontane forest (three locations), and montane forest (three locations). Group densities calculated using perpendicular distances were higher than those produced using direct distances for *S. syndactylus* in lowland forest, and for H. agilis in all habitat types (Table 21.3). The estimated group densities (estimated by averaging the estimates produced using each method) for *S. syndactylus* were highest in montane forest (5.4 groups/km^2) and lowland forest (5.0 groups/km^2), while estimated group densities in hill dipterocarp and submontane forests were somewhat lower (2.1 groups/km^2 and 3.2 groups/km^2, respectively). *H. agilis* group densities were highest in hill dipterocarp (3.8 groups/km^2) and submontane (3.6 groups/km^2) forests, and lower in lowland forests (2.0 groups/km^2).

The Distribution of Gibbons in and around KSNP

I assessed the distribution of the two gibbon species during encounters with animals in censuses of about 120 routes, comprising 400 km of transects in 25 locations ranging in altitude from 200 to 2200 m asl in and around the Kerinci-Seblat forest complex. Only one gibbon species, *S. syndactylus*, was

Table 21.3 Group density estimates for siamangs (*Symphalangus syndactylus*) and agile gibbons (*Hylobates agilis* in and around Kerinci-Sablat National Park

	N	Km^2 surveyed	Density ± SE ($groups/km^2$)	
Habitat type	siamang, agile gibbon	siamang, agile gibbon	siamang	agile gibbon
Reliable primate-to-trail				
Montane	20, 0	3.7, –	5.4 ± 0.2	
Submontane	7, 9	2.2, 2.2	3.2 ± 2.9	4.1 ± 0.4
Hill dipterocarp	18, 36	8.4, 2.2	2.1 ± 0.5	4.3 ± 1.0
Lowland	45, 17	7.3, 7.3	5.7 ± 0.6	2.3 ± 1.3
Reliable primate-to-observer				
Montane	20, 0	3.7	5.4 ± 0.2	
Submontane	7, 9	2.2, 2.9	3.2 ± 2.9	3.1 ± 0.4
Hill dipterocarp	18, 36	8.4, 10.5	2.1 ± 0.5	3.9 ± 1.0
Lowland	45, 17	4.6, 9.8	4.3 ± 0.5	1.7 ± 0.9

observed in montane forests. Siamangs were observed at all altitudes in and around KSNP from near sea level (10–50 m asl) to 2300 m asl, and the frequency of sightings was similar in lowland forest and higher-altitude (hill dipterocarp, submontane, and montane) forests. The average altitudinal level at which *S. syndactylus* was recorded was 571 m asl (range = 200–2000, *N* = 87). Siamangs were not sighted in four (two submontane, one hill, and one lowland) of 25 surveyed sites, but their great calls were heard on occasion in these sites.

Groups of agile gibbons, *H. agilis*, were more frequently observed in hill dipterocarp forest than lowland forest and fewer were encountered in submontane forest. According to Wilson and Wilson (1976), the agile gibbon normally lives at higher altitudes and is rarely seen in the lowland forest in the west of Barisan Mountains, while in eastern Sumatra they are common in the lowlands. Agile gibbons were observed at an average altitude of 505 m asl (range = 250–1100 m asl, *N* = 62).

I recorded siamangs in the eastern and western areas of the KSNP area, but densities were higher in the west, whereas agile gibbons were more common in the east and rare in the west. I did not observe agile gibbons at all in the west coast forests. Agile gibbons were probably absent from the Seblat Merah, Ipuh Ilau, Air Ikan, Sungai Melanca, and Sungai Gambir survey areas.

Gibbon Group Sizes

I recorded group sizes whenever gibbons were sighted. In both montane and hill dipterocarp forests, *S. syndactylus* had an average group size of 3.4 individuals (montane forest: SE = 0.2; *n* = 20; hill dipterocarp: SE = 0.3; *n* = 18; Fig. 21.4a), with group sizes ranging from one to five in both habitats. The

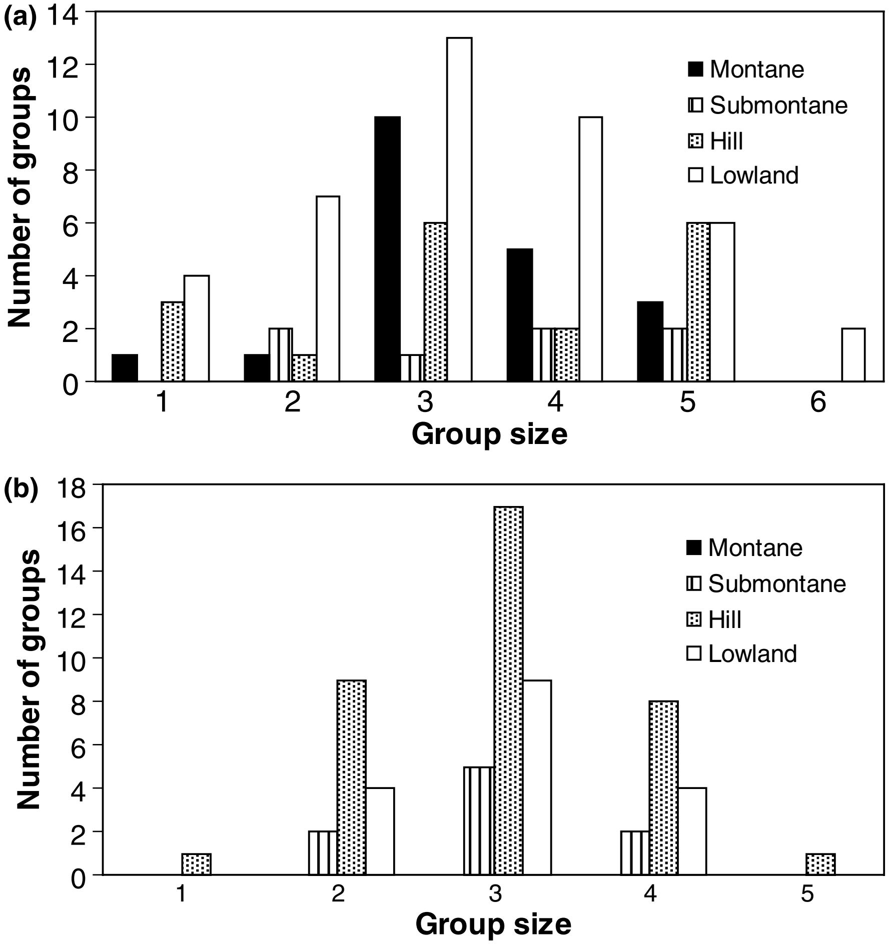

Fig. 21.4 Group sizes for siamangs (**a**) and agile gibbons (**b**) in montane forests, submontane forests, hill dipterocarp forests, and lowland forests

most common siamang social unit in these forest types consisted of one adult male, one adult female, and one immature (Fig. 21.4a). Similarly, the average group size in lowland forest was 3.5 individuals (SE = 0.5; *n* = 7), with group size ranging from one to six individuals, and a most common group composition of three to four individuals (typically one adult male, one adult female, and one or two immatures).

The average group size for *H. agilis* was 3.0 in the three habitats types in which they were found (submontane forest: SE = 0.2; *n* = 9; hill dipterocarp forest: SE = 0.1; *n* = 36; lowland forest: SE = 0.2; *n* = 17; Fig. 21.4b). A solitary individual was only observed once, in hill dipterocarp forest. The most common agile gibbon group compositions were adult pairs with one, two or three immatures (Fig. 21.4b).

Biomass of Gibbons

I calculated biomasses using published body mass information for siamangs and agile gibbons (Schultz 1973). The siamang biomass in and around KSNP was highest in the montane (151 kg/km^2) and lowland forests (135 kg/km^2), intermediate in submontane forest (93 kg/km^2), and lowest in hill dipterocarp forest (59 kg/km^2). Meanwhile, the biomass for agile gibbons was highest in hill dipterocarp forest (53 kg/km^2), followed by submontane forest (50 kg/km^2) and lowland forest (28 kg/km^2).

Discussion

The highest density of *S. syndactylus* observed in this study (5.4 group/km^2; 18.4 individuals/km^2) was in remote montane forests in KSNP. *S. syndactylus* is also found at high densities in highland forest in the Bukit Barisan Selatan National Park in southern Sumatra (O'Brien et al. 2004). However, siamang group densities in montane forests of KSNP are higher than those reported by Wood et al. (1996) for montane forest of Danau Tujuh, KSNP (1995–2000 m asl; Table 21.4) and by Marsh and Wilson (1981) for montane forests in peninsular Malaysia. Chivers and Davies (1979) reported that Sumatran siamangs (*S. syndactylus syndactylus*) are generally more abundant in higher elevation forests than their counterparts in peninsular Malaysia (*S. syndactylus. continentis*), and accordingly, in peninsular Malaysia, the mean density of siamang was higher in hill dipterocarp forest than montane forest.

Changes in primate distribution with altitude are probably correlated with changes in vegetation, e.g., tree composition, density, size, and species diversity, as well as abiotic factors, such as climate and annual rainfall (Chivers and Davies 1979). In montane forests of KSNP, only ~2% of trees sampled (N = 1033 trees from 36 families) belonged to the family Dipterocarpaceae, while higher proportions of dipterocarps were found in lower altitude forests (Yanuar 2001). Gibbons often use dipterocarps for sleep, rest, and travel, but dipterocarps provide very little food (Chivers 1972; Tenaza 1975). Caldecott (1980) reported a significant negative correlation between biomass of both primates and dipterocarps and altitude in peninsular Malaysia. The results from my study contrast with Caldecott's work, since I found higher densities of siamangs at high altitudes in KSNP, despite the rarity of dipterocarps at high elevation, and lower densities of siamangs in hill and submontane forests (Table 21.4), where trees from the family Dipterocarpaceae were most abundant.

The high density of siamangs in montane forest may result from both their ability to adapt well ecologically to montane forests on Sumatra and the lack of competition with agile gibbons in this habitat. Unfortunately, detailed information on the ecology and biology of siamangs in montane forest is not currently available. The lower densities of siamangs in hill and submontane forests may

Table 21.4 Group size and density estimates for siamangs and agile gibbons from other sites (MF = montane forest, H = hill forest, S = swamp forest, LF = lowland forest)

	Siamang		Agile gibbon			
Site	Mean group size	Density (groups/km^2)	Mean group size	Density (groups/km^2)	Habitat	References
Peninsular Malaysia						
Ulu Gombak	3.0	0.9	–	–	H	Chivers (1974)
Ulu Sempan	4.0	1.5	–	–	H	Chivers (1974)
Kuala Lompat	3.0	1.0	–	–	L	Chivers (1974)
Sungai Kenyam	No data	0.7	–	–	L	Marsh and Wilson (1981)
Rompin	No data	1.8	–	–	S	Marsh and Wilson (1981)
Telapa Burok	No data	1.2	–	–	MF	Marsh and Wilson (1981)
Sungai Dal	–	–	4.4	4.3	LF	Gittins and Raemaekers (1980)
Borneo						
Gunung Palung	–	–	4.0	No data	LF	Mitani (1990)
Sumatra						
Ranum	3.3	No data	–	–	LF	MacKinnon (1977)
Ketambe	3.0	0.8	–	–	LF	West (1981)
Bukit Barisan Selatan	3.9	3.3	2.6		LF	O'Brien et al. (2004)
	3.8	1.2	2.7	1.1	H	O'Brien et al. (2004)
Way Kambas	No data	0.7	No data	0.9	LF	Yanuar and Sugardjito (1993)
Gunung Tujuh	No data	2.7	–	–	MF	Wood et al. (1996)

be related to the relatively high agile gibbon density in these habitat types. Nevertheless, siamang group densities in these habitat types remain high relative to densities in most other areas surveyed (Table 21.4). A high siamang density (5.0 groups/km^2) was also observed in lowland forest, where agile gibbons were less common (Wilson and Wilson 1976, this study). The mean siamang density in the lowland forest of KSNP, like those of other forest types, is high compared with those reported from other lowland forest sites (Table 21.4). Clearly, the KSNP forest complex has a relatively high abundance of siamangs across various habitat types.

The highest mean densities of agile gibbons at KSNP were found in hill dipterocarp and submontane forests, with lower densities in lowland forest (Table 21.3). The overall pattern of altitudinal distribution of siamangs and agile gibbons is therefore similar to that reported by O'Brien et al. (2004) from Bukit Barisan Selatan National Park. The mean group density of agile gibbons in KSNP was higher than the densities reported for agile gibbons in primary forest throughout Sumatra (Wilson and Wilson 1976), and from Way Kambas National Park, South Sumatra (Yanuar and Sugardjito 1993). However, Mitani (1990) reported a higher mean population density of Bornean agile or white-bearded gibbons (*H. albibarbis*) in Gunung Palung National Park, West Kalimantan.

Main Conclusions

The agile gibbon and siamang share their range in the Barisan Mountains south of Lake Toba, Sumatra. The results of this study suggest that the two species reach their peaks of abundance in different forest types (agile gibbon in hill dipterocarp and submontane forests; siamang in montane and lowland forests). These differences probably relate to ecological differences across habitat types, such as differences in food availability and diversity, and forest structure. Siamang group sizes ranged from 3.4 to 3.6 in all habitat types, whereas mean agile gibbon group sizes were 3.0 in all habitat types in which agile gibbons were recorded.

There was typically an inverse relationship between agile gibbon densities and siamang densities. In habitat types where agile gibbons were relatively abundant (e.g., hill dipterocarp forest), densities of siamang were low, and in habitats when siamangs were abundant (e.g., lowland forest, montane forest), agile gibbon densities were low. Agile gibbons were also less common in the west wing of Kerinci-Seblat National Park, where siamangs were found at the highest densities.

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Chapter 22

Canopy Bridges: An Effective Conservation Tactic for Supporting Gibbon Populations in Forest Fragments

Jayanta Das, Jihosuo Biswas, Parimal C. Bhattacherjee, and S.S. Rao

Introduction

In recent years, most forests in the range of the hoolock gibbon (*Hoolock hoolock*) have become fragmented due to forest conversion and selective logging (Das et al. this volume). Therefore, protection of populations in habitat fragments is critical for the conservation of hoolock gibbons. In the Borajan Reserve in the Bherjan-Borajan-Podumoni Wildlife Sanctuary in Tinsukia district, Assam, India, changes in land use patterns and removal of feeding and sleeping trees have reduced the quantity and quality of gibbon habitat. Following dramatic loss of habitat in Borajan from 1995 to 1997, a number of hoolock gibbon groups have been observed visiting private lands to exploit isolated food resources surrounded by areas of human use. This suggests that villages with fruit trees and bamboo groves near the fragmented forests have become foraging sites for the gibbons remaining in forest fragments.

Hoolocks specialize on patchily distributed fruits, and hoolocks living in intact forests are strictly arboreal, never coming to the ground. However, in Borajan, where damage to the forest canopy is extensive, gibbons have been observed descending to the ground to cross gaps between food patches (Das 2002). While traveling on the ground, they spend a substantial period of time in vigilance against potential predators like dogs, pythons, and humans. There are also reports of falls resulting in infant deaths during gap crossing (K. Kakati pers. comm.). These observations suggest that disruptions to the forest canopy may impose substantial costs on gibbons.

We designed and built canopy bridges in the Borajan reserve to establish direct arboreal connections between food patches to allow gibbons to forage in

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isolated food patches with less risk of predation during terrestrial locomotion and reduced risk of falls. These bridges are expected to help gibbons conserve energy, to reduce stress, and to permit exploitation of unexplored food patches in the fragmented and disturbed forests. Following construction of the canopy bridges, selected hoolock groups were monitored to assess patterns of usage of canopy bridges, and to evaluate the utility of different bridge types.

Methods

Study Area

Borajan consists of 4.93 km^2 of fragmented forest located at 27°24′5″ N, 95°18′39″ E. Borajan is a part of the Bherjan-Borajan-Podumoni Wildlife Sanctuary (7.02 km^2) under the Wildlife Division, Tinsukia, Assam. Aside from the western hoolock gibbon (*Hoolock hoolock hoolock*), Borajan is also inhabited by the Bengal slow loris (*Nycticebus bengalensis*), the Assamese macaque (*Macaca assamensis assamensis*), the northern pig-tailed macaque (*M. leonina*), the rhesus macaque (*M. mulatta*), and the capped langur (*Trachypithecus pileatus pileatus*). The hoolock gibbon, capped langur, and slow loris are "Schedule I" species and the remaining primate species are "Schedule II" species under the Indian Wildlife Protection Act of 1972 (amended in 2002). The hoolock gibbon is also listed as Endangered by the IUCN (2008).

Between 1995 and 1999, 55% of the tree canopy cover in Borajan was lost. In 1995, 67% of the Forest was covered with >21% canopy, but by 1999 the area covered by >21% canopy had declined to only 30% (Fig. 22.1). The area with no tree cover also increased from 3.8% in 1995 to 8.6% in 1999 (Fig. 22.1), creating large gaps in the canopy. Between 1995 and 1997, up to 50% of the total primate population in the area was lost (Srivastava et al. 2001). On October 13, 1999, the government of Assam declared this area a Wildlife

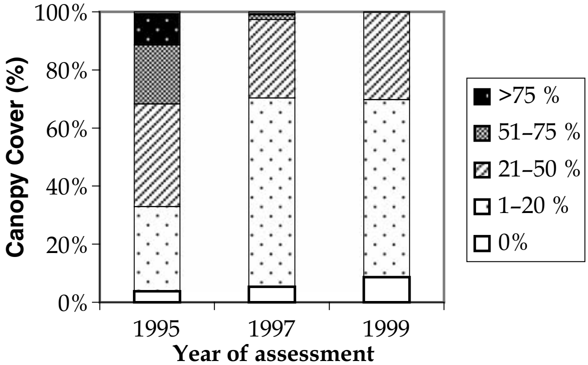

Fig. 22.1 Changes in percentage of canopy cover in Borajan from 1995 to 1999

Table 22.1 Population of Hoolock gibbons in Borajan from 1995 to 2005 (Das et al. 2005)

Year	Total groups	Breeding groups†	Total individuals
1995	11	9	34
1996	8	6	20
1997	7	5	17
1998	5	3	11
1999	5	3	11
2000	5	2	10
2001	5	2	10
2002	4	3	10
2003	4	3	9
2004	4	3	8
2005	4	3	9

†Breeding groups are defined as groups containing at least one adult male and at least one adult female.

