

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.

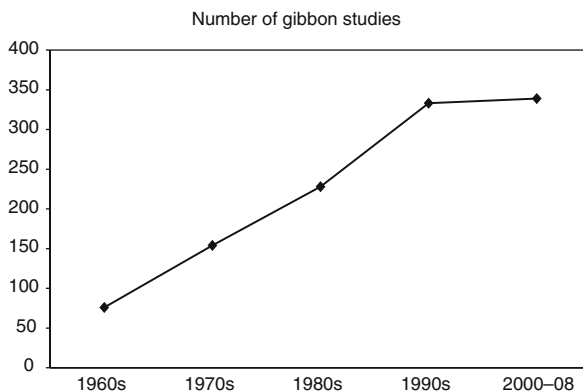
The True Neglected Apes?

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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