REFLECTOR, Center section of large structure six feet in diameter, being used to pick-up gibbon vocalizations

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Gibbon Studies in Thailand

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Primate Studies

วานรศึกษา

ชะนีศึกษาในประเทศไทย

ศาสตราจารย์เกียรติคุณ ดร.วรเรณ บรอคเคลแมน

สถาบันชีววิทยาศาสตร์โมเลกุล มหาวิทยาลัยมหิดล ศาลายา,

ธนาคารทรัพยากรชีวภาพแห่งชาติ (NBT)

สำนักงานพัฒนาวิทยาศาสตร์และเทคโนโลยีแห่งชาติ

Summary

Four of the 20 described species of gibbons occur in Thailand: Hylobates lar (white-handed gibbon), *H. pileatus* (pileated gibbon), *H. agilis* (agile gibbon), and Symphalangus syndactylus (the siamang). No species of the genera *Hoolock* or *Nomascus* occur in the country. Thailand is a special place for gibbon research for two reasons: the first study of wild gibbons was carried out in north Thailand (by C. R. Carpenter, on *H. lar*), and because Thailand has become an important center for gibbon field research and has the longest running research site, in Khao Yai National Park. This article reviews the history of discovery of the gibbons in Thailand, and summarizes the major research findings by both local and international researchers. Khao Yai Park contains the extremely valuable area where two species of *Hylobates* (*lar* and *pileatus*) overlap in a small area of forest in the Tahkong River headwaters. Research in this area has shown that the species interbreed to a limited extent, and although they differ markedly in pelage coloration and song patterns, are virtually identical in their overall ecology and behavior. At the Mo Singto study site in the park, researchers have produced important findings on *Hylobates lar* social group structure, dispersal, pair formation and vocal behavior. Gibbons live in small territorial groups, but because groups may change by the replacement of breeding adults by outside individuals, they are not necessarily nuclear families. Research is continuing on long term trends in group dynamics and demography, especially birth rates. Considerable research is also being devoted to gibbon diet and the role of gibbons in plant seed dispersal. Gibbons inhabit tropical wet evergreen, seasonal evergreen and semi-evergreen forests, but may be adversely affected by global

climate change as it causes increased warming and drying of tropical forests and the loss of important fruit tree species.

Keywords: Gibbons, Hylobatidae, Primates, Thailand

บทคัดย่อ

ประเทศไทยมีชะนี 4 สายพันธุ์ จาก 20 สายพันธุ์ ที่มีการพรรณาบันทึกไว้คือ ชะนีมือขาว (*Hylobates lar*) ชะนีมงกุฎ (*H. pileatus*) ชะนีมือดำ (*H. agilis*) และชะนีเซียมัง (*Symphalangus syndactylus*) ไม่มีสายพันธุ์ชะนีใดจากสกุล *Hoolock* หรือ *Nomascus* ประเทศไทยเป็นสถานที่วิเศษสำหรับการวิจัยชะนีด้วยเหตุผลสองประการคือ มีการศึกษาชะนีในป่าเป็นครั้งแรกในภาคเหนือของประเทศ โดย C.R. Carpenter ผู้ศึกษาชะนีมือขาว และต่อมาอุทยานแห่งชาติเขาใหญ่ได้กลายเป็นศูนย์ศึกษาวิจัยชะนีภาคสนามที่สำคัญยิ่งที่มีการใช้งานอย่างต่อเนื่องยาวนานที่สุด บทความนี้ทบทวนรวบรวมประวัติการค้นพบชะนี และสรุปการค้นพบที่สำคัญโดยนักวิจัยชาวไทยและชาวต่างประเทศ อุทยานแห่งชาติเขาใหญ่ครอบคลุมพื้นที่ที่มีคุณค่ามากที่สุดด้วยเหตุที่มีชะนีสองสายพันธุ์ (*H. lar & H. pileatus*) คือชะนีมือขาวและชะนีมงกุฎ อยู่อาศัยในอาณาบริเวณที่ค่อนข้างเล็กของป่าในบริเวณต้นน้ำลำตะคอง ผลงานวิจัยในบริเวณนี้แสดงว่ามีการสืบพันธุ์โดยผสมข้ามสายพันธุ์โดยจำกัด ถึงแม้ว่าชะนีสองสายพันธุ์นี้แตกต่างกันด้านสีขนของร่างกายและเสียงเพรียกร้องก็ตาม มันยังมีพฤติกรรมและใช้ระบบนิเวศที่เหมือนกัน

การวิจัยภาคสนามที่มอสิงโต อุทยานแห่งชาติเขาใหญ่นั้น นักวิจัยได้มีผลงานของการค้นพบที่สำคัญเกี่ยวกับชะนีมือขาวมากมาย ได้แก่ โครงสร้างของกลุ่มที่เป็นครอบครัว พฤติกรรมการเพรียกร้อง การละทิ้งครอบครัวไปจับคู่เพื่อตั้งครอบครัวใหม่ โดยปกติแล้วชะนีอยู่เป็นกลุ่ม เรียกได้ว่าครอบครัว ซึ่งมีอาณาเขตของกลุ่มเอง แต่สมาชิกในครอบครัวอาจเปลี่ยนแปลงได้เพราะมีตัวเต็มวัยที่อาจเป็นตัวผู้หรือตัวเมียจากกลุ่มอื่นเข้ามาแทนที่ ในปัจจุบัน

การวิจัยด้านพลวัตของกลุ่มและประชากรของชะนียังเป็นไปอย่างต่อเนื่องในระยะยาวมากขึ้นอีก โดยเฉพาะอย่างยิ่งอัตราการเกิดของลูกชะนี การหาอาหารและบทบาทของชะนีในการกระจายเมล็ดผลไม้ เมล็ดพันธุ์พืชของป่าดิบชื้น ป่าดิบกึ่งชื้น และป่าดิบตามฤดูกาลอันเป็นที่อยู่อาศัยของชะนี พฤติกรรมดังกล่าวนี้ อาจกำลังเปลี่ยนแปลงเนื่องมาจากผลกระทบจากสภาวะการเปลี่ยนแปลงของสภาพภูมิอากาศ ทำให้อุณหภูมิของป่าสูงขึ้น ป่าแห้งแล้งมากขึ้น ต้นไม้ที่ให้ผลไม้และอาหารสำคัญของชะนีก็ค่อย ๆ หมดไป

คำสำคัญ: ชะนี, ไฮโลบาติดี, ไพรเมต, ประเทศไทย

Introduction

Of the approximately 15 species of primates in Thailand, four are gibbons, or “lesser apes”, in Family Hylobatidae (Table 1). This includes three species in the genus *Hylobates* (*H. lar*, *H. agilis* and *H. pileatus*) (Figures 1–5) and the siamang, *Symphalangus syndactylus* (Figure 7). The siamang mostly occurs in Peninsular Malaysia and on Sumatra, but occurs near the southern border with Malaysia in Hala Bala Wildlife Sanctuary. There are no members of the gibbon genera *Hoolock* (which occurs west of the Salween River) or *Nomascus* (which occurs east of the Mekong River) in Thailand.