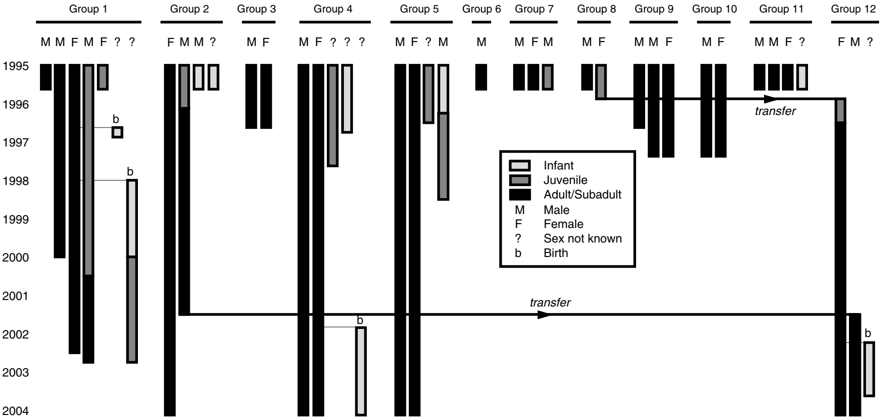

Fig. 22.2 Hoolock gibbon group compositions at Borajan from 1995 to 2004

Sanctuary specifically to conserve the endangered primates (Choudhury 2001). Hunting has not been reported in the area.

The hoolock gibbon was the primate species most affected by deforestation, with the loss of 67% of the total population between 1995 and 1999. Since 1999, the downward population trend has continued, bringing the total loss since 1995 to 74% of individuals (Table 22.1), and six of nine breeding groups (Fig. 22.2). Given the fast population decline in Borajan, this area was selected for long-term monitoring to understand the impact of habitat loss and fragmentation on hoolock gibbons, and to test methods for supporting threatened populations.

Hoolock Activity Budgets and Diets at Borajan

During a field study from October 1998 to December 2000, dramatic differences were observed in the activity patterns of gibbons in disturbed habitat (Borajan Reserve) and undisturbed habitat (Namdapha National Park) (Das 2002). The mean activity period was longer in disturbed habitat (590 min, $N = 2$ groups) than undisturbed habitat (558 min, $N = 2$ groups), and the percentage of time spent feeding was lower in disturbed habitat (42.8%, $N = 2$ groups) than in undisturbed habitat (54.3%, $N = 2$ groups). Groups spent a greater percentage of time resting in disturbed (46.2%, $N = 2$ groups) than undisturbed (33.6%, N=2 groups) forests (Das 2002). This suggests that gibbons at Borajan may use an energy-minimizing strategy to cope with reduced food availability in disturbed habitat.

In addition to spending less time feeding and more time resting, hoolocks in disturbed habitat also displayed a dietary shift relative to hoolocks in undisturbed habitat. Hoolocks at Borajan spent only 9% of their feeding time consuming fruits and 28% of their time consuming mature leaves, compared with about 62% fruit and 15% mature leaves at Namdapha. Mature leaves contain high fiber and a correspondingly lower proportion of easily digestible nutrients (Hladik et al. 1971; Hladik 1977). Moreover, mature leaves typically contain secondary chemical compounds, which can be toxic if ingested in sufficient quantities (Janzen 1975; Hladik 1978; Janzen 1978). Therefore, mature leaves are considered lower-quality gibbon food than fruits or new leaves. Time spent feeding on new leaves did not differ substantially between Borajan (12%, $N = 2$ groups) and Namdapha (14%, $N = 2$ groups). The dramatic difference in diet between the two sites suggests that hoolocks at Borajan may be forced to subsist on lower-quality foods because of low fruit availability.

Hoolock Ranging Behavior at Borajan Prior to the Construction of Canopy Bridges

As part of a long-term monitoring program, we collected behavioral data from two hoolock groups (Group 4 and Group 12) using focal animal sampling (Altmann 1974) during dawn-to-dusk follows from October 1998 to November 2001 and from March 2003 to April 2004. Both of the groups consisted of an adult male, an adult female, and an infant (Fig. 22.2).

On a number of occasions, gibbons crossed horizontal gaps in the forest canopy more than 8 m wide by bipedal walking on the ground. While crossing these gaps, they spent a substantial amount of time in vigilance. Depending on the number of people moving through the forest, the time spent in gap crossing varied from 10 min to more than 1 h. Between March and May 2003, the 1-year-old infants from both groups fell to the ground from a height of ~20 m on a total of 10 occasions while crossing gaps, without any apparent casualties.

However, in April 2004 the infant in group 12 died from injuries sustained as a result of a fall. In 1998, another infant in Borajan died under similar circumstances.

The home ranges and main food trees of two groups of hoolocks were known from the long-term monitoring program. In 2002–2003, group 12 visited the Borajan Forest Village twice per month on average. They typically stayed in the forest village for 3–4 days, apparently depending on food availability. The food trees in the village are scattered but some are connected with bamboo groves. In the village, gibbons were observed spending substantial periods of time in vigilance behavior prior to and while crossing gaps on the ground, and traveling between bamboo groves by swaying bamboo plants to bridge gaps. The gibbons did not use potential feeding trees located more than 30 m from the forest unless there were intervening bushes in which the gibbons could hide or travel. It is difficult to construct and maintain bridges longer than 25 m at low cost. Therefore, in the current experiment, nine gaps of lengths between 7 and 25 m were identified in the village and were connected with bamboo bridges. Following bridge placement, the study groups were monitored to assess patterns of usage of the bamboo bridges.

Table 22.2 Features of the canopy bridges

Bridge #	Height (m)	Length (m)	Connecting trees	
I	5	8.2	Bamboo grove	*Melia azadirachta*
II	5	8.5	*Melia azadirachta*	Bamboo grove
III	5	11.25	Bamboo grove	*Areca catechu*
IV	5	11.5	*Artocarpus heterophyllus*	Bamboo grove
V	5	12	Bamboo grove	Bamboo grove
VI	5	12	Bamboo grove	*Citrus grandis*
VII	5	21	*Citrus grandis*	*Ficus benjamina*
VIII	5	7	Bamboo grove	Bamboo grove
IX	5	7	Bamboo grove	Bamboo grove

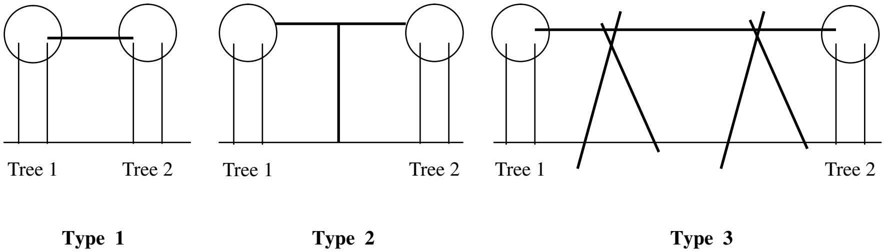

Fig. 22.3 Structure of canopy bridges

Placement of Canopy Bridges

Nine bridges made of bamboo poles were constructed and placed in the forest village habitat used by group 12 on April 28, 2003. The lengths, heights, and locations of the bridges are shown in Table 22.2. Three types of bridges were used (Fig. 22.3), to determine how bridge construction affected the patterns of usage. Bridges were used to connect food trees or food patches of species that comprise an important part of hoolock diets in the premonsoon and monsoon season (e.g., *Ficus benjamina*, *Artocarpus chama*) and to maintain a canopy linkage within the forest village.

Results

Use of Canopy Bridges

We first observed the gibbons crossing the bridges on May 13, 2003 (Table 22.2). Subsequently, they crossed bridges on 31 occasions between May 13 and June 30, 2003 (Table 22.3). The gibbons used the bridges each time they used this section of their home range. On every occasion, the adult female led the group across the bridge. Group 12 used bridges VI and VII eight times each, VIII and IX five times each, I and II twice each, and IV only once. Bridges III and V were not used during the study period (Table 22.3).

Two other sympatric nonhuman primates (capped langurs and Assamese macaques) also may have benefited from these bridges (Table 22.4). One troop

Table 22.3 Use of canopy bridges by gibbons between April 28th and June 30th, 2003

Date	Time	Group leader	Bridges used	Comments
May 13, 2003	10:00–10:05	AF[†]	IX, VIII, VII, VI	Entered village to feed
May 13, 2003	12:30–12:35	AF[†]	VI, VII, VIII, IX	Returned to the forest
May 28, 2003	7:00–7:10	AF[†]	IX, VIII, VII, VI	Entered village to feed
May 28, 2003	10:00–10:15	AF[†]	VI, VII, VIII, IX	Returned to the forest
June 18, 2003	14:30–14:50	AF[†]	IX, VIII, VII, VI	Entered village to feed; slept in a tree adjacent to the village[‡]
June 19, 2003	5:25–13:30	AF[†]	VI, VII, II, I	Crossed gaps to feed
June 19, 2003	13:30–14:15	AF[†]	I, II, VII, VI	Moved to sleeping tree adjacent to the village[‡]
June 20, 2003	5:25–9:45	AF[†]	VI, VII, IV	Returned to the forest

[†] AF = adult female (with clinging infant).

[‡] The same sleeping tree was used on June 18th and June 19th

Table 22.4 Use of the bridges by diurnal primates in Borajan Reserve during the study period

Species	Mode of locomotion†	Usual substrate‡	Bridge crossing incidents	Apparent purpose of bridge use
Hoolock hoolock	BR, BI	A	31	gap crossing, foraging, movement to sleeping tree
Trachypithecus pileatus	L, C, Q	A	1	gap crossing, foraging
Macaca assamensis	L, C, Q	A, T	2	gap crossing, foraging
M. mulatta	L, C, Q	A, T	0	n/a
M. leonine	L, C, Q	A	0	n/a

†BR = brachiation, BI = bipedalism, L = leaping, C = climbing, Q = quadrupedal running or walking

‡A = arboreal, T = terrestrial

of seven capped langurs and five individuals from a group of 20 Assamese macaques were observed crossing bridge VI and the same group of Assamese macaques also crossed bridge IV.

Gibbons employed different types of locomotion to cross different bridge types. On type 1 and type 3 bridges, gibbons were able to brachiate as there was no physical obstacle to suspensory locomotion (Fig. 22.2). However, on type 2 bridges, they walked bipedally to cross the bridge, because the pole in the middle obstructed brachiation. For connection of wide gaps, type 3 bridges appear to be most suitable because they are strong and durable, which reduces the chance of accidents due to falls.

Discussion

The population of hoolocks at Borajan was monitored as a part of a long-term study to understand the impact of habitat fragmentation and loss on primates. This population lost 25 individuals, including 6 breeding groups, from 1995 to 2005. Hunting pressure is negligible or nonexistent at Borajan and hoolock gibbons are not thought to be able to cross the surrounding tea gardens to move to the adjacent forest patches. Therefore, the disappearances likely reflect mortality resulting from forest disturbance.

Habitat fragmentation (and the resulting disruption of canopy highways) may increase gibbon mortality directly (e.g., through increased predation while crossing gaps or deaths from falls) or indirectly (through disease or starvation due to reduction in the food supply). The canopy-dependant locomotion of hoolocks restricts them to small patches of forest in Borajan and prevents them from optimally exploiting the available food resources within the forest. Differences observed in the activity patterns and diets of hoolock gibbons in undisturbed and disturbed habitat reflect the profound effects of habitat disturbance on hoolocks. As Borajan is heavily grazed by cattle and gibbons at Borajan spend a significant amount of time near the ground or on ground, they may also be at increased risk of contracting parasites.

Das and Bhattacharjee (2002) and Das et al. (2005) recommended that a number of immediate measures be taken to improve gibbon habitat quality in the Borajan area and to protect the remaining population of hoolock gibbons. Recommended measures included planting trees of important feeding and sleeping tree species (especially *Ficus* spp.), propagation of important parasitic food plants (e.g., *Hoya* spp., *Raphidophora* spp., *Ficus* spp.), and taking measures (e.g., weeding) to promote the growth of naturally growing saplings in the forest. However, newly planted saplings will take at least 5–10 years to grow to a sufficient size to provide corridors between important food patches. The rapid rate of population decline of hoolock gibbons in Borajan suggests that unless immediate measures are taken to improve habitat quality, local extinction may occur in less than 10 years. To maximize the survival and reproduction of the remaining hoolock gibbons in Borajan, it is crucial that the habitat be manipulated to allow the gibbons to exploit available but unused resources. As gibbons will not cross large gaps, this can only be done by establishing aerial connections (canopy bridges) between fragmented food patches.

During the long-term study gibbons were observed traveling efficiently through bamboo patches, which suggests that bamboo is an appropriate material for canopy bridges. Hence, single bamboo poles were used to connect the gaps with a substrate familiar for local gibbons. As the gibbons brachiate efficiently on bamboo, these bridges permit gap crossing using natural patterns of locomotion. The quick adoption and regular use of the canopy bridges by hoolocks at Borajan suggests that bamboo bridges may be an appropriate conservation tool for establishing connectivity in fragmented gibbon habitats.

Canopy bridges are an inexpensive, minimally disruptive way of manipulating the habitat to provide gibbons and other primates with access to a larger area of habitat and additional food sources while minimizing the need for the animals to behave in stress-inducing or dangerous ways (e.g., descending to the ground to cross gaps). Canopy bridges can also be integrated into ecotourism programs by strategic placement of bridges in areas accessible to tourists. Resulting revenue can then be directed into further conservation efforts. In the long run, we plan to camouflage the bridges at Borajan with vines and lianas, including *Ficus* spp., to promote a natural look and to provide additional sources of food for gibbons using the bridges.

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Chapter 23
The Role of Reintroduction in Gibbon Conservation: Opportunities and Challenges

Susan M. Cheyne

Introduction

Gibbon populations have been declining dramatically for the past 30–40 years, primarily due to habitat destruction and fragmentation through timber felling, charcoal burning, encroachment cultivation, and general bush burning for hunting (Bodmer et al. 1991) or conversion to rubber plantations (Haimoff et al. 1987), tea and pine plantations (Nijman and van Balen 1998), and recently oil palm plantations (Curran et al. 2004). Other factors contributing to their decline include the illegal wildlife trade, the use of body parts in the manufacture of traditional medicines, and hunting for food. The majority of gibbons found in rescue and rehabilitation centers come from the illegal pet trade, though many are also rescued from plantations as forests are cut down.

Gibbons in the illegal pet trade are almost always born in the wild, and infant gibbons can fetch from US $10–100 on the black market (ProFauna Indonesia, pers. comm.). This represents a great deal of money for the average family from gibbon range countries, even when the cost of a bullet and gun are considered. Therefore, trade in highly endangered gibbons continues, despite legislation against hunting throughout the gibbons' range. Without exception, the young are captured by killing the mother (usually by shooting her) and taking the infant after the mother has fallen or when the infant comes to the ground to investigate what has happened. The subsequent conditions of captivity and transport in tiny, inadequate cages cause at least half of the infants to die in transport (Rijksen and Rijksen-Graatsma 1979; Bennett 1992; Eudey 1992; Cheyne 2004). Therefore, every infant gibbon that actually reaches the market signifies a much greater loss to the population. Not only are infants lost during capture and transport, but we must also consider as lost the future infants that

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would otherwise have been born to a mother killed as a result of the pet trade. Conditions at market add to continued mortality: an infant removed from its mother experiences detrimental and sometimes fatal stress, which coupled with inadequate care results in even more deaths. Should infants live through their early years, premature death can still occur. Gibbons can become aggressive at sexual maturity, so those that have become pets are often killed before reaching adulthood as they are perceived as threats by their human owners.

The continuing pet trade decimates the natural population. Should gibbons be "lucky" enough to survive after capture and sale, they are often kept in unsuitable and unnatural conditions. In captivity gibbons are not given the types of food that they are adapted to finding in their natural habitat. They have no opportunity to find a mate, thereby contributing nothing to their species' propagation. For species that reproduce slowly, once every 2–3 years (Carpenter 1940; Chivers 1972), conditions and losses described above are a devastating blow to wild populations.

Despite the monitoring, confiscations, and education efforts of NGO's and local authorities, the illegal wildlife trade continues to deplete wild populations, increasing the number of animals living in captivity. One of the most endangered gibbon species is the Javan or silvery gibbon *Hylobates moloch* (Asquith 1995; Asquith et al. 1995). The most recent studies suggest that although a few populations number in the low thousands (Nijman 2004), most populations contain less then 100 individuals (Gates 1998; Nijman 2006). It is likely that the only way to conserve the silvery gibbon is to manage the remaining populations as a metapopulation. Gates (1998) suggests that, if the *H. moloch* housed in Indonesia and around the world in contained settings be placed in a captive-breeding program, then 85% of the species genetic diversity will be conserved. These individuals could potentially then be translocated to forests, boosting the genetic material in the wild. If such a step is to succeed, efficient rehabilitation and reintroduction guidelines and protocols must be set up to ensure that the captive-raised gibbons survive long enough to add their genes to the wild population. The crested gibbons of Indochina are also extremely endangered (Garza and Woodruff 1994) and may require metapopulation management in order to survive.

Even healthy gibbon populations are at risk. Indonesian Borneo is home to one of the largest remaining populations of gibbons; the Sebangau National Park in Central Kalimantan is estimated to hold 30,000 agile gibbons (*H. albibarbis*) (Cheyne et al. 2007). Despite these encouraging figures, the threats to gibbons in Indonesia have not abated and, indeed, may have increased. Illegal capture of infants continues, the forest is still subjected to legal and illegal logging and large tracts of forest are being converted to oil palm plantations.

Gibbons are found in several countries in South and Southeast Asia, where all populations of gibbons are vulnerable to the same threats, though not all threats apply equally to all populations. Many populations are still viable, yet face threats and are highly endangered. As habitat conversion and the illegal pet trade continue, there will be gibbons in need of rescue. As long as there is the possibility that rescued gibbons can be relocated/reintroduced to areas where they may have become locally extinct and where they can be protected, meta-population-level management should be viewed as a positive conservation plan. Unfortunately, recent history is replete with failed or mismanaged primate reintroduction attempts (MacKinnon 1977; Soave 1982; Karesh 1995). Such attempts have been unsuccessful through a combination of a lack of adequate planning, failure to assess the habitat quality in the release area, insufficient knowledge about the primates' behavior and ecology, and the lack of adequate post-release monitoring of the primates.

In this chapter, I present a history of rehabilitation and reintroduction, drawing on information from a variety of primate and nonprimate species, along with current data on gibbon reintroduction. The main reasons for past failures of reintroduction projects will also be addressed. I will conclude by highlighting possible solutions to these problems, proposing behavioral criteria for assessing the suitability of a gibbon pair for reintroduction, and discussing future directions for the conservation of both captive-raised and wild gibbons.

Rehabilitation and Reintroduction

The American National Wildlife Rehabilitation Association (NWRA) defines wildlife rehabilitation as "the treatment and temporary care of injured, diseased and displaced indigenous wildlife, and the subsequent return of healthy viable animals to appropriate habitats in the wild" (Atkinson 1997). Hannah (1989) defines rehabilitation as "training inadequate individuals in skills which allow them to survive with greater independence." The principal objectives of a reintroduction project are to establish a viable, free-ranging population in the wild of a taxon which has become globally or locally extinct in the wild (Kleiman, Stanley Price and Beck 1994).

There are two types of reintroduction: (a) *re-establishment:* the use of captive-bred animals to re-establish an extinct population and (b) *stocking reintroduction:* which involves supplementing a declining population with captive-bred animals (Viggers et al. 1993). I propose a third definition: *population reintroduction***,** which should refer to the use of wild-born, captive-raised animals to re-establish a population where it has become locally extinct. Population reintroduction can be a useful tool for gibbon conservation, but must only be conducted in areas that are adequately protected.

Global Outlook on Rehabilitation

The protection of wild populations is the first and foremost priority of conservationists, but proper management of gibbons in care facilities is important as well. Only about 50% of reintroduction projects have released threatened or endangered species or subspecies (Beck et al. 1994). These figures suggest that the potential for rehabilitation and reintroduction has yet to be realized, despite some encouraging success stories. The immediate conservation of the four genera of gibbons becomes increasingly urgent as suitable habitats and numbers of gibbons continues to diminish. Whether previous rehabilitation efforts have helped, hurt, or failed to affect the plight of gibbons (and other primates) is still an open and hotly debated topic. Despite this uncertainty, the potential importance of reintroduction and rehabilitation programs in terms of community and global education, increased awareness, and as a refuge for abandoned animals with nowhere else to go (Chivers 1991) cannot be overlooked. If the animals are not brought to rehabilitation centers, they face uncertain futures in unsuitable conditions.

Determining the Success of Reintroduction

The most obvious criterion for determining the success of a reintroduction is a resulting self-sustaining population of animals (Griffith et al. 1989). Another view suggests that if reintroduction results in a broader and more effective conservation of the habitat, then the program is a success, even if all the reintroduced animals die soon after release (Kleiman 1989). Success should be measured independently for each species, taking into account that species' behavior and life history. For gibbons, success should be measured by (1) survival post-release (i.e., finding suitable food), (2) maintenance of the pair-bond (i.e., duetting and copulating), and (3) reproduction and survival of the offspring. Another question to consider is how many deaths of released animals are acceptable in order to establish a sustainable population. Reintroduction programs can be applied to any endangered species, but the ease with which an animal can be rehabilitated and prepared for release will ultimately depend on how much the animal is required to learn in the rehabilitation center. For captive-raised monkeys and apes (who do not spend an extended period learning from their parents as would wild-raised primates), the rehabilitation time, and hence the cost of the rehabilitation process, will be considerably higher than for other species that do not have such a long learning curve. There has been very little definitive research regarding the ability of a species to adapt to new habitats (Kleiman 1996). Monitoring of reintroduced primates must be long-term and must involve comparisons with wild individuals from the same species in order to determine the success of the reintroduction (Cheyne 2004).

Primate Case Studies

If success is defined as production of a self-sustaining, reproducing population that can survive without human intervention, then the most successful primate rehabilitation project has involved a monkey, the golden lion tamarin, *Leontopithecus rosalia* (Kleiman et al. 1991). The purpose of the Golden Lion Tamarin Project was to increase the size of the wild population by returning tamarins to areas where they had become locally extinct, and the project has achieved a level of success as yet unrealized in any ape. Only pairs or intact family groups of golden lion tamarins are released. All animals are given extensive pre-release training, initially in traditional zoo cages. Subsequently, animals are given free-ranging training in wooded habitat on zoo grounds before being released into the wild. Once the animals are released, field researchers track them daily to observe their behavior and provide food, as needed. As the tamarins adapt to the forest and begin to eat natural foods, the research visits are gradually reduced to monthly observations and provisioning stops. Radio collars are fitted on several members of each family group to aid in location. After 17 years, the reintroduced population numbered 359 animals in 50 groups, including surviving founders and their offspring. Intensive post-release monitoring has contributed to the success of this project (Kierulff et al. 2002).

In an effort to conserve the highly endangered and endemic Zanzibar red colobus, (*Procolobus kirkii*), a population was translocated from an area of high human presence to a reserve. After about 20 years no net increase in the number of colobus was detected. This lack of success has been attributed to an imbalance in the age and sex composition of the translocated group and a lack of post-release monitoring (Struhsaker and Siex 1998).

Meijaard and Nijman (2000) note similar problems with attempts to translocate the proboscis monkey (*Nasalis larvatus*) in Indonesia. Here the failure has been attributed to the lack of adequate pre-translocation assessment of the release area (including failure to verify the presence of suitable natural vegetation to support proboscis monkeys), as well as the lack of post-translocation monitoring for the monkeys (Meijaard and Nijman 2000). Very few attempts have been made to assess the potential of release habitats or the reintroduced species response to their new surroundings (Fa 1994).

Recent and ongoing attempts at reintroduction of primates are still making similar mistakes. Gupta (2002) describes the release of two groups of golden langurs (*Trachypithecus geei*) in two different areas in India. A lack of proper planning and the complete absence of reintroduction and monitoring protocols following release resulted in failure of at least one of the releases. Gupta (2002) stated that after release, no monitoring was conducted and no animals were radio-collared. An entire group disappeared and the cause is not clear.

In Thailand, there are several gibbon sanctuaries. The Highland Farm in the mountains near Chiang Mai in northwest Thailand, near the border with Burma (a problematic location for a rehabilitation center due to political instability) offered a sanctuary for captive-raised gibbons. Many of the gibbons at the Highland Farm have suffered appalling injuries and are unsuitable candidates for release. In 2002, several people (including the owner) were killed at the Highland Farm, demonstrating that the area is no longer safe for a rescue center. Phuket Gibbon Rehabilitation Project (PGRP), run by the Wild Animal Rescue Foundation of Thailand, has reintroduced rehabilitant gibbons.

Though this project has been in operation since 1992, making it the longest of all gibbon rehabilitation and reintroduction projects, it is continually plagued by problems and has never permitted the scientific community to monitor the released gibbons. The PGRP has been criticized for exceeding its carrying capacity, thereby creating welfare problems for the gibbons housed there (Schoene and Brend 2002). Other problematic issues included: daily exposure of rehabilitant gibbons to large numbers of humans (though physical contact was not permitted); failure to consistently release gibbons in pairs, causing the formation of amalgamated groups at the release site (pers. obs.); and the inability of the release site (an island) to support all the gibbons, necessitating long-term provisioning. As the released gibbons are not living free from human assistance and are not in contiguous forest, those gibbons are not contributing to the wild population. The only report issued from this rehabilitation project states that all the releases have failed, with the adults separating permanently, probably due to the poor-quality (nonsexual) relationships between the released adults (DeVeer and van den Bos 2000). Many of the gibbons (along with other taxa) released from this project were chosen for release based on subjective impressions and not objective criteria. Another problem is that while a gibbon pair may have duetted and copulated in captivity, this is no indication that the association will continue once they are released. The pairs may split, one individual may disappear, or one individual may fall ill or not adapt well and have to be brought back to the center. The ultimate cause of failure must be attributed to a lack of information about the species, the release area, and the individual's response to the release area. Until the issue of proper protocols and management techniques is addressed, reintroduced gibbons will likely continue to be unsuccessful, contributing nothing to the overall survival potential of the species. The available evidence is clear: poorly planned and ill-managed releases and reintroductions of primates lead to failure of the primates to adapt to the wild, failure of the population to increase, and negligible conservation impact.

Partial reintroduction success for gibbons has only recently been achieved. The Kalaweit Gibbon and Siamang Reintroduction Project has released three pairs of gibbons in Central Kalimantan and one pair of siamangs in Sumatra (Table 23.1). Kalaweit is the only fully operational project set up for the rehabilitation of gibbons that employs medical testing techniques described by Rijksen (1974). It was founded in 1999 and does not encourage visits by tourists. Following an intensive 2-year study of pre- and post-release behavior and adaptation to the rehabilitation process (Cheyne 2004), rigorous release criteria have now been established and are in use at the Kalaweit Gibbon and Siamang Rehabilitation Program (Cheyne and Brulé 2004). If successful rehabilitation and reintroduction is to be measured by (1) survival post-release (i.e., finding suitable food), (2) maintenance of the pair-bond (i.e., duetting and copulating), and (3) reproduction and survival of the offspring (Cheyne 2004), then the Kalaweit gibbons have succeeded in two of three criteria. Only long-term monitoring will determine if they successfully raise offspring.

Table 23.1 Results from Kalaweit releases 2003–2007

Year released	Location(release area)	Species	Released animals	Provisioned?	Outcome at time of press
2003	Central Kalimantan (island)	*H. albibarbis*	Adult ♀♂ pair	No	Both alive and together, no offspring
2006	West Sumatra (island)	*Symphalangus syndactylus*	Adult ♀♂ pair	Yes	Both alive and together, no offspring
2007	Central Kalimantan (1500 ha protected area)	*H. albibarbis*	1. Adult ♂♀ pair and infant	No	All alive
			2. Adult ♂♀ pair and infant	No	All alive

Why Is Rehabilitation of Gibbons so Difficult?

There is a variety of problems facing gibbon rehabilitation: some of the gibbons will have spent their lives in tiny cages, drugged and chained, while others will have been relatively well treated and may experience difficulty adapting to life without their human owners (Cheyne 2006). Wild gibbons usually live in family groups containing an adult male and female and 1–3 offspring. These groups defend an area against other groups and territorial conflicts are not uncommon. Duets by adult males and females help defend the territory and reinforce the bond between the adults. Tame gibbons form less stable pair-bonds than untamed individuals, and their behavior towards conspecifics is unpredictable (Eudey 1992), making integration into mating pairs difficult. An understanding of the types of stereotyped behavior and the resulting central nervous system dysfunctions associated with stereotypy that captive gibbons can exhibit is essential in order to improve husbandry techniques that remove the causes. Research must differentiate between gibbons that are orphaned when young and those that have been kept for a time as pets, as their rehabilitation and care needs may vary. The failure to account for the different life histories of captive-raised gibbons has been an oversight in the past (pers. obs.).

Nonhuman primates have extensive parental care with long periods of infant and juvenile dependency (Yeager 1993). During this time the youngsters learn many critical social, behavioral, and sexual responses, e.g., the ability to call and communicate with others, how to manipulate and handle food, and how to avoid predators. Grouping juvenile gibbons is useful for socialization and to identify compatible individuals, but groups of juveniles should not be released, only bonded pairs, matching the social grouping of wild gibbons. Gibbons do not mate with just any member of the opposite sex; a bond must be formed. There are many examples of captive pairings of gibbons that did not result in pair-bonding or mating (pers. obs.). If a bond has already been established in the rehabilitation center, then a large social hurdle has already been overcome. Another option is to place an older (>4 years) individual with an adult same-sex companion in the hope that the adult will adopt the juvenile and teach the juvenile. Having an adult gibbon teaching a youngster is preferable to having a human teach the gibbon the necessary survival skills, but there is a potential drawback to the pairing of adults and juveniles. If the adult and juvenile are not compatible, the juvenile may develop a fear of conspecifics leading to problems when forming a pair-bond later. This substitute parent idea was effective in a single case involving two *H. lar* males (Cheyne, unpubl. data), but it remains unclear whether this strategy would work for most gibbons.

While efforts are being made to rehabilitate gibbons, the increase in the numbers of gibbons being brought to rehabilitation centers and the lack of suitable release sites has resulted in a shift in emphasis from rehabilitation to a search for humane housing for the newcomers. As a result there has been less focus on rehabilitation. Until this issue is addressed, the centers will continue to fill up with animals that face an indeterminate period in a cage. Some "pet" gibbons may have spent much of their life being free to roam (albeit in a human environment), and may not adapt well to being caged.

Long-term monitoring of the animals to determine their reactions to the new environment and to account for any deaths/disappearances is essential to determine the success of the reintroduction program, and to make necessary adjustments in protocol. If the released animals do not live long enough to breed, then their conservation value is zero (Cayford and Percival 1992).

Wild vs Rehabilitant Gibbons: The Resource Allocation Dilemma

Critics of rehabilitation and reintroduction (e.g., Bennett 1992) would argue that these centers detract from efforts to protect and conserve the remaining wild populations. But, rescue, rehabilitation, and reintroduction of captive-raised gibbons need not be at the expense of the conservation and protection of wild populations. Education and cooperation with local people, government, and authorities is essential if any conservation program is going to succeed, and rehabilitation projects are in a position to contribute significantly to this effort. Rehabilitation projects generally have substantial contact with local people (perhaps more so than researchers working at specific sites in remote areas), due to travel to rescue animals and community education and outreach programs to highlight the need to return animals to the wild (Agoramoorthy 1997, 1998; Siregar et al. 1998; Supriatna and Manullang 1999; Commitante 2005). A particular example of the potential conservation impact of rehabilitation programs is Kalaweit FM, the radio station started by the Kalaweit Gibbon and Siamang Rehabilitation Project. This radio station is aimed at young audience and broadcasts popular music, current affairs programs, and comedy shows. Five times per hour, conservation messages are broadcast on a variety of topics including bat hunting, forest fires, and the keeping of gibbons and other wild animals as pets. Establishing sites for research on wild gibbons and developing release sites for the reintroduction of rehabilitant gibbons both contribute to the amount of land that has protected status, thus increasing the area of forest where gibbons can be found. Agreements between local people and the rehabilitation center can ensure that land is set aside for the reintroduction of gibbons (A. Brulé, pers. comm.). These agreements involve protection of the land in exchange for social benefits provided by the project for the local community such as money for schools, jobs for local people, and provision of medical care when needed. Rehabilitation centers can also support law enforcement by providing a receiving point for animals confiscated by Forestry officials or police.

Research stations establish a presence in an area and highlight the importance of the area for conservation, and rehabilitation projects have the contact with local communities to disseminate the conservation message. Ultimately, both wild research and rehabilitation projects are working for the same goal: the protection of the habitat and the animals. There are currently three main areas of concern for gibbon conservation (Pruett-Jones et al. 2000): (1) a lack of effective communication about the plight of gibbons, both within range countries and internationally; (2) a lack of wildlife law enforcement in range countries and lack of awareness of the laws already in place; and (3) failure to prioritize unprotected populations for surveys and protection. Fragments of forest containing gibbon populations must be identified and surveyed and country-wide Population and Habitat Viability Analyses conducted to highlight the gaps in knowledge and pinpoint areas in need of protection.

With adequate cooperation between researchers working with wild populations and reintroduction centers, resources can be managed to achieve two goals: (1) management and protection of wild populations and (2) rehabilitation, reintroduction, and management of the wild-born, captive-raised population.

Avoiding the Problems of the Past

For rehabilitation to succeed, equal care and planning should go into both the pre-release and post-release phases. Past experience has allowed researchers to identify several factors that affect the success of the release of previously captive animals, including negative impacts on the native flora and fauna, mortality due to animals being unused to natural predators in the release site, poaching for food or the pet trade, inter- and intraspecific competition, lack of familiarity with food and water resources at the release site, and poor habitat quality at the release site.

Pre-release planning requires a detailed understanding of the animals' biology and behavior in the wild and of welfare and husbandry techniques for care of these animals in captivity (Cheyne 2005; Cheyne, Chivers and Sugardjito 2005). Different species have very different social needs and behaviors. Rehabilitation centers set up for one species should *never* attempt to rehabilitate or reintroduce another species unless sufficient expertise is available (Cheyne 2005).

Behavioral Assessment Prior to Release

A survey of 145 reintroduction projects (Beck 1995) found that only 11% showed a measurable success, while another study found a success rate of 25% (22 of 87 projects: Fischer and Lindenmayer 2000). As these failures involve substantial financial and opportunity costs as well as unnecessary suffering and deaths, there is a pressing need to improve the success rate. Post-release behavioral problems have been cited as the main reasons that reintroduction of captive animals has failed (Konstant and Mittermeier 1982; Lindburg 1992; Beck et al. 1994; Ware 2000; Junge 2001; Gadsby 2002; Gupta 2002; Hu and Jiang 2002; Kierulff et al. 2002; Strum 2002; Cheyne 2004). Reintroduced black-and-white ruffed lemurs (*Varecia variegata variegata*) failed to avoid predators, find food, and negotiate the complex arboreal environment (Britt et al. 1999). African wild dog reintroduction failed in part because the animals were unable to avoid predators and could not capture their own prey (Mills 1999; Frantzen et al. 2001). Kleiman et al. (1991) noted that golden lion tamarins that had little prerelease training had a lower survival rating than those individuals that had extensive prerelease training. These are just three examples of a problem that is rife throughout reintroduction programs: the release of animals that do not fulfill a set of behavioral criteria.

Reintroduction protocols must have adequate medical testing in place before releases should even be discussed. Inadequate medical testing of rescued animals is unacceptable as it raises the possibility of human or animal diseases being transmitted to other animals. Primates can carry and become infected by several human diseases including Hepatitis A, B and C, *Herpes simplex,* and tuberculosis (Smith et al. 1969; Viggers et al. 1993; Mootnick et al. 1998; Warren et al. 1998; Kilbourn et al. 2003). Little information is available about human–primate zoonosis and how these diseases can then be passed between primates. Rescue/rehabilitation centers must carry out full medical testing and keep up-to-date on the latest scientific information regarding disease transmission; to do otherwise is highly irresponsible.

These examples highlight the importance of developing natural behaviors in captive animals prior to release. Captivity affects many behaviors because the conditions are often very different from the wild environment (Darwin 1868; Price 1970; Frankham et al. 1986; Lickliter and Ness 1990; Stunz and Minello 2001). This difference is exacerbated in animals that have been kept as pets, as conditions differ from natural environments more for pets than for animals housed in zoos involved in reintroduction projects. Unless individuals with behavior similar to that of wild animals are preferentially released, many animals will die needlessly (McPhee and Silverman 2004).

Based on the behaviors essential for survival in wild animals, which can be used to gauge suitability for release, I propose a checklist of behaviors that rehabilitant gibbons must show before release (Cheyne 2004). A pair of opposite sex gibbons must have been established and must meet the following prerequisites:

1. The gibbons should be able to move around the enclosure well, and most of this movement should be by brachiation. Enclosures must have adequate supports inside to encourage appropriate locomotion, i.e., flexible supports that are not fixed and that encourage the gibbons to learn balance.
2. No more than 5% of time should be spent on the ground for any purpose. Gibbons should be at the top of the cage for at least 40% of the time and should not be sleeping on the floor at all. Gibbons do not make nests and require a suitable tree cavity or platform on which to sleep.
3. The pair should spend at least 7% of total activity time in positive pair association (grooming, copulating, and playing). At least 3% of total activity time should be spent allogrooming.
4. At least 6% of total activity time should be spent duetting.
5. They should be copulating successfully, and each member of the pair should be able to successfully initiate copulation with the other.
6. Activity budgets should approximate those of wild conspecifics in all major categories, i.e., feeding (type or food, e.g., nonfig fruit, figs, young leaves, flowers, and invertebrates), resting, and traveling (Table 23.2).