In this article I will attempt to give a brief history of scientific research on gibbons in Thailand, in which I have played an active role. My main activities as a gibbon researcher in Thailand (particularly in Khao Yai Park) have been detailed in a brief biographical article (Brockelman 2013). I am less knowledgeable about research on other primates such as macaques and langurs (leaf monkeys), and will defer to other scientists to describe the history of research on these groups. Many scientists and their students have been involved in gibbon studies here, and

I will not attempt to discuss everyone's contribution, but only what I consider to be the major events and issues.

Although other countries such as Indonesia and China have more primate species, and gibbons, Thailand has a special importance for the study of gibbons, for two reasons. The first reason is that the first field study ever conducted on gibbons in the wild was carried out in Thailand. The second reason is that more papers have probably been published on gibbons in Thailand than in any other country. Thailand also now has the longest running gibbon study site in Asia, in Khao Yai National Park, which has been active for more than 40 years. However, now other countries such as China, Viet Nam and Malaysia are catching up and there are scientists who study gibbons in all the habitat countries.

The first gibbon study

Studies of primate ecology and behavior in the wild began in the 1930s. One of the first primatologists to look at primates in the wild was the American Dr. Clarence Ray Carpenter, who pioneered in the study of howler monkeys and spider monkeys on Barro Colorado Island, Panama. 1n 1937, he mounted an expedition to Southeast Asia with several other anthropologists to study and collect primates, especially gibbons in Thailand. His resulting monograph, "A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*)", was published in 1940. (Carpenter 1940) It is a classic work, and it established the basic character of the social structure and behavior of the white-handed gibbon that has proven to be accurate and has led to many additional studies on different species in other countries of Asia. Carpenter's field study lasted only

three months, and was carried out at Doi Chiang Dao (now a wildlife sanctuary), in northern Thailand. Carpenter observed 21 groups of gibbons in forest patches at the base of the big mountain. Sadly, there are no more gibbons left in that area now, because all the forest patches in the lowlands have been cleared, and the remaining gibbons have been hunted out by local tribal and Thai residents.

After observing the gibbons in the wild, Carpenter and his anthropologist colleague Harold J. Coolidge (from Harvard University) shot 24 individuals from his study groups, and more from other places, to obtain scientific museum specimens. The skeletons of these specimens are still kept in the Peabody Museum of Harvard University, where they have provided most of the information that we have about the size and anatomy of the species. In no country are researchers allowed to collect primate specimens in this manner today, but in 1937 it could be justified by the need for new studies of the structure and evolution of gibbons and all other primates, about which little was known at the time. Besides, in the 1930s gibbons and other primates were still abundant in the forests all over most of Thailand, whereas today nearly all species are classified as "Endangered" with extinction.

Carpenter's findings

What did C. R. Carpenter discover about the behavior of wild gibbons? He found that gibbons were unlike any of the monkeys and apes, as known at the time. Most monkeys and apes live in large groups that roam over large areas of forest or savannah habitat in search of food. They have rather complex social behaviors and dominance hierarchies that regulate the collective behaviors and

dynamics of the group. This was seen in captive groups in zoos and primate study centers, and was beginning to be documented in the wild. Carpenter found, however, that his gibbon groups were small (about four individuals, on average) and mostly consisted of a mated pair of adults and their offspring. They were highly territorial, and defended relatively small areas (much less than one square kilometer) of the forest for their own use. They defended their territories by chasing back and forth across the (unmarked) boundaries, and also seemingly by a large amount of calling and singing. They were the most vocal and noisy of all primates. Their diet consisted mostly of succulent, ripe fruits of trees.

The male and female of a gibbon group were appeared to be devoted to each other, and spent a lot of time grooming and singing together. Carpenter recorded and attempted to describe the form and context of their vocal sounds, and identified nine different call types. Without access to his original sound recordings, we cannot figure out in some cases what calls he was describing. Although Carpenter identified the common loud vocalizations if the adults as "Type I" and "Type II" calls (the great call and the shorter male phrase, respectively), he did not recognize these calls as integral parts of the highly stereotyped duets that mated gibbons give. It was not until the subsequent work of John Ellefson on the white-handed gibbon in Malaysia (Ellefson 1974) that the organization of the duet was better understood. During the duet bout, the female sings series of hoots called "great calls" at intervals of 1.5 to 2 minutes, which are immediately followed by the male's shorter burst of hoots, sometimes referred to as a coda (a classical musical term). Ellefson's work (a Ph.D. thesis) also supported and extended Carpenter's observations on aggression, territorial behavior, intra-group behavior and food habits. One aspect that both Carpenter and Ellefson addressed

was the problem of how gibbons disperse and form new groups. And how long do pair bonds and groups last? In a single limited study these aspects can only be speculated on. It was not until long term studies of white-handed gibbons in Khao Yai Park were carried out that answers were revealed.

Gibbon phylogeny, then and now

Ellefson's work suggested that the social behavior of a species may be rather uniform throughout its range. But what about other species? Are gibbons all uniformly monogamous and territorial and fruit-loving? The answer to this is somewhat mixed. First, we should address the long-running debate about how many species of gibbons there are. The respected anthropologist Prof. Adolph A. Schultz, in an introductory chapter to Carpenter's monograph, commented that the number could be somewhere between 3 and 12, depending on which authority you consulted. At that time there was no DNA analysis, and limited skeletal material was available.

Dr. Schultz also displayed the prevalent theory of the phylogeny of the primates, in which both humans and gibbons branch off the main ape stem at about the same time, with humans slightly closer to the great apes than to the gibbons. We now know that humans are much closer to great apes than to gibbons and, in fact, are nested *within* the great ape family. There is now no such thing as a "great ape" clade or monophylogenetic group, unless you consider humans to be apes (which most anthropologists now consider humans to be). All "great apes", including the orangutan, are now placed in the family Hominidae along with us (*Homo*) (see Mittermeier et al. 2013 for our current understanding of primate phylogeny). The next closest family is the gibbon family, Hyobatidae

(sometimes called the "lesser apes"), which now has four recognized genera (see Thinh et al. 2010 for a recent treatment). The Hylobatidae diverged from the Hominidae somewhere around 16 million years ago. That's how close we are to gibbons. It is likely that the ancestor of all the apes (Hylobatidae and Hominidae) was a tree-living ape, and that much later the chimpanzee, bonobo, gorillas and humans became more ground-dwelling.

How many species in Thailand?