Selecting a Suitable Site for Release

Before releasing gibbons into a natural habitat, the project must specify the following: whether the release will occur within the gibbons' original demographic range; whether there is a pre-existing population at the release site; the history of the reintroductees, i.e., whether they are captive born and if they have any previous experience in the wild (Kleiman 1996); if the area has suitable habitat to support the gibbons (Cheyne et al. 2006), and if the area is suitably well protected.

Reintroduced gibbons should not be released into existing communities or into places where there are conspecific populations (IUCN/SSC 2002). Kierulff

Table 23.2 Activity budgets of wild, rehabilitant, and reintroduced gibbons. All values are given as percentages of total observation time

Species[a]	*S. s.*	*H. k.*	*H. m.*	*H. ag.*	*H. p.*	*N. c.*	*Ho. h.*	*H. al.*	*H. al.*	*H. al. & H. m.*
Reference[b]	CH	WH	KA	GI	SR	SH	AH	CY	CY	CY
Groups[c]	3 (W)	1 (W)	1 (W)	1 (W)	4 (W)	4 (W)	15 (W)	20 (W)	2(RI)	2 (RC)
Feed	31–56	34	32	29	22	29	52	32	37	18
Rest	35–52	54	40	29	39	18	28	26	37	49
Travel	8–20	11	23	10	24	37	8	16	24	20
Social	2	–	–	–	7	4	4	18	–	8
Sing	1–3	2	5	5	8	11	3	8	2	7

[a] *S.s.* = *Symphalangus syndactylus; H.k.* = *Hylobates klossii; H. ag.* = *Hylobates agilis; H. al.* = *Hylobates albibarbis; H. m.* = *Hylobates muelleri; H. p.* = *Hylobates pileatus; N. c.* = *Nomascus concolor jingdongensis; Ho. h.* = *Hoolock hoolock*.

[b] CH = Chivers, Raemaekers and Aldrich-Blake (1975); WH = Whitten (1980); KA = Kappeler (1981); GI = Gittins (1982); SR = Srikosamatara (1984); SH = Sheeran et al. (1998); AH = Ahsan (2000); CY = Cheyne (2004).

[c] W = wild; RI = reintroduced; RC = in a rehabilitation center.

(2000) determined that golden lion tamarins released back into their historical range (an area where the animals were historically found but where they are no longer present due to past hunting pressures) have a greater chance of establishing a self-sustaining population.

Due to the pressures of logging and cultivation, it is becoming increasingly difficult to find suitable forest that can be used for reintroduction [i.e., otherwise healthy forest with no wild gibbons (Kleiman et al. 1991)]. If hunting or deforestation was the primary cause of a local extinction, then evidence must be presented to show that the problem has been eliminated or drastically reduced prior to the establishment of a reintroduction program. Every effort must be made to find a release habitat that resembles the natural habitat as closely as possible. The site should be evaluated for the availability of suitable food types, water, and sleeping sites (Abbott 2000). Also, it is essential that there are enough emergent trees from which gibbons can call (allowing the call to carry), and trees high enough to afford the gibbons protection from predators while they are sleeping (Whitten 1980). Vié and Richard-Hansen (1997) and Nettelbeck et al. (1999) suggested additional criteria for a release site, stating that it must provide the trophic requirements of the animals and should be close to the project, so as to limit transportation time and stress to the animals. Contact between gibbons and human observers should be avoided, as it is critical that the gibbons develop a distrust of humans; otherwise, they are potential targets for hunters. Sufficient distance from humans (in terms of settlements, plantations, roads, and livestock) is important to avoid the gibbons raiding crops and being shot as pests. Accordingly, finding appropriate release sites is difficult, and requires intensive surveying of potential locations.

The IUCN/SSC Reintroduction Specialist Group state in its *Guidelines for Non-human Primate Reintroductions* (2002): “reintroductions should only take place when the taxon’s habitat requirements are satisfied and likely to be sustainable for the foreseeable future. If the taxon’s basic habitat and ecological requirements cannot be determined, the animals should not be released.” The only way to meet these requirements is to conduct a habitat analysis of the release site, both pre- and post-release (Cheyne et al. 2006). An accurate analysis of the release area is essential if the released animals are going to survive into the future and become nutritionally independent as soon as possible post-release. Due to the lack of accurate and reliable data on the behavior of released gibbons, it is essential that all stages of the rehabilitation and release process be monitored and documented.

Post-Release Monitoring

Rehabilitation and reintroduction programs have a huge responsibility toward the animals they are returning to the wild. We must ensure that the animals concerned not only are ready for release but also can adequately cope after release. Currently, there are no precedents for gibbon rehabilitation and reintroduction, and even if there were, each pair should be treated as a separate case in need of post-release monitoring (Cheyne and Brulé 2004). Though we may be able to predict how a pair will react, we cannot simply release animals and hope for the best.

The main causes of death in released gibbons have been starvation, hunting, disease, and aggressive territorial disputes (Bennett 1992). These problems can be avoided through adequate medical screening before the release, release of the gibbons into a habitat that can provide sufficient food (provisioning of food for the gibbons after release should be considered only in exceptional circumstances: provisioned gibbons are not fully reintroduced gibbons), and long-term post-release monitoring. There is a greater than 90% chance that the released gibbons will die from the above causes if the project is inadequately planned and supervised (Bennett 1992). Post-release monitoring is vital to ensure that the gibbons are adapting, to counter any problems that arise, and to collect data on the pre- and post-release process. The IUCN/SSC Re-introduction Specialist Group (2002) lists post-release monitoring as one of the essential steps in any rehabilitation process.

Hannah (1986) observed that chimpanzees' (*Pan troglodytes*) chances of survival were greatly increased if they were radio-collared before release. Animals that had not been seen at the feeding site for several days could be tracked and, if necessary, brought back to the center. When none of the chimpanzees were collared, only 50% survived; whereas when 30% of individuals were collared, 60% survived; and when all released individuals were collared, 95% survived (Hannah 1986). The most obvious problem with radio tracking is the risk that the collars will affect the gibbons' behavior or movement within the canopy (e.g., through the collar becoming entangled in vegetation) and social interactions within the pair/group through increased aggression or a reduction in the pair-bond. Radio collars have been used on a number of primate species successfully, e.g., chimpanzees (Hannah 1986), red-tailed guenons (Jones and Bush 1988), black spider monkeys (Karesh et al. 1998), savanna baboons (Sapolsky and Share 1998), and golden lion tamarins (Kierulff 2000). Despite the risk, Creel et al. (1997) believe that the benefits of studying radio-collared animals outweigh the potential risks. In a recent study by Agoramoorthy and Hsu (1999), 24 released chimpanzees were fitted with radio collars around their necks and this did not measurably affect their behavior, nor did the chimpanzees try to remove the collars. Despite the evidence suggesting the value of radio collars, they have not been used on reintroduced gibbons. I suggest that radio collars should not be used on reintroduced gibbons until their effect on gibbon behavior and movement has been more fully studied under a controlled, captive situation.

Since the released gibbons will be semihabituated, it is hoped that after a short time, their home ranges and daily travel routes will be known, making following and observation easier than if the gibbons were fully wild. Without adequate post-release monitoring, rehabilitation projects have no way of determining if the rehabilitation process is adequately preparing the gibbons for a life in the wild. Post-release monitoring programs must collect data on the gibbons' behavior, ranging, ecology, socialization, breeding, and interactions with other animals in the release area (e.g., other primates, other mammals, and birds). The importance of daily post-release monitoring, involving observations of the gibbons for the full active period, cannot be overemphasized. Thus the case for radio collars is very strong, assuming that adequate tests are carried out prior to the use of collars on wild gibbons. Some basic points to remember for the release of gibbons are:

1. After transport to the release site, the gibbons should be allowed at least 24 h to recover from the journey, while housed in a suitably sized cage.
2. Gibbons must be released together.
3. Logistics must be in place to allow for post-release monitoring.

Discussion

Rehabilitation and reintroduction projects must incorporate collaboration between several disciplines including nutritionists, physiologists, behavioral biologists, and veterinarians. This holistic approach is favored by the US Fish and Wildlife Service. Without the collation and distribution of information, information that may prove useful to the various disciplines remains inaccessible. Data on all aspects of the rehabilitation and reintroduction process should be shared among centers and sanctuaries and made available to researchers to facilitate communication, prevent repetition of mistakes, and improve on successes. Rehabilitation centers must not operate in a vacuum and new projects should make every effort to gather information from other rehabilitation projects and to work together; to do otherwise would be to ignore the data already available and is irresponsible. There are few case studies on gibbon rehabilitation, so it is hoped that this article will serve as the first of many, and that the guidelines suggested herein can be improved upon as more information is gathered.

Summary and Conclusions

Any strategy to save gibbons and their habitats must involve an integrated approach. Steps taken should include:

- Rehabilitating and reintroducing gibbons taken from captivity and the illegal pet trade in a humane environment with expert care;
- Discouraging local people from keeping gibbons as pets;
- Alerting foreigners to the fact that keeping and trading in gibbons is illegal;

- Promoting gibbons as flagship conservation species for the rain forests of Southeast Asia;
- Providing conservation education for locals and foreigners about the gibbon's role in the rainforest and the threat that humans pose to gibbons;
- Conserving suitable gibbon habitat in large enough areas to allow large populations of wild and reintroduced gibbons to live and breed;
- Law enforcement, education, and dissemination of information to people living in and around protected areas. Consideration must also be given to providing for people whose livelihoods depend on the forest.

Tropical forests continue to disappear at a phenomenal rate and the illegal pet trade continues with no sign of abating. The number of gibbons being kept in captivity will only increase as their forest homes are opened up for plantations, logging concessions, and for other types of human use. Rehabilitation can work in conjunction with habitat protection in terms of protecting areas for reintroduction and establishing rehabilitation training centers where there are already wild gibbons. The gibbons can be housed in areas where there is a wild population to encourage the rehabilitant gibbons to sing, but the rehabilitant gibbons should never be released in this area. Rehabilitation and reintroduction is becoming the only viable option to secure a healthy future for the hundreds, possibly thousands of pet gibbons all over the world. The low profile of the gibbon worldwide is an obstacle to gaining recognition for the problems facing gibbons.

On a large scale, the governments of gibbon range countries need to provide local people with alternatives to deforestation and hunting for food or the illegal pet trade, as these are two of the main causes contributing to habitat destruction and the dramatic decline in gibbon numbers. There are many hundreds and probably thousands of wild-born gibbons living in captivity as pets or tourist attractions. These wild-born, captive-raised animals may be an important resource for conserving gibbon species. Rehabilitation and restocking may be the only viable option for repopulating areas that have been devastated by hunting, but will be successful only if the process is carried out properly. Rehabilitation of captive-raised gibbons is possible, but the process has yet to be perfected. Both failures and successes must be shared and the process constantly evaluated and changes implemented.

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Chapter 24
Saving the Small Apes: Conservation Assessment of Gibbon Species at the 2006 Asian Primate Red List Workshop

Danielle J. Whittaker

The body of work assembled in this volume makes it clear that gibbons play an important ecological role in their environment, but unfortunately both gibbons and their habitats are in decline throughout their distribution range. Understanding the threats to wild populations is an important first step in conservation planning. In September 2006, several gibbon researchers were invited to participate in the Asian Primate Red List Workshop in Phnom Penh, Cambodia. Thomas Geissmann has prepared an excellent report of the results of this workshop as it pertains to gibbons (Geissmann 2007), and I will only summarize the overall conclusions of the workshop in this chapter.

The researchers who assessed the status of gibbons at the Workshop included Noviar Andayani, Bill Bleisch, Warren Y. Brockelman, Thomas Geissmann, Colin P. Groves, Nguyen Manh Ha, Saw Htun, Long Yongcheng, Eric Meijaard, Sanjay Molur, Vincent Nijman, Ben Rawson, Matt Richardson, Jatna Supriatna, Carl Traeholt, Rob Timmins, Joe Walston, Danielle J. Whittaker, and Jiang Xuelong. The assessments resulting from the Workshop appear in the 2008 version of the IUCN Red List.

The World Conservation Union's Red List of Threatened Species (IUCN 2008) is a comprehensive review of threatened taxa across the globe. The categories for taxa that have been evaluated and for which sufficient data exist are, in increasing order of risk, Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CE), Extinct in the Wild (EW), and Extinct (EX). The criteria used to define each category include small or declining population size and small or declining geographic range; details and guidelines are described in the IUCN's Red List Categories and Criteria (version 3.1: IUCN 2001).

Sixteen purported species of gibbons were assessed at the workshop, three of which were divided into a total of 12 subspecies. The new status assessments for each taxon are summarized in Table 24.1, with the previous assessments (2003

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Table 24.1 Previous (2000, 2003) and most recent (2006) Red List assessments of gibbon taxa

Taxon	Previous assessment	2006 assessment
Hoolock hoolock	EN	EN
Hoolock leuconedys	EN	VU
Hylobates agilis	LR/NT	EN
Hylobates albibarbis	LR/NT	EN
Hylobates klossii	VU	EN
Hylobates lar	LR/NT	EN
H. l. yunnanensis	CR	DD[1]
H. l. vestitus	LR/NT	EN
H. l. lar	LR/NT	EN
H. l. entelloides	LR/NT	VU
H. l. carpenteri	LR/NT	EN
Hylobates moloch	CR	EN
Hylobates muelleri	LR/NT	EN
H. m. muelleri	LR/NT	EN
H. m. funereus	LR/NT	EN
H. m. abbotti	LR/NT	EN
Hylobates pileatus	VU	CR
Nomascus concolor	EN	CR
N. c. concolor	EN	CR
N. c. furvogaster	CR	CR
N. c. jingdongensis	CR	CR
N. c. lu	EN	CR
Nomascus gabriellae	VU	EN
Nomascus leucogenys	EN	CR
Nomascus siki	DD	EN
Nomascus nasutus	CR	CR
Nomascus hainanus	CR	CR
Symphalangus syndactylus	LR/NT	EN

[1] More recent data suggest that this subspecies may already be extinct (see text).
CR, critically endangered; DD, data deficient; EN, endangered; LR/NT, Low Risk/Near Threatened; VU, Vulnerable. The category "Low Risk" was abandoned by the IUCN in 2003.

for *Nomascus nasutus* and *N. hainanus*; 2000 for all other species) for comparison. In cases where the taxonomy has changed between assessments (i.e., *Bunopithecus hoolock* is now *Hoolock hoolock*; *Nomascus leucogenys siki* is now *Nomascus siki*), only the new taxonomic name is given.

The current situation of the small apes is dire. Of the 28 taxa assessed, 19 (68%) increased in threat level by one or two categories since the previous assessment. Only two decreased in threat level; for the Javan gibbon, *H. moloch*, this change was due to the availability of better information, not due to an actual decrease in threat. Eight of the 28 taxa (29%) are considered Critically Endangered, while another 17 taxa (61%) are categorized as Endangered and two are considered Vulnerable (7%). No taxa are in the lower-risk categories of Least Concern or Near Threatened.

In the 2000 assessment, the Yunnan white-handed gibbon, *H. lar yunnanensis*, was categorized as Critically Endangered; at the 2006 workshop, this subspecies was considered Data Deficient. Since the workshop, a team of scientists conducted a survey in China's Yunnan Province throughout this taxon's known range. The team concluded that this gibbon subspecies is locally extinct in China and that, unless populations have survived in neighboring Myanmar, it is likely to be globally extinct (Holden 2008; Müller 2008). Gibbons have had a prominent role in Chinese art and literature for more than two millennia (Van Kulik 1967). The extinction of the white-handed gibbon in China therefore represents an incalculable loss not only to biodiversity but also to the Chinese cultural heritage. Two other taxa in China are also on the edge of extinction: only about 50 Cao-Vit crested gibbon (*Nomascus nasutus*) individuals remain in China and Vietnam, and the Hainan crested gibbon (*N. hainanus*) population has been reduced to fewer than 20 individuals (Mittermeier et al. 2007). These gibbons are, by far, the most endangered apes on the planet.

While gathering data is critical to defining conservation needs, and further information about the status of many gibbon populations is still urgently required, research is only a first step. We must do more. It is our hope that publications such as this volume will contribute to a greater public interest in saving these wonderful animals, as well as providing encouragement and support for conservation professionals and gibbon researchers and enthusiasts already working to develop effective conservation policies. It may be too late for some populations and taxa, but others can and should be saved. If we are to have any hope of bringing the small apes with us into the next century, the time for action is now.