The three most common species of gibbons in Thailand are in the genus *Hylobates*. The most familiar gibbon to everyone is the white-handed gibbon, *Hylobates lar* (Figures 1, 2), which occurs throughout most of the country except the Southeast. It was Joe T. Marshall, Jr., who established that the pileated gibbon, *Hylobates pileatus* (Figures 3, 4), is the species that occurs throughout the Southeast and also in Khao Yai National Park. Most species of *Hylobates* were once considered by most scientists to be subspecies of *Hylobates lar*, because morphologically they could not be distinguished as separate species (Creel and Preuschoft 1984). Many species were also polymorphic for fur coloration, or polychromatic (Fooden 1969), causing confusion and making it difficult to separate them into clear species. Marshall observed them carefully in the wild, and found that pelage color, and also their vocalizations, clearly separated *lar* and *pileatus* into two distinct species, and that in a small area of Khao Yai Park they intermingled (Marshall et al. 1972) in partial sympatry. ("Sympatry" means that the species' geographic distributions overlap, and hence the species are in contact with one another in the wild. The converse term is "allopatry", meaning that the species' ranges do not overlap.) Joe Marshall and his wife Elsie, who

always accompanied him in the field, showed that all the gibbon species known or suspected at the time had highly distinctive duetted song patterns (Marshall and Marshall 1976). Differences in song pattern appeared to be the most useful characteristics in separating the species of gibbons.

Marshall also mapped out the range of the black-handed or agile gibbon *Hylobates agilis* (Figure 5) in southern Thailand. Paul Gittins, a student from Cambridge University who studied the species in Malaysia (Gittins 1980; 1982), found that the ranges of *H. lar* and *H. agilis* overlapped slightly in the headwaters of the Muda (=Mudah) River in northern Peninsular Malaysia (Brockelman and Gittins 1984), with the agile gibbon extending southward from the Muda to the Perak River which flows southwestward. On the eastern side of the peninsula it was known that *H. agilis* extended southeastward to the Kelantan River. It was not clear how far north *H. agilis* extended, before Marshall (1981) surveyed its distribution in remaining forest fragments in eastern peninsular Thailand with the help of its acoustic song patterns. Marshall found that the agile gibbon extended north into Thailand and was bordered in the west by the Thepha River in Yala Province. It must also occur in the Hala-Bala mountains of Narathiwat and Yala Provinces, but no one has dared to survey most of the area due to the presence of insurgents. Marshall (1981) considered that his findings demonstrated that *H. agilis* was a separate biological species from *H. lar* because it was separated from it on all sides by rivers, and the species did not grade into each other anywhere. The intrusion of *H. agilis* into the range of *H. lar* in the peninsula was a secondary phenomenon (perhaps from Sumatra during a glacial low sea-level stand). Subsequent analysis of DNA has shown that the two species are phylogenetically distinct at the species level (Thinh et al. 2010) despite their morphological similarities.

Later, Treesucon and Tantithadapitak (1997) also discovered that the siamang (Figure 6), as well as the agile gibbon, occurs in the mountains of Bala Wildlife Sanctuary near the southern Thai–Malaysian border. Further survey work in Hala Bala by Nongkaew et al. (2018) has shown that the population of the siamang in Thailand is likely to be less than 100, which by itself is considered to be critically endangered. It is isolated from other larger populations in Malaysia by deforested agricultural areas.

The taxonomy of gibbons and the meaning of "species"

In 1979, the International Primatological Society held its 7th congress in Bangalore, India. It this meeting, several gibbon researchers, including David Chivers, Holger Preuschoft, John MacKinnon and myself, decided that it would be timely to organize an international workshop focused on the ecology, behavior and evolution of the gibbons, as many studies on gibbons had been carried out during the last two decades that should be compared and synthesized into a new and better understanding of the family in the context of all the apes. Prof. H. Preuschoft of Bochum University agreed to pursue the organization and financial support of a relatively small workshop-type meeting in Germany, and in July of 1980 the meeting was held at the renovated Schloss Reisensburg castle in Ulm, southern Germany. It was an extremely productive and enjoyable meeting (especially the informal discussions over delicious white wine), and resulted in the production of a volume covering virtually all aspects of gibbon biology in 46 chapters (Preuschoft et al. 1984). If one could draw any general conclusions from the large amount of research presented in the book, they might be (1) the overall behavioral and ecological similarity of the gibbons; (2) the difficulty of

resolving a consistent phylogeny of the gibbons, due to the morphological and genetic similarity of many of the taxa; (3) the importance of vocalizations and certain pelage characters in distinguishing closely-related forms. Much attention was focused on the lar-group taxa (most of those now placed in genus *Hylobates*), and considerable debate arose concerning whether these should be considered full species or subspecies, with morphologists preferring to call them subspecies, and ecological and behavioral researchers preferring to consider them full species. Clearly, there is disagreement among primatologists as to how one defines a "species". Lar-group species include *agilis*, *lar*, *moloch*, *muelleri*, *pileatus*, and usually *klossii*. This issue was settled convincingly only in the case of *H. lar* and *H. pileatus*, where study of the overlap area in Khao Yai National Park in Thailand showed a preponderance of parental types and limited evidence of interbreeding (Brockelman and Gittins 1984). However, new data presented by Sompoad Srikosamatara (Srikosamatara 1984) showed that the pileated gibbon in Southeast Thailand was virtually the same behaviorally and ecologically as *H. lar*. If *H. lar* and *H. pileatus* are so easily recognizable as species, then why haven't they evolved ecological differences? This is a still a puzzle that impinges on the question of how speciation occurs.

The meeting in Germany in 1980 generally recognized the existence of nine species of gibbons (Brockelman and Chivers 1984). They were all still placed in the genus *Hylobates*; subsequently there were divided into the four existing genera. The number of species has increased over the last decades to 20, with the addition of six new species in genus *Nomascus* (in addition to *N. concolor*), two new species in *Hoolock*, and three new species of *Hylobates* (in addition to *H. muelleri*) on the island of Borneo (see Mittermeier et al. 2013). The additions

have occurred not because new distinct undescribed populations have been discovered, but mainly because existing recognized species have been split into two or more new species. In other words, many populations formerly considered to be subspecies have been elevated to full species. The subspecies of *H. lar* (including *H. lar entelloides* and *H. lar carpenteri* in Thailand, *H. lar lar* in Malaysia and *H. lar vestitus in* Sumatra), however, have not been considered distinct enough to be elevated to species status.

The growth in the number of species of gibbons, and of primates in general, has resulted largely from abandoning of the Biological Species Concept (BSC) by many, if not most, taxonomists. The most common definition of the BSC, developed and most strongly articulated by Mayr (1963), affirms that species are "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". Essential aspects of the BSC are listed by Mayr (1963) as (1) distinctness of populations, (2) species as populations and not individuals, and (3) reproductive isolation. As speciation is a gradual process, it is recognized that intermediate cases will exist, and that natural hybridization may occur between species that are in contact to variable degrees, even between those in sympatry (living in the same area together). However, unlimited hybridization that would swamp out differences between the gene pools should not occur, due to the presence of reproductive isolating barriers (RIB), acting either before fertilization or after (Futuyma and Kirkpatrick 2017). In vertebrates, such barriers commonly consist of visual, acoustic or chemical differences in characteristics important in mating or mate recognition.

Use of the BSC requires that the mechanisms preventing free interbreeding be determined in areas of contact between species in the wild (and not in captivity where conditions are not normal). Thus, it is not easy to apply the test to allopatric populations separated by space or by physical barriers. "Distinctness" is often used as a kind of proxy for evaluating the potential of reproductive isolation. The common practice is to evaluate the degree of morphological or genetic similarity and compare it with that found between closely-related species in parapatry or sympatry. This is an inexact science because the amount of morphological or genetic difference needed to prevent hybridization is variable among taxa and cannot be precisely defined. As a result, many systematists now apply the Phylogenetic Species Concept (PSC) which defines a species as "an irreducible (basal) cluster of organisms diagnosably different from other such clusters, and within which there is a parental pattern of ancestry and descent", as proposed by Cracraft (1989). Professor Colin Groves of Canberra University, our most influential primate systematist in recent decades (now deceased), championed the use of the PSC in primate taxonomy (Groves 2012), including gibbons. This has resulted in the Hylobatidae now comprising a mixture biological species, especially those with clearly different vocal patterns, and allopatric sibling species, or semispecies that are unlikely to be biological species, due to their very close morphological, acoustic and genetic similarity. The three species of *Hylobates* that occur in Thailand, however, all appear to be biological species, based on two contact zones between them, and on acoustic differences in their song patterns. There are very few contact zones between the species of gibbons, which are nearly all allopatric with only one clear case of sympatry (the siamang, which overlaps the ranges of *H. lar* and *H. agilis*). Deforestation of

lowland river valleys has eliminated nearly all places of potential contact between gibbon species, and three species are confined to islands (*Hylobates klossii* on the Mentawai Islands of Indonesia, *H. moloch* on Java and *Nomascus hainanus* on Hainan Island). These species are allopatric and the test of reproductive isolation cannot be directly applied.

The process of speciation

One characteristic of sibling species, in addition to the difficulty of distinguishing them, is that their divergence has occurred within their present ranges. Well-marked biological species, on the contrary, are older and often have changed their ranges in response to environmental change or competition from other species. Contact zones between these species, such as *H. lar* and *H. pileatus* in Khao Yai Park, are regarded as "secondary". Examples of sibling species in gibbons that have diverged in place likely include four species of *Nomascus* in Vietnam, the three *Hoolock* species, and most species of *Hylobates* (excepting *H. albibarbis*) on the island of Borneo.

I have discussed the problem of defining species in some detail because it is important for an understanding of how the species and genera of gibbons evolved, and why they are now distributed as mostly allopatric forms. The use of the PSC has given us an understanding of the relationships and phylogeny of the family, but fails to tell us how gibbon species got to be distributed as they now are, and anything about the genetic, behavioral and ecological relations between them. The PSC, as useful as it has been, faces the same problems and challenges in all other groups of organisms. To study all these aspects, we must

focus our research on interactions between species where they come together in contact zones such as the one between *H. lar* and *H. pileatus* in Thailand's Khao Yai National Park. This relatively small contact area has proved to an exciting laboratory for the study of speciation, and ecological and behavioral relations between species, and considerable research remains to be done there.

***Hylobates lar* and *H. pileatus* in Khao Yai National Park**

The first published observations of gibbons in the area where *H. lar* and *H. pileatus* come into contact were made by Joe T. Marshall and myself during the 1970s. Marshall had observed *H. pileatus* in contact with *H. lar* during the 1960s, but around 1975, in the area east of the Tourism Organization bungalows (now managed by the Department of Parks), Joe and I started hearing gibbons with rather peculiar sounding great-calls and male solos. At first we thought that the gibbon calls might just be individually variable, perhaps depending on the mood of the singer, but that turned out not to be the case. The gibbons with odd calls (for example, great calls intermediate in number of notes between *H. lar* and *H. pileatus*) also had odd-looking pelage (Figure 6). We then realized that were looking at natural hybrids. We started to record their duets and male solos. These natural hybrids were mated adults that duetted in the normal way; a hybrid could be mated to a normal *H. lar* or *H. pileatus* adult, or to another hybrid. Some hybrids tended to resemble and sound more similar to either of the parental species, suggesting that they were probably back-crosses to those species. In other words, the hybrids were observed to be completely healthy and viable.

The association between odd-sounding calls and odd-looking pelage indicates that call patterns are likely to be under genetic control. I accumulated a lot of sound recordings during the 1970s and 80s, and was able to test the hypothesis that call patterns were largely inherited, and not learned from their parents. It had been known from observations of interspecific crosses of gibbons in zoos that hybrids had odd-sounding vocalizations. In Khao Yai, Marshall and I found mixed-species or hybrid groups in which the adults were of unlike genetic type, for example, an *H. lar* and an *H. pileatus*, or one of these mated with a hybrid. In some of these groups, the young female offspring were starting to practice their great calls in synchrony with their mothers' calls. I asked whether these young females were learning their call patterns from their mothers, or inheriting a different, hybrid pattern. The latter turned out to be the case (Brockelman and Schilling 1984); the young females gave calls with a pattern somewhere between that of their mother and the genetic type of their father. They did not learn the great call pattern from their mothers. Each female sang with her own cadence, which was not influenced by the cadence of the other. This remarkable feat shows that the great call is basically a fixed action pattern that is not under the conscious control of the singer. Furthermore, the father's genes influence the development of the daughter's call, even though males do not give these calls during duets. Evidence that great call patterns are inherited was also published by Geissmann (1984), who studied zoo gibbons of the same species.

The finding that song patterns in the Khao Yai gibbons are genetic traits gives us more tools in which to study hybridization and introgression in the contact zone between the species. During the 1970s I surveyed and identified by song the pelage 133 groups in the contact zone, and developed a hybrid index

based on pelage characters (Brockelman and Gittins 1984). Twenty groups were mixed species pairs or contained a hybrid individual, and 19 individuals were judged to have hybrid pelage characters, all of which also had odd vocal patterns. The preponderance of pure *H. lar* and *H. pileatus* individuals in the zone, and the relative rarity of mixed pairs, makes it clear that the gibbons do not pair randomly, and that there is a premating isolating barrier that probably involves behavioral mating preferences. This mating barrier will prevent or reduce the exchange of genes between the species, or introgression of genes from one species into the other. Exactly how much introgression is occurring can only be determined by analysis of individual DNA, because the phenotypes of individuals are affected by the relative dominance and penetrance of alleles, and our ability to discriminate phenotypes is limited.