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Index

A
Abbott, I., 489
Abbott's gray gibbon, *see H. muelleri abbotti*
Abrams, P., 154
African cercopithecines, 135
African wild dog, *see Lycaon pictus*
Agile gibbons, *see Hylobates agilis*
Aglaia, 170
Agoramoorthy, G., 52–53, 485, 490
Ahsan, M.F., 4, 134, 137, 140, 141, 190, 245, 251, 349, 397, 488
Alaotran gentle lemur, *see Hapalemur griseus alaotrensis*
Alberts, S., 328
Alcántara, J.M., 198
Aldrich-Blake, F.P.G., 488
Ali, R., 390, 391, 397, 400, 441, 442, 456
Allied rock-wallaby, *see Petrogale assimilis*
Altizer, S.M., 366
Altmann, J., 337, 470
Altmann, S.A., 221
American National Wildlife Rehabilitation Association, 479
Anchal Reserved Forests, 413
Andayani, N., 4, 16, 67, 76, 83, 93, 104, 105, 106, 499
Andelman, S.J., 230
Anderson, J., 411
Andrews, P., 124
Anthony, H.E., 438
Anzenberger, G., 339
Aotus spp., 289
  and pup retrieval behavior, 291
The Apes: Challenges for the 21st Century, in 2002, 8
Aquilaria malaccensis, 166
Arborophilia davidi, 389
Arcady, A.C., 92
Arcese, P., 367
ARF, *see* Anchal Reserved Forests
Arnason, U., 25
Artabotrys, 170
Asian elephant, *see Elephas maximus*
Asian Primate Classification (2004), 15
Asian Primate Red List Workshop 2006, 497
Asian rain forests
  gibbons (Hylobatidae), seed dispersers, 190
Asiatic black bear, *see Ursus thibetanus*
Asquith, N.M., 93, 478
Assamese macaque, *see Macaca assamensis assamensis*
Atkinson, M.W., 479
Auditory census methods
  for *Hoolock leuconedys*, 441
  and for *Nomascus gabriellae*, 388–389
  vocalization study, for population density estimate, 390–392
Aung, Moe, 435
Avahi occidentalis, 294
Avise, J.C., 76, 84
Ayala, F., 136
Ayeyarwady (Irrawaddy) river, 118
Azusa, H., 37

B
Baboons, *see Papio spp.*
Baker, M.C., 91
Balai Konservasi Sumber Daya Alam (BKSDA), 38
Banack, S.A., 196, 201
Banteng, *see Bos javanicus*
Barelli, C., 6, 266, 290, 313–324, 328, 349, 353, 364–366, 368, 371
Barito River in Borneo, 20, 22
Barito Ulu research area, Central Kalimantan, Indonesia, 4, 190
Barnett, A., 456

- Barry, J.C., 123
- Bartels, E., 192, 196, 201
- Bartlett, T.Q., 5, 137, 140, 141, 213, 217, 219, 221, 222–223, 228, 241, 243, 246, 248, 249, 255, 258, 265–273, 295, 301, 350, 369–370, 398
- Basabose, A.K., 181
- Batchelor, B.C., 29, 52, 64–65, 73
- Bateson, P.B., 330–331, 357
- Bats, role in seed dispersal, 196–197
- Batu Islands, 65
- Baudoin, C., 285, 290–291, 293, 299
- Beck, B.B., 479–480, 486
- Becker, P.M., 192, 201
- Begon, M., 161
- Belian, *see Eusideroxylon zwageri*
- Bellwood, P., 27, 29
- Benefit-of-Philopatry Hypothesis, 299
- Bengal slow loris, *see Nycticebus bengalensis*
- Bennett, E.L., 52–53, 182
- Bennett, J., 477–478, 484, 490
- Bennett, P., 349
- Bernstein, I.S., 426
- Bester-Meredith, J.K., 328
- Betumonga, in North Pagai, 74
- Bhattacharjee, P.C., 474
- BigDye Terminator Ver. 3, 0 cycles sequencing kit, 44
- Biogeography, of gibbons
  - paleoenvironmental history of Southeast Asia, 27–30
  - paleontological records, 26
    - evidence from sites of Lang Trang in Vietnam and Niah in Malaysian Borneo, 27
    - fossil record until Pleistocene, 26, 27
    - Punung faunal assemblage on Java, 27
- Biological Species Concept (BSC), 77
- Bird fruit, 194
- Birkhead, T.R., 348
- Bishop, M.G., 121, 122
- Biswas, J., 409, 467
- Black-crested gibbons, *see Nomascus concolor*; *Nomascus nasutus*
- Black-shanked douc langur, *see Pygathrix nigripes*
- Blanc, L., 400
- Blate, G.M., 198, 199
- Bleisch, W., 136, 151, 250–251, 348, 499
- Blundell, A.G., 166
- Bodmer, R.E., 477
- Boesch-Achermann, H., 347, 370–371
- Boesch, C., 370
- Boonratana, R., 52–53
- Borajan Reserve, Assam, India, 4
- Bornean frugivores
  - feeding competition with gibbons, 161–188
  - width of seeds dispersed by, 191–192, 197
- Bornean gibbon, *see Hylobates muelleri*
- Bornean rainforest, gibbons in, 162
  - competitive interactions among primate species, 162
  - vertebrate frugivores in, 162, 163, 165
- Bornean white-bearded gibbons, *see Hylobates albibarbis*
- Borneo, 17, 19, 22, 27–31, 32, 37, 47, 48, 121, 123, 190, 197, 199, 202, 245, 397, 478
- Borries, C., 327, 350, 367
- Bose, J., 426
- *Bos gaurus*, 389, 439
- *Bos javanicus,* 389*, 489*
- Boyd, R., 348
- Brandon-Jones, D., 13–17, 29, 37, 64, 104, 105, 136, 435
- Brend, S.A., 482
- Brickle, N.W., 389
- Bricknell, S.J., 266, 272
- Britt, A., 486
- Brockelman, W.Y., 4, 5, 7, 22, 51, 92, 125–127, 135, 211–234, 241, 244, 248, 249, 253, 258–259, 265–267, 273, 297, 301, 340, 348–351, 355, 364–365, 369, 371–372, 375–376, 390–391, 391, 395, 397–398, 402, 411
- Brotherton, P.N.M., 213–214, 222–223, 225, 231, 280, 285–287, 289–291, 293, 294, 298, 302, 305
- Brown, R.E., 328
- Brown, W.L., 135, 138
- Bruce, E., 136
- Brugiere, D., 456
- Brulé, A., 257, 482, 490
- Buchan, J.C., 327, 339
- Buckland, S.T., 391, 397
- Buech, R.R., 285
- Bukittinggi Zoo, 66
- *Bunopithecus*, *see* Hoolock
- *Bunopithecus sericus*, 15, 120
- Burley, N.T., 327–328
- Burton, K.M., 22
- Bush, B.B., 490
- Byers, J.A., 367
- Byrne, R.W., 347

C
Cabang Panti Research Station (CPRS), 166
Cadigan, F.C., 456
Cain, M.L., 200
Cairina scutulata, 389
Callithrix jacchus, 280, 297
Caldecott, J., 255–256, 461
Caldwell, C.A., 370
California mouse, *see Peromyscus californicus*
Calkins, J.D., 327–328
Callicebus moloch, 289
Cameron, E.Z., 332
Candidate priority areas, 414
Canis simensis, 288
Canis lupus, 288
Cannon, C.H., 161, 164–166, 168, 182
Canopy bridges, in gibbon conservation, 467–468
  usage of canopy bridges, 472–473
Cantoni, D., 328
Cao-Vit crested gibbon, *see Nomascus nasutus*
Capped langur, *see Trachypithecus pileatus pileatus*
Capricornis crispus, 289, 294, 298, 299
Carpenter, C., 221–223, 248, 301–302, 365, 478
Carranza, J., 368
Carter, C.S., 285
Case, T.J., 162
Castellan, N.J.J., 58
Castor canadensis, 290
Catchpole, C.K., 92
Cayford, J., 484
Cebuella pygmaea, 297
Cercopithecus monkeys, 162
Cervus eldii, 389
Cervus unicolor, 439
Chambers, K.E., 6, 353
Chaplin, G., 111–127
Chapman, C.A., 193
Chapman, L.J., 189
Charif, A., 54
Charif, R.A., 94
Charles-Dominique, P., 162
Charnov, E.L., 163, 216
Chasen, F.N., 52–53, 65, 74
Chatterjee, H.J., 4, 13–32, 37, 113, 120, 136, 190, 241
Cheirogaleus medius, 288, 291, 296
  parentage analysis of, 288
Cheney, D., 347
Chen, N., 136, 151, 250–251, 348
Chetry, D., 426
Cheyne, S.M., 7–8, 67, 84, 257, 477–492
Chimpanzee, *see Pan troglodytes*
China, 7
Chit, Saw, 435
Chivers, D.J., 8, 14, 22, 30, 51, 92, 124–125, 134, 136–137, 141, 153–155, 165, 182, 190, 196–197, 200, 203, 212, 216, 221–224, 245, 248, 250, 265, 272, 294, 300, 328, 332, 334–335, 338, 348–349, 388, 398, 411, 453, 461–463, 477–478, 486–489
Choo, G.M., 246
Chuang-Dobbs, H.C., 339
Ciochon, R.L., 112, 113
Civets, role in seed dispersal, 192
Clarke, E.A., 353
Classification systems, in for gibbons, 13–14
Clement, M., 44
Clements, T., 387, 388, 389, 391, 398, 400
Clouded leopard, *see Pardofelis nebulosa*
Clutton-Brock, T.H., 134, 138, 141, 152, 211, 214, 215, 225, 327, 368
Coates-Estrada, R., 162, 181
Cochrane, E.P., 189
Cody, M.L., 161
Coker, P., 412
Colwell, R.K., 181
Commitante, R., 485
Common marmoset, *see Callithrix jacchus*
Common muntjac, *see Muntiacus muntjak*
Community-wide feeding competition
  comparisons of dietary overlap, 166, 173–174
    dietary composition over time by plant part, 167
    dietary specialization of vertebrate frugivores by family and species, 172–173
    diets comparison by using index of dietary identity, 169–170
    distribution of feeding tree sizes among vertebrate species, 170
    food items included in diets and major vertebrate competitors, 174
    major competitors, 173–174
  effects of food availability on dietary overlap, 176
  in peat and non-peat forests, 175–176
Conklin-Brittain, N.L., 165
Connell, J.H., 161, 181, 189–190

Conservation landscapes in Assam, for primate conservation, 423
  See also Hoolock gibbons
Conservation, of gibbons
  assessment in Asian Primate Red List Workshop 2008, 497–499
  difficulties of, 483–484
  global outlook on, 479–480
  poaching, in Mahamyaing Wildlife Sanctuary, 449–450
  population decline of, 477–479
  pre-release and post-release plannings for, 485–491
  rehabilitation and reintroduction of, 479–483
  in Sumatra, population decline, 453
  techniques, 467–468
    methods in, 468–472
    usage of canopy bridges, 472–473
    wild *vs*. rehabilitant gibbons, 484–485
Cooper, G., 161
Cords, M., 347
Corlett, R.T., 189, 191–193, 196, 198, 201
Cowlishaw, G., 256, 290, 353, 365, 397–398
CPA, *see* Candidate priority areas
Cracraft, J., 37
Creel, N., 14, 22, 24, 51, 136
Creel, S.R., 490
Crested gibbons *(Nomascus spp.), see Nomascus; Nomascus concolor; Nomascus nasutus; Nomascus gabriellae; Nomascus siki; Nomascus spp.; Nomascus hainanus; Nomascus leucogenys*
Cronin, J.E., 47
Crook, J.H., 215, 216
Cunningham, C.L., 370
Curran, L.M., 163–164, 198, 477
Curtin, S.H., 219
Curtis, D.J., 285, 316
Cynomys gunnisoni, 295, 299

D
Dacryodes, 196
Dahl, J.F., 313, 317–318, 323
Dalling, J.W., 190
Dallmann, R., 4, 16, 51, 64, 91–106
Daly, M., 366
Danielle, J.W., 3, 4, 7, 73, 499
Dao, V.T., 15, 22
Darwin, C.R., 214, 487
da Silva Mota, M.T., 339
Das, J., 7, 409–431, 435–436, 439, 445, 467–475
Davidson, P., 402
Davies, A.G., 163, 182, 461
Davies, N.B., 301, 348
Davis, J.L., 77
DCRF, *see* District Council Reserved Forests
Deaner, R.O., 370, 371
Defendability index (D-index), 267–268, 270
Delacour, J., 53
Demes, B., 211–212, 256
den Boer, P.J., 161
Dendropithecus, 26, 112
DeSalle, R., 75, 77
Deschner, T., 323
DeVeer, M.W., 482
de Vos, J., 27, 29, 112–113
Diamond, J.M., 161
Di Bitetti, M.S., 219
Dielentheis, T.F., 328, 338
Dietary overlap, 164
Diets of gibbons
  degree of diet specialization, 162–163
  dietary composition over time by plant part, 167
  dietary identity, below null model, 170
  diet comparison, 137, 138, 142, 143
    living sympatrically *vs*. allopatrically with siamangs, 145, 152
  diets at CPRS and variation across season, 166, 179–180
  diets, less diverse during HFP than LFP in peat forests, 173
  folivory/frugivory relationships, 143, 144
    folivory link to body mass in, 143–145, 151, 152
    food-switching in, 125
  major vertebrate competitors, 163–164, 174
  in Peat and non-peat forests diet overlap
    with vertebrates, 175–176
    during LFP and HFP, 176
    during LFP, HFP, and masts in, 177
  primate fruits consumption, 194–195
  relationship between food availability and diet breadth, 163
  relatively unspecialized in diets, 170, 195
  unique food items included in diets, 174
Di Fiore, A., 163
Digby, L.J., 285, 289, 297–299, 366
Dik-dik, *see Madoqua kirkii*
Dionysopithecus, 26, 112

Diospyros, 170
Dipterocarpus turbinatus, 439
Dispersal-vicariance analysis (DIVA), 30
District Council Reserved Forests, 413
Dixon, A., 339
Dizon, A.E., 83
Dog-faced bat, 170
Dolman, P.M., 162
Dong Phayayen–Khao Yai Forest Complex, 350
Douroucouli, *see Aotus spp.*
Doust, H., 121, 122
DPKY, *see* Dong Phayayen–Khao Yai Forest Complex
Dring, J.C.M., 65
Duckworth, J.W., 387, 390, 401–402
Duckworth, W., 167
Dudgeon, D., 52–53
Dunbar, R.I.M., 5, 214, 215, 222–225, 230, 242–243, 249, 265, 268, 272–274, 291, 295–296, 301, 338, 340, 347, 367, 369
Dunlap, A.S., 366
Durio, 196
Dusky titi monkeys, *see Callicebus moloch*

E
Eames, J.C., 387, 401
Early catarrhines/hominoids, 112
Eastern hoolock gibbon, *see Hoolock leuconedys*
Eastern Mueller's gibbon, *see Hylobates muelleri muelleri*
Eberhard, W.G., 366
Eccard, J.A., 161
Eeley, H.A.C., 162
EIA, *see* Enzymeimmunoassay
Eisenberg, J.F., 215
Elder, A.A., 6, 18, 125, 133–156, 190, 202, 245, 246, 252
Eld's deer, *see Cervus eldii*
Elephas maximus, 389, 439
Ellefson, J.O., 137, 140, 141, 221–223, 248, 265, 348, 349
El Niño/Southern Oscillation, 154, 255
Emlen, S.T., 163, 213–214, 221, 230, 243, 265, 299, 327, 340
Emory, K.O., 65, 84
Endozoochory, 197, 199, 200, 202
Engelhardt, A., 314, 322–323
ENSO, *see* El Niño/Southern Oscillation
Enzymeimmunoassay, 316
EPCs, *see* Extrapair copulations
EPP, *see* Extrapair paternity
Esser, A.H., 257–258
Estimated strip width, 456
Estrada, A., 162, 181
ESU, *see* Evolutionarily Significant Units
ESW, *see* Estimated strip width
Ethiopian wolves, *see Canis simensis*
EU-ASAC, *see* European Union Assistance on Curbing Small Arms and Light Weapons in Cambodia
Eudey, A.A., 135, 477–478, 483
Eulemur fulvus rufus, 291
Eulemur mongoz, 280
Eulemur rubriventer, 291
European Union Assistance on Curbing Small Arms and Light Weapons in Cambodia, 400
Eusideroxylon zwageri, 166
Evans, B.J., 65–66, 389
Evolutionarily Significant Units, 37, 75, 77
Evolutionary niches of gibbons, 164
  fruit patches used, smaller, 165
  niche defined, 126, 181–183
  niche divergence, 135
  similarity in feeding niches with major competitors, 164–165
    fruit patches used, smaller, 165
Excoffier, L., 44, 78
Extrapair copulations, 249, 279, 286–289, 349, 362
Extrapair paternity, 279
  incidence of, 286–289

F
Fa, J.E., 481
Fan, P., 4, 273
Fashing, P.J., 301
Fat-tailed dwarf lemurs, *see Cheirogaleus medius*
Fecal hormone analysis, for *H. lar* reproductive status, 314–315
  genital skin swelling, changes in, 320–321
  hormone concentrations, storage procedure on, 321
  hormone profiles, 318–320
  methods in, 314–318
  See also Hylobates lar
Feeroz, M.M., 4, 435
Female dispersion hypothesis, 272
Ferguson, D.K., 126

Fernandez-Duque, E., 285, 289–291, 293, 296
Ficus spp., 245
Fiedler, K., 368
Fietz, J., 285, 287–288, 291, 293, 296, 366
Figs, 245
Fischer, J., 486
Fischer, J.O., 301–302
Fischer, K., 368
Fleagle, J.G., 26, 112, 154, 155, 211, 398
Fleming, K., 118
Fleming, A.S., 339
Fleming, T.H., 161, 164
Flenley, J.R., 29–30
Fleury, M.C., 456
Fogden, M.P.L., 192, 193, 198
Folivory, link to Body Mass in gibbons, 143–145
Foltz, D.W., 285, 287
Foraging, of gibbon, 215–216
  foraging and food patch size, 216
  territory, knowledge of, 216–220
Fork-marked lemur, *see Phaner furcifer*
Forschhamer, M.C., 161
Fossil records, of gibbons, 111
  ancestral stock, west of Mekong, 120
  bifurcation of lineage, 120
  deposits of latest Miocene or earliest Pliocene age, 112
  distribution and dispersal
    alternating periods of exposure and inundation of Sunda platform and, 118
    biological and ecological factors influencing, 111
    dispersed west of Paleo-Salween, 121
    environmental changes in Pleistocene, 124–125
    environmental deterioration of Pleistocene and impact on, 124–125, 127
    expansion and factors, 121
    impact of large rivers, 118
    southward dispersal, 127
  distribution of fossil gibbon localities, 118–119
  distribution of fossil hylobatids through time, 119
  distribution and relation to changing sea levels and landforms, 113–123
  in Holocene re-radiation of, 123
  Middle Pleistocene, westward expansion of, 120
  Miocene fossil record of Eurasia and East Africa, 112
  nature of records, 112–13
  occurrences of fossils of Hylobatidae, 114–117
  radiation origin, estimated time for, 113, 118
  rare elements of fossil record, 113
Francis, C.M., 167
Frankham, R., 37, 487
Frantzen, M.A.J., 486
Frazier, C.R.M., 328
Fredriksson, G.M., 192, 196, 198
French Guiana, 165
Fruit types
  bird fruit, 193–194
  generalist fruit, 194
  primate fruit, 194
Fuentes, A., 5–6, 73–74, 85, 212, 241–259, 273, 279, 280, 285, 328, 340, 348–350, 364
Fürtbauer, I., 353–354
Futuyma, D.J., 181

G
Gadsby, L., 486
Gaharu, *see Aquilaria malaccensis*
Galdikas, B. M. F., 8, 124, 200
Galetti, M., 192, 196, 201
Ganzhorn, J. U., 135, 181
Garber, P.A., 340–341
Garcia, J.E., 456
Garcinia, 170
Gaston, A.J., 340
Gates, R., 478
Gaur, *see Bos gaurus*
Gautier-Hion, A., 135, 162, 164
Gautier, J.P., 91
Geissmann, T., 4, 15–22, 24, 30, 37, 39, 51–52, 64, 66, 73, 77, 91–106, 118, 120, 124, 135, 136–138, 212, 290, 301, 338, 348, 354, 387–388, 402, 435, 453, 499
Generalist fruit, 194
Genital skin swellings, for *H. lar* reproductive status, 313–314
  genital skin swelling, changes in, 320–321
  hormone profiles, 318–320
  methods in, 314–318
Gentry, A.H., 139, 153, 155
Geological ages, epochs or sub-epochs, 113