A certain degree of post-mating isolation also occurs in the contact zone, in which offspring of mixed or hybrid groups may be at some disadvantage. Joe Marshall and I noticed that mixed groups sometimes contained more than one adult female, which were always of unlike types. The average number of young per female averaged less than that of single females in single-species groups. Thus, a confusion or disturbance of the normal mating system of gibbons causes some depression in the average fitness of females in mixed species or hybrid groups.

Study of the genetics of the zone of contact and hybridization have been late in getting started. A study by Matsudaira et al. (2013) discovered mitochondrial haplotypes of *H. pileatus* in some *H. lar* individuals on the western side of the edge of the contact zone, providing evidence for introgression.

A recent study by Darunee Markviriya and colleagues of the Biology Department of Mahidol University (unpublished) analyzed both nuclear and mitochondrial DNA, and found evidence for introgression of *H. pileatus* nuclear DNA, but not mtDNA, into the *H. lar* population, but no evidence of introgression of *H. lar* DNA into the *H. pileatus* population. The reason for this asymmetrical pattern is not known. All phenotypically hybrid individuals showed evidence of admixture of nuclear DNA from the two species. More work needs to be done here combining analysis of vocal characteristics with DNA analysis.

Ecological and behavioral interactions

Studies of the ecological and behavioral relations between *H. lar* and *H. pileatus* have also been carried out, to determine if there any differences between the two species that facilitate their coexistence. A study by Suwanvecho and Brockelman (2012) on aggression and territorial behavior between the species found that the species were interspecifically territorial, which means that their territories did not overlap more than conspecific territories did (both species are territorial in themselves). This means that the species treat each other as ecologically equivalent competitors, and that their ecological niches could be virtually identical. A follow-up study by Asensio et al. (2017), utilizing more groups, including mixed species groups, reinforced this conclusion and also found that their fruit diets did not differ in any significant way. The biogeographical implications of these findings are profound, as they suggest that competition may prevent the species of *Hylobates* from existing in stable sympatry, and explains why the species of gibbons are allopatric. Competition might even have prevented the different genera (*Hylobates*, *Nomascus* and *Hoolock*) from overlapping in

distribution, which is a situation (intergeneric territoriality) virtually unheard of in the vertebrates. But this begs the big question: why haven't the gibbons been able to diverge ecologically so species can live together peacefully, as have the macaques, leaf monkeys, guenons (of Africa) and other genera of monkeys, in which several species can occupy the same forest? I merely pose the question; to answer it would require much digression and speculation.

Studies of behavior of *H. lar* in Khao Yai

Less than one kilometer in the forest west of the Khao Yai National Park visitors' center, a hilly area, inexplicably called "Mo Singto" (lion hill), is densely populated with *H. lar* gibbon groups. Convenient of access, these groups have been the objects of many kinds of research since about 1980, when researchers started to name them and map their territories. "Group A" was the first to be observed, and it consisted of two adults and a juvenile in early 1980, until a new baby was born in late 1980. This infant, called Actionbaby, would be followed throughout its life until its death. All individuals in all groups within an area of about two sq. km would be named and followed to obtain information about births, movements between groups, reproductive status and deaths. There are 12 groups in the Mo Singto under study by our team from Mahidol University and now the National Biobank of Thailand (my current host institution). Additional groups have been studied by other researchers. The Mo Singto population is the most intensively studied gibbon population in Asia, and studies by colleagues from many countries have involved such topics as vocal behavior, group formation, structure and dynamics, dispersal, birth rates, diet, ranging and feeding behavior, and seed dispersal mutualisms. Much work is still in progress and being analyzed

and written up for publication. The number of studies of this populations is too numerous to recount here in detail, so in the remainder of this paper I will cover only some of the noteworthy highlights of Mo Singto research.

The husband-and-wife team of Jeremy and Patricia Raemaekers from Scotland were the first serious researchers at Mo Singto. They studied the vocal repertoire of the "lar" gibbons in detail (Raemaekers et al. 1984), and carried out playback experiments to determine if territory holders were very disturbed by strange duets heard within their territory (they were) (Raemaekers and Raemaekers 1985). The Raemaekers constructed a trail network throughout Mo Singto and mapped most of the groups there, which has greatly aided subsequent research.

Additional studies of vocalizations were later carried out by Clarke (2012; 2015) and Terleph et al. (2015). Clark et al. (2012), taking an informational approach, found that the gibbons respond vocally in distinctive ways to different types of predators, which potentially include pythons, eagles, and large cats. Clarke et al. (2015) also analyzed the structure and context of the low-intensity "hoo" calls that gibbons give in several different circumstances. Terleph et al. (2015) analyzed the acoustic properties of *H. lar* female great calls and found a high degree of individual distinctiveness.

Breeding structure and group formation in *H. lar*

The social group structure and breeding system of gibbons have been a major interest of several researchers at Mo Singto. From earlier, short-term studies of gibbons the close nuclear family-like group composition implied that gibbons were all monogamous. This view began to be challenged, especially

following numerous bird studies that showed, using DNA analysis, that extra-pair paternity of species with varying degrees of paternal care of the young was often a significant cost to the male of the pair, sometimes as high as 50 percent. Was this also the case with gibbons? Ulrich Reichard, who started studies at Mo Singto in 1992, observing three different groups in detail, observed extra-pair copulations (EPC) on several occasions, in which a paired female copulated with a male not her mate (Reichard 1995). Another phenomenon often seen is groups containing extra adult males (see review by Reichard 2009). Without knowing the histories of all the groups, it is difficult to distinguish extra males from maturing subadult males in their natal groups. However, in many cases over the years, the extra males were known not to be maturing members of the groups, and in many cases they were known to be relatives of the breeding male in the group, as a result of various kinds of group disturbances and changes. It is difficult to be sure that an extra male is not a relative of other group members. Having two unrelated adult males in a group would suggest a polyandrous breeding structure rather than monogamy (see reviews by Reichard (2003) of monogamy in gibbons, and of the social breeding system at Mo Singto (Reichard 2009). Some important evidence bearing on this issue was presented by Barelli et al. (2013), who compared the paternity of the primary male mate of the group with that of an extra male present in the group during the conception of an offspring. Of 11 infants born under these conditions, 10 were shown to be the offspring of the primary male. While this confirms that extra-pair paternity can occur, it also supports the idea that monogamy, not polyandry, is the dominant mating system of lar gibbons, even though some groups appear as though they might be polyandrous. Paternity of the dominant male may typically be on the order of 90 percent.

Polygyny, in which a male mates with more than one female in the group, is even rarer in the genus *Hylobates* (although it is common in the genus *Nomascus* east of the Mekong River). Two females carrying infants were once seen in the lar population in Khao Yai, which lasted only a few weeks before one female left (unpublished observations), and another similar situation was seen in *H. pileatus* in Khao Soi Dao Wildlife Sanctuary, which was also probably a temporary arrangement (Srikosamatara and Brockelman 1987).