Geographic distributions of gibbons, 17–22, 32
  - areas of sympatry among species, 18
  - of species in genus *Hylobates,* 17
  - of species in genus *Nomascus,* 21
  - of species in genus *Symphalangus*, 18

Germain's peacock-pheasant, *see Polyplectron germaini*
Getz, L.L., 285, 299
Ghiglieri, M.P., 216
Giant ibis, *see Pseudibis gigantea*
Gibbon evolutions
  - diameter of feeding trees and major competitors, 178
  - ecological flexibility, 124–125
  - exhibit individual-specific characteristics, 92
  - great-calls, 92
  - in Holocene re-radiation of, 123
  - major vertebrate competitors, 163–164, 174
  - role in seed dispersal in Bornean dipterocarp forests, 190

Gibbon-like primates
  - and nature of fossil records of, 112

Gingerich, P.D., 154
Girman, D.J., 285, 287–289, 300–301
Gittins, S. P., 14, 22, 92–93, 96, 135–137, 140–141, 216, 219, 221, 248, 251, 294, 328, 338, 347–349, 351, 365–366, 376, 407, 421, 435, 441, 445, 462, 488
Golden langurs, *see Trachypithecus geei*
Golden lion tamarind, *see Leontopithecus rosalia*
Golden Lion Tamarin Project, *see Leontopithecus rosalia*
Goldizen, A.R., 367
Goldizen, A.W., 297, 338, 340, 348, 367
Goldstein, P.Z., 77
Gomendio, M., 366
González-Solís, J., 162
Goodman, M., 26
Goossens, B., 285, 287, 300
Gorillas, 8
Goss-Custard, J.D., 215
Gouat, P., 285, 289, 299
Gould, S.J., 154
Goustard, M., 397–398
Gowaty, P.A., 212
Graham, M., 266
Graham, R.W., 125
Grand, T.I., 211–212
Granger, W., 15, 120
Grant, P.R., 161
Gray, E.M., 287
Gray wolves, *see Canis lupus*
Great call phrase, 54, 55
  - female silvery gibbon, and components
    - accelerando-decelerando of wa-notes, trill, 96
    - slow pre-trill phase, 96
    - termination phase, 96

Great ape-gibbon split, 113
Green peafowl, *see Pavo muticus*
Green, S., 91
Grether, G.F., 216
Griffith, B., 480
Griffith, S.C., 366
Gromko, M.H., 367
Gross, M.R., 339
Groves, C. P., 13–17, 22, 30–31, 37, 39, 48, 52, 53, 64–66, 74, 85, 93, 104–105, 136, 403, 409–411, 425, 435, 438, 453, 499
Guangdong Provinces of China, 123
Gubernick, D.J., 285, 294, 296, 327–328
Guillotin, M., 135, 162, 165
Gunung Lawét, 105
Gunung Palung National Park, West Kalimantan, Indonesia
  - Cabang Panti Research Station (CPRS) in, 166
  - competition and niche overlap between gibbons and frugivorous vertebrates in, 161–165
  - vertebrate frugivores, highest degree of dietary overlap with gibbons at, 175

Gunung Pangrango complex, 105
Gupta, A.K., 153, 155, 417, 421–422, 481, 486
Gurmaya, K.J., 93
Gursky, S., 285, 293, 297
Guttman, L., 98
Gu, Y.M., 27, 112–113, 120
Gyps bengalensis, 389

H

Habitat characteristics, of hylobatid communities, 244–245
  - *See also* Hylobatid communities

Habitat fragmentation and gibbon mortality, 473
Habitat requirements, 7
Habitat-saturation hypothesis, 299
Hacia, J.G., 370
Hafen, T., 91–92

Haimoff, E.H., 14, 22, 51, 54, 91–92, 96, 151, 250, 347, 348, 441, 477
Hainan crested gibbon, *see Nomascus hainanus*
Hainan Provinces of China, 123
Hairston, N.G., 161
Hall, L.M., 22, 23, 28, 106
Hall, R., 22, 28, 106, 118
Hamilton, M.B., 190
Hannah, A.C., 258, 319, 479, 490
Hapalemur griseus, 288–289, 298, 299
Haq, B. U., 118
Harper, J.L., 161
Harrison, T., 112–113
Harvey, P.H., 66, 85, 134, 138, 141, 152, 211
Hasegawa, M., 78
Hayano, A., 37, 44, 47
Hayashi, S., 22–223, 24, 37, 44, 106
Hayssen, V.D., 124, 332
Heaney, L.R., 29–30
Heistermann, M., 6, 313–324
Heng Duan Mountains, 118
Hepp, G.R., 163
Herrera, C.M., 189, 198
Hery, W., 37
Heymann, E. W., 135, 367
High fruit periods (HFP), 176
Highland Farm, gibbons in, 481
Hilton-Taylor, C., 93, 105
Hirai, H., 4, 15, 17, 37–48
Hladik, C.M., 134, 135, 153–154, 470
Hladik, V., 470
Hla, Naing, 435
Hylobates agilis, 222, 397, 453
  genetic differentiation, between Sumatra and Kalimantan, 37
  chromosome composition data, 43
  clustering analyses of mtDNA haplotypes, 44
  Sumatran and Bornean agile gibbons and Eastern Mueller's gibbons, relationships, 43
  inversion polymorphisms, 38
  microsatellite DNA (mtDNA) analysis, 47
  migration
    of gibbons in Sundaland, 48
    of *Hylobates muelleri* and *H. agilis* from Sumatra to Borneo, 47
  pelage pattern of *Hylobates agilis albibarbis*, 39
  population status and distribution of
    biomass of, 461
    density estimates and distribution of, 458–489, 461–463
    group sizes for, 459–460
  reciprocal translocations, 38
  relation between genetic parameters, 45
    pelage pattern of *Hylobates agilis albibarbis*, 39
    stasipatric speciation model, 47
  whole-arm translocation (WAT8/9), in *Hylobates* and Sumatran agile gibbons, 40, 43, 47
Hodges, J.K., 314, 316
Hodges, K.E., 285, 289, 296, 299
Hodgkison, R., 192–194, 196–198
Hodun, A., 91
Hoelzer, G.A., 74
Holden, C., 501
Holder, K., 367
Hominoids-large, chances of survival, 124–125
Hooijer, D. A., 27, 112–113
Hoolock hoolock hoolock gibbons, 3, 4, 251, 397, 468
  activity budgets and diets, at Borajan, 470
  characteristics of, 251–252
  conservation landscapes in Assam for, 423
  distributed to west in India and Bangladesh, 17
  distribution of, 409–410, 417–419
  extinction risk of, 424–425
  group size and composition, 421–422
  in India, distribution status of, 411–412
    altitudinal distribution of, 421
    assessment methods for, 412–414
    outside protected areas, 416, 426–431
    in protected areas, 415–416
  population estimates for, 422
Hoolock hoolock leuconedys, 17, 407, 420, 424
  See also Hoolock leuconedys
Hoolock leuconedys
  census in Mahamyaing Wildlife Sanctuary, 436, 439, 448–449
    census methods, 441–442
    forest assessment methods, 443
    forest canopy cover, 446
    gibbon densities and forest condition, 446–468
    group densities in, 443, 445
    mean group and total population size assessment, 445–446
    workshop and training exercises, 439–440

  distribution of, 410–411, 416, 419–421
  and protected areas in Myanmar, 436–439
Hormone analysis, *see* Fecal hormone analysis
Hor, N.M., 387
Horton, K.E., 370
Hosken, D.J., 366
Howe, H.F., 189–190, 193, 199–200
Hrdy, S.B., 366–367
Hsu, M.J., 490
Hubbell, S.P., 161
Hubrecht, R.C., 366
Huck, M., 287, 298, 340–341
Hudieliangzi (Butterfly Hill), 27
Huelsenbeck, J.P., 76–77
Hu, H., 486
Hukaung–Bumhpabum reserves, for hoolock gibbons, 438
Hulme, P.E., 198
Human impacts, in hylobatid communities, 254–258
  See also Hylobatid communities
Hunan Provinces of China, 123
Hung, V. L., 122
Hunt, K.D., 165
Hunt, K.E., 314, 323
Hutchinson, G.E., 164
Hydnocarpus anomala, 193
Hylander, W.L., 153–154
Hylobates, 4, 14
  constituent members, 15
  distribution of species, in Southeast Asia, 17
  "dweller in the trees", 13
  features of, 246–249
  and *Symphalangus*, comparison of, 252–253
Hylobates agilis
  Hylobates agilis agilis, 39
  Hylobates agilis albibarbis, 4, 16
  Hylobates agilis unko, 16, 39
Hylobates albibarbis, 15, 37, 39
  populations, at CPRS, 166
  diet comprising of, 166
  See also Hylobates agilis
Hylobates gabriellae, 15
Hylobates lar, 4, 15, 16, 135, 152, 212, 217, 221, 222, 224, 226, 228, 249, 254, 257, 265, 266, 271, 272, 280, 290, 313, 349, 453
  daily path length and home range size, 269–270
  daily path length, variation in, 271
  fecal hormone analysis, for reproductive status, 313–324
    genital skin swelling, changes in, 320–321
    hormone concentrations, storage procedure on, 321
    hormone profiles, 318–320
    methods of measuring in, 314–318
  female reproductive status in, 313–314
  fig eaters, 133
  genital skin swellings analysis, for reproductive status, 313–324
  H. lar carpenteri, 16
  H. lar entelloides, 16, 376
  H. lar lar, 16
  H. lar vestitus, 16
  H. lar yunannensis, 16, 501
  home range use and defendability in, 265–273
  hormone concentrations, storage procedure on, 321
  hormone profiles, 318–320
  of Khao Yai Thailand, populations, 125
  mating system of
    females and males, mating strategies of, 362–363
    variable social organization and mating system in, 363–368
  maximum number of defendable females, 272–273
  in Mo Singto - Klong E-Tau, 350
    mixed species groups, 351–352
  multimale polyandry, resource distribution and territorial/female defense, 368–369
  resource abundance and rainfall, 266, 268–269
  social organization of, 356–357
  social organization and mating system of, 348
  sociosexual flexibility and advanced cognitive abilities of, 370–372
Hylobates hoolock, 17, 435
Hylobates hoolock hoolock, *see Hylobates hoolock*
Hylobates klossii, 3, 4, 15, 17
  an endangered species, 53
  areas for conservation in Pagais, 85–86
  between-population divergence in, 82
  closely related Javan silvery gibbon, behavioral characteristics, 73
  conservation planning for, 85–86

Hylobates klossii (*cont.*)
  discriminant functions, represents differing variance percentages, 59
  endangered, 85
  endemic to the Mentawai Islands, 51, 64–67, 73
    gene flow among, 83–84
    and possible explanations for, 64–67
  Evolutionary Significant Unit (ESU), 67
  examining subspecific taxonomy of, 53
  gene flow in recent and historic time, 84
  lineage sorting in, 84
  methods used for analysis of songs
    discriminant analysis results, using song material, 62
    Discriminant Function Analysis (DFA) for identification, 57–62
    discriminant scores of gibbon groups, 61
    "leave-one-out" method, 61
    MDS analysis, to visualise vocal similarities/dissimilarities, 58, 62–63
    quantification of acoustic characteristics, 57
    reclassification procedure used, 61
  patterns of vocalization, songs, 51
  phylogenetic relationships analysis
    by using Bayesian analysis, 76, 78
    by using neighbor-joining algorithm and bootstrap replications, 76
  phylogeography and methods used to study
    analysis of molecular variance (AMOVA), 78
    DNA sequencing, 76
    Markov Chain Monte Carlo simulations, 77
    molecular pairwise distance matrix, 80
    population genetics in, 78
    sampling sites in Mentawai Island, 75–76
  population aggregation analysis (PAA) of, 79, 81
  shared haplotypes between Siberut and South Pagai, 83
  in Siberut National Park, 85
  song structure in, 54–55, 57
    male and female, 55–56
    number of song bouts recorded and analyzed, 56
    sonograms of female song phrases, 60
    stylized sonograms of song phrases, male/female, 55
  vocal diversity studies in, 66, 67
    field sites for recording and data collection, 54
  vocal *vs.* geographic distance in, 62–63
Hylobates leucogenys, 15
Hylobates moloch, 4, 15, 52, 64, 73, 91–94, 96, 105, 254, 280, 478, 500
  Hylobates moloch moloch, 16, 93
  Hylobates moloch pongoalsoni, 16, 93, 104
Hylobates moloch, variability in songs, on Java, 91
  acoustic analysis of song bout, 94–96
  division into distinct populations, 94
    Central Java, 94
    Gunung Halimun complex, 94
    Gunung Pangrango complex, 94
    Ujung Kulon complex, 94
  map showing area inhabited, 93
  field recordings and analysis, 94
  great-call phrases of female, 91, 92, 94
    consisting single wa-notes and wa-phrases, 91, 92
    main components, 96
  molecular studies on, 106
  rarity of male singing in, 92
  significant inter-individual differences in great-call variables, 92–93
  sonogram of great-call phrase by female silvery gibbon, 96
  studies on mitochondrial DNA sequences, 105
  variability between populations, 102–104
    discriminant analysis of great-call data, 102–103
  variability within and between individuals songs, 99–102
  vocal "representative of family" female, 91
Hylobates muelleri, 4, 15, 40, 222, 245, 300, 397
  Hylobates muelleri abbotti, 16, 40
  Hylobates muelleri funereus, 16, 40
  Hylobates muelleri muelleri, 16, 40
  localities, 123
  See also Hylobates albibarbis; Hylobates agilis; Hylobates agilis albibarbis
Hylobates pileatus, 15, 17, 348, 351, 397
Hylobatidae, 15, 37
  characteristics of, 111
  divisions and geographic distributions of, 16

  fossils, 114–117
  relative lack of behavioral diversity within, 126
Hylobatid communities, 133, 241
  area of origination for lineage, 120
  competition between species, 134–137
  descendants of small Miocene apes, 112
  dietary and habitat data, overarching patterns in gibbon ecology, 135–138, 140, 141
  diets analysis and understanding in, 136–138
  distribution of fossil through time, 119
  earliest fossils, latest Miocene or earliest Pliocene, 120
  ecological flexibility, 124–125
  ecological variation to variable social organization, 253–254
  ecology, 133–134, 155
  effects of Body Mass on energetics, 134
  folivory link to Body Mass in gibbons, 151–152
  frugivorous nature, 140–141
  future prospectives of, 301–302
  genetic distances among genera of, 135–136
  impact of interspecific competition on diets, 148–150
  infanticide and, 296
  Late Pleistocene, fossils within the Pearl River drainage, 123
  morphological consequences of large body size, 153–154
  polygynous groupings in, 297
  resource availability and diet, relationship between, 138, 145–148, 153
  ripe-fruit specialists, 133
  social organization, human impacts, and population viability, 254–258
  social organization, hypotheses and predictions for, 243
  taxonomy of, 242
  variation and flexibility, ecological bases for
    distribution and habitat characteristics, 244–245
    resource use, patterns of, 245–246
Hypogeomys antimena, 291, 296

I
IBI, *see* Interbirth interval
Ihara, Y., 340
IIRS, *see* Indian Institute of Remote Sensing
Imai, H.T., 46–47
India, 7
Indian Institute of Remote Sensing, 414
Indian Wildlife Protection Act of 1972, 468
Indochina Bioprovinces, 120
Indo-Malaysian Islands, 27
Indonesia, 4, 7
Indonesian Borneo, gibbon population in, 478
Indonesian Ministry of Forestry's Department for the Protection and Conservation of Nature, 38, 329, 341
Indonesian Research Authority, 38
Infanticide and monogamy, 296
  See also Monogamy
Inskipp, T., 167
Interbirth interval, 249
International Primatological Society symposia, 3
Interspecific competition, ecological effects of, 161–162
Isbell, L.A., 298–299
Islam, M.A., 4, 435
IUCN Red List 2008, 85, 387, 411, 499
IUCN Red List Categories and Criteria, for gibbon, 500
IUCN Species Survival Commission, 93

J
Jablonski, N. G., 4, 26, 29–30, 111–127
Janis, C. M., 124
Janson, C.H., 155, 213, 216, 219, 231, 337, 367
Janzen, D.H., 164, 190, 470
Japanese serow, *see Capricornis crispus*
Japan International Cooperation Agency, 390
Jauch, A., 38
Java, Indonesia, 27
Javanese primates, 105
Javan or silvery gibbon, *see Hylobates moloch*
Jennions, M.D., 327
Jepson, P., 453
Jiang, X., 4, 212, 273, 348
Jiang, Z., 486
JICA, *see* Japan International Cooperation Agency
Johnson, A., 397
Johnson, K., 327

Johnstone, R.A., 366
Jolly, A., 215, 348
Jones, W., 490
Jordano, P., 198
Joshi, A.R., 201
Junge, R.E., 486
Jungers, W.L., 134, 136, 139

K

Kalaweit Gibbon and Siamang Rehabilitation Project, 485
Kalimantan, 135
Kapos, V., 255, 256
Kappeler, P.M., 66, 92, 96, 104, 137, 140, 213, 215, 222, 225, 242, 243, 248, 280, 285–286, 291, 293, 347, 348
Karesh, W.B., 479, 490
Karig, D.E., 65, 73
Katz, A., 486
Kawabe, M., 52–53
Kawamichi, T., 285, 289, 293, 294, 298, 299, 302
Kay, R.F., 153–154, 211
Keith, S. A., 4, 7, 17, 51–68, 83, 85
Keller, L., 366
Kelley, J., 123–124, 256
Kempenaers, B., 289
Kent, M., 412
Kerby, J., 350–351
Kerinci-Seblat National Park (KSNP)
  gibbon population status and distribution in
    biomass in, 461
    density estimates and distribution in, 458–459, 461–463
    group sizes for, 459–460
    study sites and methodology for, 454–456
Ketambe, 4
Khan, M.R.A., 407
Khan, M.Z., 314, 323
Khao Yai National Park, gibbons in
  mating system of
    females and males, mating strategies of, 362–363
    sexually active gibbons in, 359–360
    variable social organization and mating system in, 363–368
    mixed species groups, 351–2
    social groups and solitary individuals, identification of, 354–356
    social organization of, 356–357
  multimale polyandry, resource distribution and territorial/female defense, 367–368
  social organization and mating system of, 348
  sociosexual flexibility and advanced cognitive abilities of, 370–372
Khao Yai National Park, 4, 20, 249
  daily path length and home range size, 269–270
  daily path length, variation in, 271
  defendability, 271–272
  maximum number of defendable females, 272–273
  resource abundance and rainfall, 266, 268–289
  study site and animals in, 266
Kierulff, M. C. M., 481, 486–487, 490
Kilbourn, A.M., 486
Kim, H., 44
Kingdon-Ward, F., 438
Kinnaird, M.F., 329
Kinzey, W.G., 216
Kishimoto, R., 285, 289, 293–294, 298–299, 302
Kitamura, S., 193, 198, 350
Kitchener, A.C., 64–66, 74, 85
Kit fox, *see Vulpes macrotis*
Kleiber, M., 134
Kleiman, D.G., 221, 279, 285, 291, 294, 302, 327, 328, 348, 479–481, 486–487, 489
Kloss, C. B., 52–53, 65, 74
Kloss's gibbon, *see Hylobates klossii*
Knott, C.D., 181–182
Kobold, S., 73
Kocher, T.D., 76
Koehler, U., 38
Koenig, A., 156
Koenig, W.D., 367
Kokko, H., 327, 340
Komers, P.E., 213, 214, 222, 223, 225, 231, 280, 285, 290–291, 294, 302, 305
Konrad, R., 4, 51, 64, 91, 387, 402
Konstant, W.R., 486
Krau Game Reserve, Malaysia, 162
Krebs, C.J., 392
Kudo, H., 347
Kurland, J.A., 52
Kutai National Park, 165
Kyoto University, Japan, 38