Are all gibbon groups nuclear families (in which all the young are offspring of the two adults present), or are other compositions possible? This question bears importantly on how new groups form, and how they may change (Brockelman et al. 1998). It was realized as early as 1983, when a young subadult male from Group F entered the adjacent Group A's territory and displaced the resident male, suddenly creating a non-nuclear family. As if to reinforce the point, the new male's two younger brothers soon joined him in Group A. Gibbon group dynamics then became a new ball game. A new group may form when a subadult female from one group pairs with a subadult male from another group, and settles into new territorial space. However, at Mo Singto there is virtually no extra space for new territories, so that a more common method of obtaining a mate is to invade a nearby territory and challenge the resident adult of the same sex. This is a common method of forming a new pair bond in both sexes, and the challenger always wins. The fate of the displaced adult is rather variable: he or she may leave the territory and disappear (most displaced females), remain in the territory but assume a subdominant status, at least for a while, disperse into another group's territory as a guest resident, or, rarely, be killed by the usurper. The process of new pair formation and dispersal of young adults is a subject still

being actively studied at Mo Singto. In any event, the idea that groups can remain for very long as nuclear families has been pretty much disproved at Mo Singto. Moreover, the commonness of non-nuclear families disturbs and complicates a lot of theory about the evolution of social behavior, both within and between groups. Savini et al. (2009) suggested that ecological factors such as resource richness can favor groups with extra males that may help to defend larger territories.

Infanticide?

In primate research, the existence of "male takeovers" immediately calls to mind the possibility of infanticide, a phenomenon that has stimulated great controversy and new research since the 1970s. The proponents of the evolutionary theory of infanticide argue that if a new male kills an infant that is not his own, he may increase his fitness if it allows the female to come into estrus sooner (Hrdy 1979; van Schaik 2000a). The theory is generally accepted by primatologists and there is much evidence to support it, but evidence for infanticide in gibbons is relatively sparse. According to theory, the reduction of the birth interval caused by infanticide will be greater in species with a long lactation period relative to the gestation period (in gibbons, about seven months) (van Schaik 2000b). Gibbons have a relatively high ratio of lactation to gestation period of about 3.1, which should make them prime candidates for infanticide. Direct observations of infanticide are lacking, but this may be due to the relative rarity of male take-overs while the adult female resident is carrying an infant, and the general difficulty of observing behavior high in the forest canopy. Nevertheless, there is indirect evidence for infanticide, as in virtually all cases of male take-overs while the female was carrying an infant, the infant disappeared

shortly afterward, and in one case a dead infant with injuries was recovered (see reviews by Borries et al. 2011; Ma et al. 2019).

Diet and foraging

The remainder of this review will deal with studies of the ranging behavior, diet and role of gibbons in plant seed dispersal. Studies of diet and ranging have been facilitated by the creation of a large forest dynamics plot of 30 hectares, roughly covering the territory of Group A and parts of those of Groups B and C (Brockelman et al. 2011; Brockelman et al. 2017). This plot was initiated before 2000, and there have been three complete 5-year censuses of all trees present since then. A total of approximately 265 tree species reaching 1 cm in diameter at 1.5 m height have been tagged, identified, mapped and stored in the plot database. This Mo Singto Plot has become part of the international network of ForestGEO plots coordinated by the Smithsonian Tropical Research Institute in Washington, D.C. One of the purposes of this plot was to completely inventory the plant diet of the gibbons, and to study the ranging and foraging behavior of Group A in detail.

Study of gibbon groups in and around the Mo Singto Plot has shown that gibbons have a detailed knowledge of fruit sources and appear to travel directly to fruit trees that are completely out of sight, in distant parts of their range (Asensio et al. 2011). This knowledge allows the gibbon group to forage more efficiently and selects for a smaller territory, which is easier to defend (Brockelman et al. 2014). Gibbons in seasonal forest such as in Khao Yai must modify their diet and ranging behavior in response to seasonal changes in their food species (Bartlett 2009). In winter when fruit is in short supply, the gibbons

travel shorter distances and reduce the amount of time spent in social behavior. Food finding is made more complicated by the fact that most trees and lianas that they depend on are irregular fruiters, meaning that they do not fruit every year, or fruit only in occasional years (Suwanvecho et al. 2017).

Studies of seed dispersal

The preferred foods of gibbons are succulent fruits, which are also eaten by other mammals and birds. Many types of drupes and berries are eaten by gibbons and the seeds are always swallowed and defecated alive, ready to germinate and grow into seedlings. An example is a wild type of plum, *Prunus javanica*, the subject of a special study of seed dispersal on the Mo Singto Plot (McConkey and Brockelman 2011). While many other mammals and birds shared the fruit, gibbons appeared to be qualitatively the most reliable seed dispersers, but not the most important quantitatively. Some species of fruits eaten by gibbons tend to drop to the ground and are also consumed by terrestrial mammals such as sambar deer and elephants, which may disperse them outside of the forest (Chanthorn and Brockelman 2008; Brodie et al. 2009; McConkey et al. 2018). Other types of fruits have a more intimate, mutualistic relationship with gibbons—those with hard husks or leathery covers that prevent birds from feeding on them, and perhaps also protect them from insect damage. These include the wild relatives of some familiar fruits sold in our markets: rambutans, mangosteens, khatorn, and others. Our studies of dispersal of these species has revealed that gibbons are the most reliable dispersers that remove the propagules from the fruiting tree, increasing the survival probability of the seeds (McConkey et al. 2014, 2015, 2018; Tongkok et al. 2020). The role of animals in dispersing

seeds of forest trees underscores the importance of conserving them, especially primates such as gibbons, as part of our efforts to conserve forest ecosystems in tropical environments (e.g., Brodie et al. 2009; 2013).

Will the gibbons survive?

Gibbons in Thailand are largely, but not entirely, confined to broad-leaved evergreen, or seasonal evergreen, forest. It is important to know the habitat limits of gibbons and other species in order to understand how they may respond to future climate changes. Much research is now being carried out on how climate warming, CO2 level and changes in precipitation will affect the world's tropical forests. It was found that in Huai Kha Khaeng Wildlife Sanctuary, western Thailand, gibbons can feed on selected trees in neighboring patches of deciduous forest in the dry season, but they cannot survive throughout the year in this forest type (Light et al. 2021). In Mae Hong Son Province, northern Thailand, gibbons are found in a mosaic of evergreen and mixed deciduous forest that has become highly fragmented by the agricultural practices of tribal groups (Yimkao and Srikosamatara 2006). Local Karen communities cherish and usually conserve gibbons, but other minority ethnic groups hunt them and may drive them to local extinction without enforcement of protection measures. Pileated gibbons in the Khao Ang Ru Nai Wildlife Sanctuary in Southeast Thailand survive well in what has been termed "dry evergreen", or "semi-evergreen", lowland forest which has a high proportion of deciduous tree species (Phoonjampa et al. 2011). Pileated gibbons reach their maximum density in the very moist seasonal evergreen forest on the mountain slopes of Khao Soi Dao Wildlife Sanctuary in extreme southeastern Thailand of around five groups, or 15–20 individuals,

per square km (Brockelman and Srikosamatara 1993). Gibbon density in the more peripheral, lowland parts of the sanctuary has already been reduced by poaching (Phoonjampa and Brockelman 2008).