L
Laccopithecus, 112
Laccopithecus robustus, 26, 112
Lactation, in *Symphalangus syndactylus*, 331–332
  See also Symphalangus syndactylus
Lagerstroemia spp., 400
Laland, K.N., 253
Laman, T.G., 166
Lambert, J.E., 134, 244
Lambert, F.R., 201
Lan, D.– Y., 125, 134, 136–137, 140–141, 151, 248, 251
Langurs, *see Semnopithecus phayrei*
Lappan, S., 3–9, 124, 137, 139–141, 152, 212, 224, 248–250, 272–273, 285, 293–294, 297, 300–302, 327–341, 349, 350, 364, 366–371, 426
Late Miocene, 26, 28, 29, 123, 126, 127
Lawes, M.J., 162
Lazaro-Perea, C., 369
Ledbetter, D.H., 38
Legok Heulang Research Station, Java, Indonesia, 4
Leigh, S. R., 124, 337
Leighton, D.R., 51, 92, 181, 217, 231, 245–248, 265, 279, 301, 348, 350, 365, 367, 398
Leighton, M., 161–168, 180, 181, 182, 192, 193, 196, 198, 212, 214, 217, 220, 222, 243, 245–246
Lembaga Ilmu Pengetahuan Indonesia (LIPI), 38
Leontopithecus spp., 297
Leontopithecus rosalia, 480–481
Lepilemur edwardsi, 294, 295
Lepilemur ruficaudatus, 289, 300
The Lesser Apes: Evolutionary and Behavioural Biology, 3
Levine, J.M., 190
Levin, S.A., 190
Levins, R., 163–164, 242
Lewontin, R.C., 242
Lickliter, R., 487
Life history parameters, 124
Lifjeld, J.T., 339
Ligon, J.D., 299
Limited Production Forest, 86
Limnopithecus, 112
Lindburg, D.G., 486
Lindenmayer, D.B., 479, 486
Lindsey, N., 167
Line transect method, for gibbon estimation, 456
Linn, Z., 435
Listening area, definition of, 442
Listening posts, 441
Longo, S.B., 241–242
Long-tailed parakeets, specialized in frugivory, 170
Long, V., 27
Lowe, J.J., 29
Lowen, C., 272, 301
Low fruit periods (LFP), 176
LPs, *see* Listening posts
Lucas, P.W., 192, 201
Lufeng deposits, 26
Lundberg, A., 301, 348
Lycaon pictus, 288, 289, 301, 486
Lynam, A.J., 350

M
Macaca assamensis assamensis, 468
Macaca fascicularis, 165, 219
Macaca leonina, 468
Macaca mulatta, 439, 468
Macaca nemestrina, 165, 216
Macaca pagensis, 52, 64, 74
Macaca pagensis siberu, 74
Macaca siberu, 64
Macaques, 8
Macaranga spp., 193
MacArthur, R.H., 161, 163–164
Macdonald, D.W., 327
Macedonia, J.M., 91
MacKinnon, J.R., 133–138, 139–141, 154, 179, 216, 219, 297, 462, 479
MacKinnon, K.S., 133, 135–137, 139–141, 154, 179, 216, 219, 297, 454
Maddison, D.R., 77
Maddison, W.P., 77
Madoqua kirkii, 289, 293
Maeda, T., 92
Mahady, S., 288, 296
Mahamyaing Wildlife Sanctuary, *H. leuconedys* census in, 436, 448–449
  forest canopy cover, 446
  gibbon densities and forest condition, 446–448
  group densities in, 443, 445
  mean group and total population size assessment, 445–446
  workshop and training exercises, 439–440

Malagasy giant jumping rat, *see Hypogeomys antimena*
Malagasy strepsirhines, 135
Malcolm, J.R., 327
Male parental care, importance of, 221
Malone, N.M., 5, 6, 212, 241–258, 340–341, 364, 366, 370, 371
Manly, B.F. J., 58, 169
Mann-Whitney U tests, 139
Mano, T., 52–53
Manullang, B.O., 485
Manu National Park, Peru, 162
Marbled cat, *see Pardofelis marmorata*
Markham, R., 124
Marler, C.A., 328
Marler, P., 92
Marlowe, F., 327–328
Marshall, E.R., 14, 15, 51, 95, 137
Marshall, A.J., 133–134, 140, 147, 161–183
Marshall, J.T., 14, 15, 18, 21, 37, 40, 51, 53, 92, 93, 95, 105, 133, 135, 137, 435–437
Marsh, C.W., 456, 461, 462
Marsh, H.D., 286, 461, 462
Martarinza, M., 478
Martin, P.M., 330, 357
Martins, M.M., 339
Ma, S., 15, 22
Masataka, N., 91–92
Mate competition theory
  female mates resources, 229–230
  in gibbon, 214
  male and female, territoriality and resources competition in, 230–231
  mate-guarding and monogamy, 231–232
  parental investment and mate competition, asymmetry of, 228–229
Mather, R., 22, 51, 92, 245, 477
Mating system, of Khao Yai gibbons
  females and males, mating strategies of, 362–363
  sexual behavior data collection, 357–359
  sexually active gibbons in, 359–362
  variable social organization and mating system in, 360–365
Matthews, L.H., 317
Matthew, W. D., 15, 120
Maynard, Smith, J., 154
McConkey, K.R., 4, 7, 134, 135, 137, 140, 141, 163, 179–180, 189–204, 220, 245–246
McFarland, M.J., 216
McGrew, W.C., 258, 339
McGuire, B., 285, 296, 299–300
McInroy, J.K.E., 328
McKenny, B., 389
McKey, D.B., 163, 189
McKnight, S.K., 163
McNeely, J.A., 73
McPhee, M.E., 487
Meehan, H.J., 196
Meijaard, E., 481, 499
Mekong river, in Yunnan Province of China, 118
Meldrum, D. J., 26, 112
Melnick, D. J., 74
Menken, S.B.J., 397
Mentawai Islands, in Southeast Asia, 52
  and nonhuman primates endemic to, 52, 64
  North Pagai, 74
  primate species in, 74
  sampling sites in, 75
  Siberut, 74
  Sipora, 74
  South Pagai, 74
Mentawai langur, *see Presbytis potenziani*
Mentawai leaf monkey, *see Presbytis potenziani*
Mentawai macaque, *see Macaca pagensis*
Merker, B., 66, 94, 95
Micropithecus, 112
Microsatellite DNA (mtDNA), 44, 45, 47
Microtus ochrogaster, 280, 288, 289, 295
Milliman, J.D., 65, 84
Mills, M.G.L., 486
Milne-Edwards sportive lemurs, *see Lepilemur edwardsi*
Milton, K., 163, 216
Mimura, N., 67
Minello, T.J., 487
Miocene hominoids, 112
Mirmanto, E., 191
Mitani, J.C., 91–92, 135, 166, 216, 222, 225, 227–228, 231, 248, 267–268, 271–272, 279, 290, 295, 301, 348, 350, 365, 367, 462, 463
Mitered leaf monkeys, *see Presbytis melolophos*
Mitiri, M.N., 189–190, 193, 200
Mittermeier, R. A., 486, 501
Moe, A., 435
Moe, T. K., 435
Möhle, U., 316
Mohnot, S.M., 407, 412

Molecular clock estimates, 113
Møller, A.P., 348
Molur, S., 411, 425, 435–436, 499
Monfort, S.L., 490
Mongoose lemur, *see Eulemur mongoz*
Monkeys of Siberut and taxonomic distinction between, 53
Monogamy, 5
  definition of, 280–286
  evolutionary causes of, 290–291
    ecology, 294–295
    infanticide, 296
    paternal care, 291–294
    predation risk and reproductive success, 296–297
  in mammals, 279–286, 287
  mechanisms maintaining, 289–290
  social structure and mating patterns
    broader social networks, 300–301
    flexible grouping and mating, 297–300
    relatedness within groups, 300
Moore, A., 290
Moore, G.F., 73
Mootnick, A. R., 15, 37, 136, 251, 317, 407, 435, 486
Morino, L., 5, 279–302, 313, 329, 366
Moritz, C., 83
Morland, H.S., 285
Morley, R. J., 29, 124
Morris, R.C., 53
Morse, D.H., 154
Mo Singto – Klong E-Tau, gibbon in, 350–351
  See also Khao Yai National Park
Mound-building mice, *see Mus spicilegus*
  and pup retrieval behavior, 291
Moustached tamarins, *see Saguinus mystax*
Mueller-Dombois, D., 191, 412
Mukherjee, R.P., 248, 251–252, 421
Müller, A.E., 347
Müller, K.-H., 272
Muller-Landau, H.C., 190, 200
Müller, S., 38, 136
Multidimensional scaling (MDS), 58
Multifemale gibbon groups, formation of, 375–376
Multimale gibbon groups, formation of, 372–375
Multimale polyandry, in Khao Yai gibbons, 368–369
Mundinger, P.C., 92
Muntiacus muntjak, 439
Murray, C.M., 163
Murrell, D.J., 190
Mus spicilegus, 289, 290, 295
Myristica spp., 193

N
Nadler, R.D., 313–318, 323–324
Nadler, T., 489
Naing, H., 435
Nasalis larvatus, 481
Nathan, R., 190, 200
National Geographic Society Publications Index (NGSPI), 8
National Protected Area, 402
Natuna Island, 121
Nature and Wildlife Conservation Division, 436
Neff, B.D., 290, 339
Nei, M., 76
Nephelium rambutan-ake, 194
Ness, J.W., 487
Nettelbeck, A.R., 217, 223–224, 489
Neudenberger, J., 353–354
Nguyen, Cu, 387, 401, 499
Nguyen, D. H., 122
Niche divergence, 165
Niche overlap and impact on resource availability, 135
Niche partitioning and resource overlap, *see* Evolutionary Niches
Nievergelt, C.M., 285, 287, 289, 297–300
Nie, W., 38
Nijman, V.H., 4, 73, 92–93, 255, 397, 477, 478, 481, 499
Nikolei, J., 52–53
Nixon, K.C., 77
Noble, R. A., 121–122
Nomascus concolor, 247–248, 273, 348, 397
  Nomascus concolor concolor, 17
  Nomascus concolor furvogaster, 17
  Nomascus concolor jingdongensis, 17
  Nomascus concolor lu, 17
Nomascus, features of, 247–248
Nomascus gabriellae, 17
  conservation, 387
  habitat requirements of, 398–400
  site population estimates and population trends, 400–403
  vocal behavior, 397–398
Nomascus leucogenys, 17
Nomascus leucogenys siki, 17
Nomascus siki, 17, 404, 498
Nomascus nasutus, 8, 500, 501

Nomascus hainanus, 8, 500, 501
Nomascus leucogenys, 402
Nomascus spp., 3, 4, 14, 64
Norconk, M.A., 216
North American beaver, *see Castor canadensis*
North Pagai Island, 52, 74
Norusis, M.J., 58
Nottebohm, F., 92
Nowak, R.M., 13
NPA, *see* National Protected Area
Nunes, S., 339
Nunn, C.L., 366, 397–398
Nurcahyo, A., 134, 137, 139, 141, 152, 329, 334
NWCD, *see* Nature and Wildlife Conservation Division
NWRA, *see* American National Wildlife Rehabilitation Association
Nycticebus bengalensis, 468
Nycticebus coucang, 289, 295

O

Oates, J. F., 91, 163, 181, 216
O'Brien, T.G., 7, 135–136, 155, 182, 248, 256–257, 328–329, 337–338, 391, 397, 449, 461–463
Odling-Smee, J., 253
Oka, T., 285, 286, 287, 300
Oktavinalis, H., 253
Old World monkeys, 52
Olsen, J. W., 112–113
Opdyke, N.D., 29
Orange-necked partridge, *see Arborophilia davidi*
Orangutans, 8, 199–202, 347
Orgeldinger, M., 124, 290, 301–302, 348
Oring, L.W., 213–214, 221, 230, 243, 265, 327
Osborn, T., 387
Ostner, J., 316, 322
Overdorff, D.J., 267, 285, 291–293
Owens, I., 349
Oyama, S., 244

P

Paciulli, L.M., 53–54, 73–74, 85–86
Packard, J.M., 288
Pagai Islands, 74, 75, 86
Paleo-Malacca river, 123
Paleo-North Sunda river, 123
Paleo-rivers of Sundaland, courses and drainages of, 122
Paleo-Siam-Chao Phyra river, 121
Paleo-South Sunda river, 123
Palombit, R.A., 133–135, 137, 140–141, 150, 155, 212, 215, 224, 226, 231, 241–244, 246, 248–250, 252, 255–267, 272–273, 286, 291, 294, 296, 297, 300–302, 328, 340, 349, 364, 366, 369, 371
Panthera tigris, 389
Pan troglodytes, 490
Pan, Y., 26, 112
Paoli, G.D., 166
Papio spp., 8, 162
Pardofelis nebulosa, 389
Pardofelis marmorata, 389
Parental investment (PI) and mate competition, in gibbon, 228–229
Parental investment theory, 213–214
  resource territoriality, evidence for, 227–228
  territorial defense mate, 225–227
  types of investment, 220–221
    grooming, 223–224
    guarding against predators, 223
    infanticide, protection against, 224–225
    play and infant carrying, 224
    territorial resource defense, 221–223
Parker, G.A., 367
Parsons, R.E., 53
Parus major, 226
PA, *see* Protected areas
Paternal care
  in monogamous mammals, 292–293
  and monogamy, 291–294
  See also Monogamy
Paterson, H.E.H., 161
Patris, B., 285, 290, 291, 293, 299
Pavo muticus, 389, 391
Payne, J.B., 167, 192, 198
Pearl and Red Rivers, 120
Peart, D.R., 166
Percival, S., 484
Pereira, H.M., 66, 231
Peres, C.A., 155, 162, 165
Perlindungan Hutan dan Konservasi Alam (PHKA), 38
Perodicticus potto edwardsi, 280
Peromyscus californicus, 292
Perwitasari-Farajallah, D., 37
Peters, S.A., 92

Petrie, M., 289
Petrogale assimilis, 286, 289, 291
Petropseudes dahli, 291, 294
Pfeyffers, R., 52–53
PGRP, *see* Phuket Gibbon Rehabilitation Project
Phaner furcifer, 289, 295
Phillips, K.A., 216
PHKA, *see* Indonesian Department of Forestry and Nature Conservation
Phoonjampa, R., 441, 448, 449
Phrase, single vocal activity, 54
Phuket Gibbon Rehabilitation Project, 481
Phylogenetic relationships, in gibbons, 22
  divergence dates issues, 25–26
  great ape-gibbon split, 25–26
  molecular phylogeny in, 26
  phylogenies based on morphological and molecular characters, 23
  relationships among the concolor groups, 22–23
Phylogenetic Species Concept (PSC), 77
Pianka, E.R., 163, 165, 181
Piedade, H.M., 272
Pig-tailed langur or simakobu, *see Simias concolor*
Pilbeam, D., 124, 154
Pimley, E.R., 285, 293, 297
Pizo, M.A., 199
Platnick, N.I., 77
Platodontopithecus, 26, 112
Pliopithecidae *(Pliopithecus)*, 112
Poirier, F. E., 27, 113
Põldmaa, T., 367
Polet, G., 387, 400
Polygynous mating system, in primates, 348–349
Polyplectron germaini, 389
Population aggregation analysis (PAA), 77
Population reintroduction, definition of, 479
Population simulation models, for hoolock gibbons, 425
Population viability, in hylobatid communities, 254–258
  See also Hylobatid communities
Porter, C. A., 26
Posada, D., 76
Post, E., 161
Poulson, J.R., 162, 164
Prairie dogs, *see Cynomys gunnisoni*
Prairie voles, *see Microtus ochrogaster*
Pratt, T.K., 201
Presbytis comata, 105
Presbytis melalophos, 219, 334
Presbytis potenziani, 52, 64, 74, 280
  Presbytis potenziani potenziani, 64
  Presbytis potenziani siberu, 74
Preuschoft, H., 3, 14, 24, 53, 136, 211–212, 256
PRF, *see* Proposed Reserved Forests
Price, E.C., 272, 301, 339
Price, E.O., 487
Price, S.M.R., 479
Primate fruit, 194, 196
Primate Research Center, Bogor Agricultural University, Indonesia, 38
Primate Research Institute, 38
Proboscis monkey, *see Nasalis larvatus*
Procolobus kirkii, 481
Proconsulidae, 112
Propliopithecus, 112
Proposed Reserved Forests, 413
Protected areas, 436
Prouty, L.A., 14, 15, 435
Proximate cues and male parenting behavior, 339
Pruett-Jones, M., 485
Prunus javanica, 194
Pseudibis gigantea, 389
PT Minas Pagai Lumber Corporation, 74
PT Minas Pagai Lumber logging concession, 86
Purvis, A., 22, 23
Pygathrix nigripes, 389, 397
Pyke, G.H., 165

Q
Qinghai-Xizang (Tibetan) Plateau, 125

R
Raaum, R.L., 26
Rabinowitz, A.R., 196, 201, 438
Radespiel, U., 135
Raemaekers, J. J., 124, 133–137, 139–141, 154–155, 162, 165, 211–212, 216, 219, 221–222, 246, 248, 250, 253, 265–267, 271, 290, 328, 332, 338, 349, 353, 355, 367, 372–373, 375–376, 397, 400, 462, 488
Raemaekers, P.M., 222, 290, 328, 353, 397, 400
Ralin, D.B., 91
Ralls, K., 285, 300–301