If climate change affects the tropical forests, especially seasonal forests, by making them drier and more deciduous (discussed in Brockelman et al. 2017), gibbons that inhabit relatively dry seasonal and semi-evergreen forests will be adversely affected and may find themselves in shrinking habitats. Unlike bird species, gibbons and most other mammal species will not be able to shift their ranges northward in Thailand, because they are limited to their current forest patches, and may be limited to their preferred forest type Srikosamatara and Doungkhae 1982). And farther northward, there are only seasonal forests which are also becoming drier. One characteristic of gibbons which may help them survive climate change is their dietary flexibility. The loss of gibbons from our forests will be felt not only by us fellow apes, but by the fruiting trees, lianas, and other plants and animals of the forest.

Acknowledgements

I acknowledge all my colleagues too numerous to list here, for their help and inspiration, but I am particularly indebted to and proud of my former students and Thai colleagues who have staked their careers in primate and gibbon research, ecology, and conservation and carried on: Anuttara Nathalang, Chalita Kongrit, Chanpen Saralamba, Intanon Kolasartsanee, Janya Jadejaroen, Nantiya Aggimarangsee, Pathom Yimkao, Ramesh Boonratana, Rungnapa Phoonjampa, Sompoad Srikosamatara, Suchinda Malaivijitnond, Surapon Duangkhae, Sutthirak Nongkaew, Udomluk Suwanvecho, Uthai Treesucon and Wirong Chanthorn.

I thank the National Research Council of Thailand for allowing me to extend my research here for so long, and the National Science and Technology Development Agency (NSTDA), my current funding agency, for their continued support. I am grateful to Anak Pattanavibool and his assistant Mayuree Umponjan of Wildlife Conservation Society–Thailand for their frequent support of gibbon surveys. Finally, I am ever grateful to my wife Chariya and our daughters Anne and Jill for their tolerance, help and love.

Table 1. Species of gibbons native to Thailand

Latin name	English name	Thai name	Range in Thailand
Hylobates lar	white-handed gibbon	ชะนีมือขาวหรือ ชะนีธรรมดา	North, central, west and south, west of Tepha R.
Hylobates agilis	agile gibbon	ชะนีมือดำ	Far south, east of Tepha R.
Hylobates pileatus	pileated gibbon	ชะนีมงกุฎ	Southeast
Symphalangus syndactylus	siamang	ชะนีเซียมัง	Far south in Bala mountains

Figure 1. Black color morph of *Hylobates lar*, or white-handed gibbon, with black infant, in Khao Yai National Park. Black color appears to be controlled by a single dominant allele (Brockelman, 2004). As a consequence, dark females may give birth to dark or light offspring. (Photograph by Kulpat Saralamba.)

Figure 2. Light color male *Hylobates lar* in Khao Yai National Park. In this species, color is not related to sex: either sex may be dark or light in color. (Photograph by Kulpat Saralamba.)

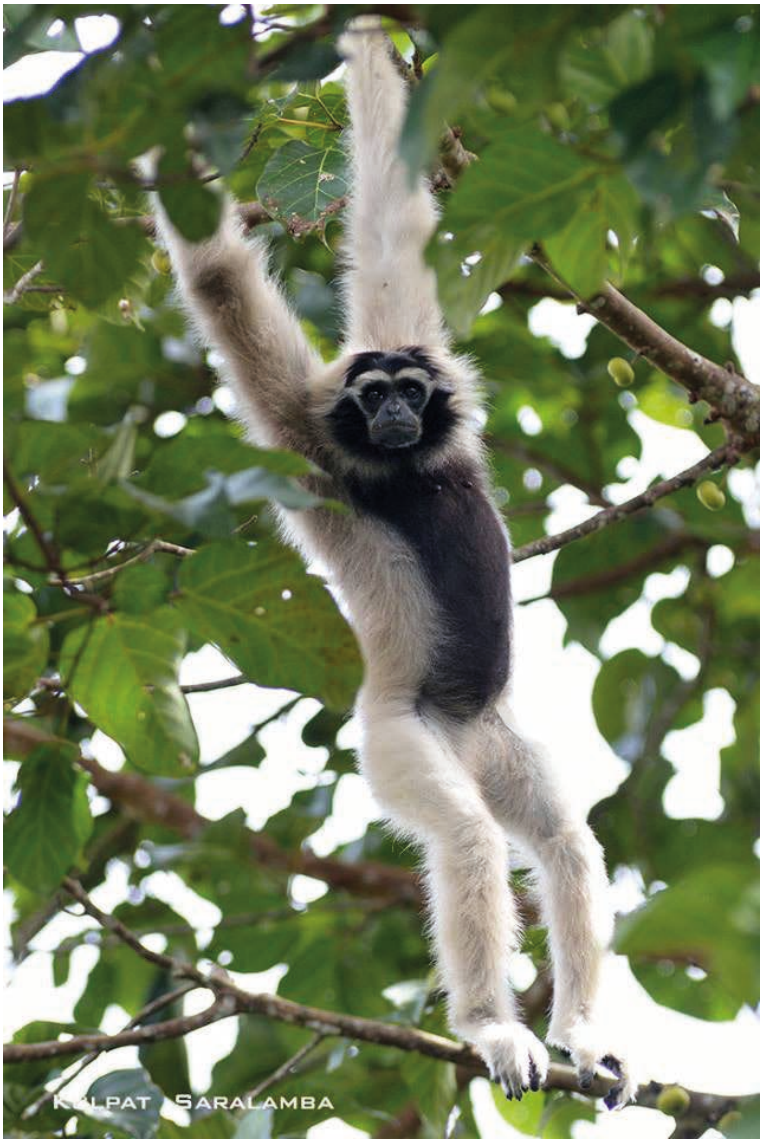

Figure 3. Female *Hylobates pileatus*, or capped gibbon, in Khao Yai National Park. This species is sexually dichromatic, meaning that color pattern is sex-specific. (Photograph by Kulpat Saralamba.)