Rankin, D.J., 327
Rao, S.S., 467
Rasoloharijaona, S., 285, 294–295
Ravosa, M.J., 154
Rawson, B.M., 7, 387–403, 499
Red-bellied lemur, *see Eulemur rubriventer*
Red-tailed sportive lemurs, *see Lepilemur ruficaudatus*
Reed, K.E., 155, 162
Re-establishment of population, definition of, 479
Reeve, H.K., 366
Reeve, N., 353
Rehabilitation of gibbons, 481–483
  difficulties of, 483–484
  global outlook on, 479–480
  post-release monitoring, 489–491
  pre-release plannings for
    behavioral assessment before release, 486–487
    site selection for, 487–489
  of wild *vs.* rehabilitant gibbons, 484–485
Reich, A., 288
Reichard, U., 4, 5, 212–214, 217, 222–226, 230, 242–243, 248, 249, 254, 255, 258, 266, 268, 272–273, 286, 290, 294–295, 297, 301, 313, 315, 340–341, 347–374
Reintroduction of population, success determination of, 480
Rendall, D., 347
Renton, K., 163
Reproductive effort (RE), 229
Reproductive status of *H. lar*
  hormone concentrations in, 321
  hormone profiles in, 318–320
Reserved Forests, 413
Resource use patterns, of hylobatid communities, 246–249
  See also Hylobatid communities
Rey, P.J., 197
RF, *see* Reserved Forests
Rhesus macaque, *see Macaca mulatta*
Ribble, D.O., 285, 287, 293–294
Richard-Hansen, C., 489
Richardson, P.R.K., 366, 499
Richards, P.W., 189
Rijksen-Graatsma, A.G., 477
Rijksen, H.D., 199–200, 453, 482
Robbins, D., 241
Robbins, A.M., 347
Robbins, M.M., 347
Roberts, R.L., 285, 299
Robson, C.R., 387, 401
Rock-haunting possum, *see Petropseudes dahli*
Rock-wallaby, *see Petrogale assimilis*
Rödel, H.G., 163
Rodents, 191
Ronquist, F., 30, 76–77
Roos, C. I., 15, 22, 23, 37, 52, 64–66, 74, 77, 106, 120, 136, 212, 435
Rosell, F., 285, 293, 302
Ross, C., 66, 85, 353
Rotundo, M., 291
Round, P.D., 266
Rourea minor, 194
Roy, K., 125
Rubenstein, D.I., 230
Rufous lemur, *see Eulemur fulvus rufus*
Ruggeri, N., 401, 402
Runcie, M.J., 285, 291, 293, 294–295
Russo, S.E., 189, 193
Rutberg, A.T., 214, 216, 279, 285, 291, 305
Ryder, O.A., 77

S
Sæther, B., 161
Saguinus spp., 162, 297
Saguinus mystax, 298
Saitou, N., 76
Salween river, 118
Sambar, *see Cervus unicolor*
Sangchantr, S., 285
Santiria, 196
Santos, C.V., 339
Sapolsky, R.M., 490
Savini, T., 223, 226, 227, 266, 353, 368, 371, 376
Saw, C., 435
SBCA, *see* Seima Biodiversity Conservation Area
Schilling, D., 51, 92, 375
Schneider, S., 44, 78
Schoene, C.U.R., 482
Schoener, T.W., 161, 163–165
Schradin, C., 339
Schülke, O., 219, 227, 285, 287, 289, 293, 295, 296, 348, 363
Schultz, A.H., 13–14
Schupp, E.W., 189
Schwab, D., 347
Schwarzenberger, F., 316
Sebastian, A.C., 52–53

Seddon, N., 366
Seed dispersal by gibbons, in Bornean dipterocarp forests
        fruit and plant types, species over/under-selected and not eaten, 194
        plant species consumed by gibbons, 195
    diet overlap with
        hornbills and barbets, 196
        Prevost's squirrel, orangutans, and macaques, 195
    dispersal of lianas with primate fruits, 201–202
    dispersal modes by different frugivore taxa, 199
    dispersal niche of gibbons and its overlap, 202
    and enhancement of gene flow, 190
    food plants selection, and frugivore's seed dispersal niche, 192–193
    frugivores in, 191–192
    frugivores influence on survival probability of seeds, 198
    fruit types categories in, 193–197
    main seed dispersal agents in, 192
    role and comparison with other frugivorous animals, 190, 196–197 seed depositions and distances covered, 199–200
    seed dispersers and coevolutionary relationships, 189
    size of seed and impact on dispersal, 196–197
    smaller fruit patches role, 197–198
Seed dispersers, effective, 200
Seed predation and seed death, 198
Seed predators, 191–192
Seima Biodiversity Conservation Area, 387
    Nomascus gabriellae conservation in
        intensive study plots, monitoring methods, 390–391
        outcomes of intensive study plots, 392–395
        site population estimates, 390–392, 395–397, 401–403
        site population trends, 389–390, 395–397, 400–401
        study site, methods of, 388–390
Senior, B., 397
Sexual relationships, in primates, 347–348
Sexual selection, in gibbon, 215–216
Shackleton, N.J., 29
Shafer, C.L., 85
Share, L.J., 490
Sharman, M., 224
Sharpe, F., 285, 293, 302
Shea, B., T., 337–338
Sheeran, L. K., 137, 140, 141, 248, 250, 348, 485, 488
Sheldon, B.C., 339
Sherman, P.W., 290
Siamang, *see Simia syndactyla*
Simia syndactyla, 13
    body mass, 134
    competitive advantage over smaller gibbons, 154
    diet and differences with other gibbons, 138, 143, 150–151
    fig seekers, 13, 133
    habitat, 134
    interbreeding, 135
    interspecific competition with other gibbons, 135
    niche divergence, 135
    as true folivores, 13, 133
Siberut Island, 74
Siberut National Park, 53, 74
Siberut populations, 74
Siddiqi, N.A., 251, 421
Siegel, S., 58
Siex, K.S., 481
Silk, J.B., 348
Sillero-Zubiri, C., 285, 288, 366
Silvered langur, *see Trachypithecus germaini*
Silverman, E.D., 487
Silver, S.C., 84
Silvery gibbon, *see Hylobates moloch*
Simakobu, *see Simias concolor*
Simao, I., 199
Simia concolor, 13
Simia hoolock, 13
Simias concolor, 52, 64, 74
    Simias concolor concolor, 64
    Simias concolor siberu, 64, 74
Simmen, B., 162, 163
Simons, E. L., 112, 154
Sinaga, R.M., 478
Sinakak islet, in South Pagai, 74
Single large or several small (SLOSS) concept, 85
Singleton, I., 347
Sipora, 52
Sipora Island, 74
Siregar, R.S.E., 485
Slagsvold, T., 226
Slater, P.J.B., 92

Slow loris, *see Nycticebus coucang*
Smallwood, J., 200
Smith, B.H., 154
Smith, H.G., 327, 486
Smith, R.J., 134, 136, 139
Smith, T.B., 201
Sneath, P.H., 58, 98
Soave, O., 479
Social group, definition of, 354
Social networks, in monogamous species, 300–301
Social play, in *S. syndactylus*, 334–335
Social preference, importance of, 288
Social structure and mating patterns, in monogamous species
  broader social networks, 300–301
  flexible grouping and mating, 297–300
  relatedness within groups, 300
Socioecology of gibbons, flexibility
  dietary studies, 6
  ecological adaptations and social monogamy, 5
  flexibility limits, 7
  role in ecological communities, 7
  social and mating systems in, 5
Sody, H.J.V., 104–105
Soini, P., 367
Sokol, R.R., 58
Solitary individual, definition of, 354
Soltis, J., 367
Sommer, S., 285, 286, 287, 293, 296
Sommer, V., 212, 214, 223–224, 230, 242, 243, 258, 280, 313, 350, 353, 363, 366, 369, 370
Song bout, 55
Song “series of notes”, 51, 54
Song vocalizations, suitable for reconstructing the phylogenetic relationships, 92
South American platyrrhines, 135
Southeast Asia, 27
  environmental effects of Quaternary glaciations, 29
  gibbons radiation pattern in, 30–32
  paleoenvironmental history of, 27–30
  paleogeography of, 27
South Pagai Island, 52, 74
Southwick, C.H., 456
Species-specific song characteristics, genetically determined, 92
Spectral tarsier, *see Tarsius spectrum*
Spencer, P.B.S., 285–287, 289, 293
Spratt, D.M., 479, 486
Squirrel, 191
Srikosamatara, S., 137, 140, 141, 212, 216, 220, 222, 230–231, 244, 246, 348, 351, 375, 389, 391, 397–8, 402, 441, 488
Srivastava, A., 468
Stacey, P.B., 299, 367
Stanger, K.F., 91
Steenbeek, R., 52–53
Sterck, E.H.M., 298–299
Stevenson, P.R., 135, 162, 164
Stiles, E.W., 201
Stocking reintroduction of population, definition of, 479
Stockley, P., 366
Storm, P., 113
Streicher, U., 489
Strier, K.B., 314
Struhsaker, T.T., 162, 255, 412, 481
Strum, S.C., 162, 181, 486
Stunz, G.W., 487
Sugardjito, J., 14, 22, 37, 39–40, 51, 53, 92–93, 105, 435, 438, 462–463, 486, 487, 489
Sumatra, 4, 16, 17, 27
  gibbon population decline in, 453
Sun bear, *see Ursus malayanus*
“Sundaland” or the Sunda Shelf, 27, 121
Sunda Platform geologic province, 121
Sun, L., 285, 290, 295
Supriatna, J., 93, 105, 106, 485, 499
Sus scrofa, 439
Sussman, R.W., 340
Suwanvecho, U., 223–224, 234, 241, 253, 376
Suwelo, I.S., 454
Swofford, D.L., 44, 76, 78–79
Sympatric hylobatids, 135, 136, 138
Sympatric primates, 135
Symphalangus syndactylus, 4, 14, 249–250, 271, 280, 294, 327–328, 349, 368, 397, 453
  characteristics of, 249–250
  and *Hylobates*, comparison of, 252–253
  infant care, patterns of, 327–328
    infant carrying behavior of female, 332–333
    infant carrying behavior of male, 333–334
    infant survivorship, 337–338
    lactation, 331–332
    males in proximity with infants, 335–336

    - mother and infant, proximity patterns between, 335–336
    - in polyandrous groups and monogamous groups, 337
    - social grooming interactions, 335
    - social play and infants, 334–335
  - population status and distribution of
    - biomass of, 461
    - density estimates and distribution of, 458–459, 461–463
    - group sizes for, 459–460
  - *Symphalangus syndactylus continentis*, 17
- *Systema Naturae*, 13
- Systematics and history, of gibbons, 13–17
  - *See also* Fossil record of gibbons; Hylobatidae
- *Syzigium*, 196

T

- Taggart, S.J., 348
- Takacs, Z., 22–3, 25, 52, 73, 77, 91, 136, 153
- Takenaka, O., 285, 286, 287, 300
- Taman Nasional Kerinci-Seblat, *see* Kerinci-Seblat National Park (KSNP)
- Tamarin, *see Saguinus spp.*
- Tanaka, H., 37, 44
- Tanaka, Hiroyuki, 37
- Tan, C.L., 135, 285
- Tangtham, N., 266
- Tantravahi, R., 38
- Tardif, S., 339
- *Tarsius spectrum*, 280, 297
- Taylor, B.L., 83
- Tchernichovski, O., 92
- Teferi, T., 285, 294, 296, 328
- Tenaza, R.R., 51, 73, 74, 85–86, 92, 214, 248, 301, 348, 461
- Terborgh, J., 213, 216, 231, 367–368
- Terminal Miocene, 113
- Terrestrial birds, frugivory by, 192
- Territorial behavior, definition of, 232
- Territorial defense
  - definition of, 232
  - importance of, 227
  - in Khao Yai gibbons, 368–369
- Territoriality and resources competition, in gibbon, 230–231
- Territorial resource defense, in gibbon, 221–223
- Territory, knowledge of, 216–220
- Testis-specific protein Y-encoded (TSPY) gene, 43, 44
- Thailand, 135
- Thalmann, U., 294, 347
- Thom, M.D., 366
- Thompson, C.J.H., 44
- Thorpe, W.H., 55, 92
- Tichy, H., 285, 286, 287, 293, 296
- Tiger, *see Panthera tigris*
- Tilson, R.L., 51, 92–93, 96, 214, 221, 225, 243, 248, 251–252, 255, 279, 280, 301, 348, 407, 421, 435, 441, 445
- Timmins, R.J., 401–402
- Tordoff, A.W., 401
- Tougard, C., 113
- Townsend, C.R., 161
- *Trachypithecus auratus*, 105
- *Trachypithecus geei*, 481
- *Trachypithecus germaini*, 397
- *Trachypithecus pileatus*, 468
- Traeholt, C., 387–388, 390, 399, 400, 401–403
- Tranh, V.N., 453
- Tran, Q.N., 401
- Traveset, A., 198–199
- Travis, S.E., 299
- Treecuson, U., 355, 372
- Trill phrases, 55
- Trivers, R.L., 213, 214, 220–221, 227–230, 234, 327, 367–368
- Trivers–Wrangham model, in gibbon, 214
- Trocco, T.F., 91
- Tropical forests, ecological role of gibbons in, 4
- Tua Pejat, 74
- Tufted ground squirrels, 170
- Tun, Yin, U., 438
- Tuttle, R.H., 211
- Tyler, D. E., 25–26, 112, 113

U

- Uhde, N.L., 223, 371
- Ujhelyi, M., 370
- Umponjan, M., 137, 140, 141, 155–156
- Ungar, P.S., 103, 134, 162, 192, 196, 219–220
- Urinary estrogen measurements, in *H. lar* reproductive status, 314
- *Ursus malayanus*, 389
- *Ursus thibetanus*, 389

V

- Vallayan, S., 245
- van, Balen, S., 477

van den, Bergh, G. D., 27, 29, 113
van den, Bos, R., 482
van der, Pijl, L., 189, 193
van, Kulik, R. H., 501
van, Schaik, C.P., 5, 213–215, 222–225, 230, 234, 242, 243, 244, 265, 268, 272–273, 280, 286, 291, 295, 296, 337–338, 347, 367, 369–370
van, Tuinen, P., 38, 40, 43, 45–47
Varsik, A., 485
Vasey, N., 135, 267, 285
Verdú, M., 198–199
Vié, J.C., 489
Viggers, K.L., 479, 486
Vigilant, L., 76
Village Reserved Forests, 413
Vincent, A., 221
Vocal differences analysis, 91
Vocalization patterns, songs, 51
Vogler, A.P., 75, 77
Voris, H. K., 121, 122
VRF, *see* Village Reserved Forests
Vulpes macrotis, 301

W
Wahungu, G.M., 135
Wahyono, E.H., 93, 105
Waits, L., 367
Walker, M.J.C., 29
Waller, M.S., 51, 66
Walsh, P.D., 83
Walston, J., 388, 389
Walter, G.H., 161
Wang, Y., 15
Ware, D., 486
Warren, K.S., 486
Waser, P.M., 162, 164–165, 232
Watanabe, K., 52–53
Waterman, P.G., 134, 246
Way Canguk Research Station, Sumatra, Indonesia, 4, 329
WCS-IP, *see* Wildlife Conservation Society-Indonesia Program
WCS, *see* Wildlife Conservation Society
Webb, C.O., 166
Webb, J.N., 327
Weir, J.E.S., 201
Welch, C., 486
Wenny, D.G., 190
West-Eberhardt, M.J., 253
Western hoolock gibbon, *see Hoolock hoolock hoolock* gibbon
Western, J.D., 181
West, K., 134
Westneat, D.F., 366
Whaling, C., 92
Wheatley, B.P., 165
Wheeler, Q.D., 77
Whelan, C.J., 199
White-cheeked crested gibbon, *see Nomascus siki*
White-handed gibbon, *see Hylobates lar*
White, M.J., 47
White-rumped vulture, *see Gyps bengalensis*
White-winged duck, *see Cairina scutulata*
Whitington, C., 190, 216, 353, 355
Whitmore, T.C., 245
Whitney, K.D., 200
Whittaker, D.J., 3–9, 17, 22, 25, 52–54, 64–67, 73–86, 499–501
Whitten, A. J., 51, 65, 66, 73, 74, 84, 134, 137, 140, 141, 221, 248, 314, 453, 488, 489
Whitten, J.E.J., 74
Whitten, P.L., 328
Whittingham, L.A., 340, 348
Wich, S.A., 164, 165, 168, 399–400
Wiens, F., 285, 289, 293, 295
Wiens, J.A., 161
Wijayanto, H., 37
Wildlife Conservation Society, 388
Wildlife Conservation Society-Indonesia Program, 329
Wildlife trade, effects on gibbon population, 477–479
Wild pig, *see Sus scrofa*
Williams, G.C., 214, 215, 367
Willson, M.F., 199
Willughbeia spp., 194
Wilson, C.C., 453, 459, 459, 463
Wilson, E.O., 135, 138
Wilson, W.L., 453, 456, 459, 461, 462, 463
Win, Z., 435
Wittenberger, J.F., 214, 221, 243, 255, 279, 280
Wittig, R., 370
Wolff, J.O., 285, 288, 296, 366
Wolf, J.O., 288, 296
Wong, S.T., 192, 196, 201
Wood, H., 461, 462
Wood, J. W., 124
Woodroffe, R., 221
Woodruff, D.S., 22, 23, 76, 106, 478
World Conservation Union's Red List of Threatened Species (IUCN), 499

World Wildlife Fund 1980, 73
Wrangham, R.W., 162–166, 214, 216, 227, 229–231, 265, 295
Wright, H.W.Y., 328
Wright, P.C., 328, 338
Wright, S., 82
Wu, R.K., 26, 112

X
Xuan, Dang, N., 387, 401–402

Y
Yamagiwa, J., 181
Yamaguchi, A., 92
Yangzi river, 118
Yanuar, A., 7, 367, 397, 453–464
Yap, S. Y., 123
Yasui, Y., 367
Yeager, C.P., 84, 183, 483–484
Yellow-cheeked crested gibbon, *see Nomascus gabriellae*
Ylönen, H., 161
Yongcheng, L., 499
Yunnan Plateau, 120

Z
Zabel, C.J., 348
Zanzibar red colobus, *see Procolobus kirkii*
Zaramody, A., 285
Zar, J.H., 331
Zeeve, S.R., 52–53
Zeh, D.W., 366
Zeh, J.A., 366
Zehr, S.M., 22, 24, 26, 77
Zeitoun, V., 113
Zhang, Y.P., 17, 22, 23
Zhenhe, L., 250
Ziegler, T.E., 314, 316
Zimmerman, J., 386, 391, 398, 400
Zinner, D., 285, 289, 293, 300, 347, 348
Zitzmann, A., 285, 289, 293, 295
Zizyphus sulvensis, 194
Zong, G., 27, 112–113
Zuberbühler, K., 347