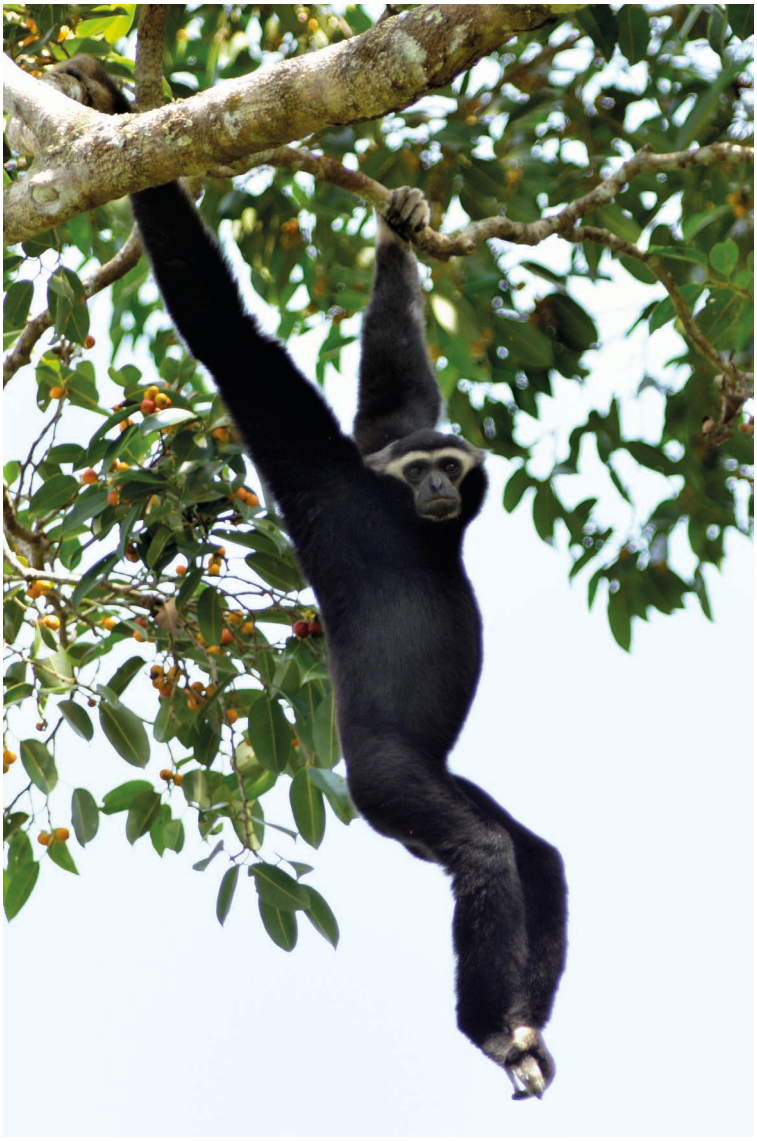

Figure 4. Male *Hylobates pileatus* in a fig tree, in Khao Yai National Park. This species has white eye brows, but not a complete face ring. Adult males always have black body coloration, but juveniles of both sexes have coloration resembling that of adult females. (Photograph by Kulpat Saralamba.)

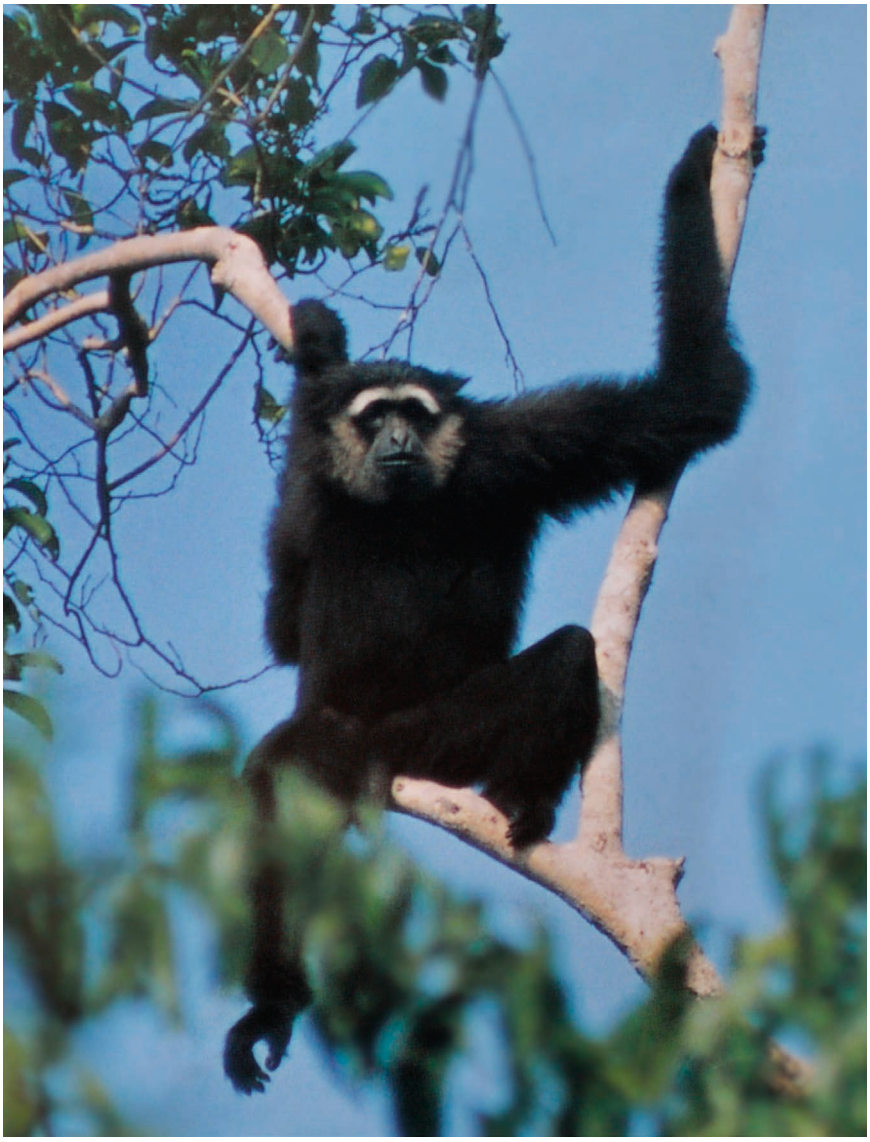

Figure 5. Male *Hylobates agilis*, called the agile gibbon or black-handed gibbon, in Hala Bala Wildlife Sanctuary, southern Thailand. Its face pattern contrasts with those of *H. lar* and *H. pileatus*. Like *H. lar*, it is asexually dichromatic in body color. This species is more widespread in forests of Peninsular Malaysia and Sumatra. (Photograph by Kulpat Saralamba.)

Figure 6. A male siamang in a the Khao Khieo zoo in Thailand. A small population of siamang survives in Hala Bala Wildlife Sanctuary, but they have not been studied intensively or photographed in the wild there. Both sexes are black in color. They are larger in size than all other gibbon species. The siamang has been studied in the wild in peninsular Malaysia and southern Sumatra, where they are more abundant. (Photograph by Kulpat Saralamba.)

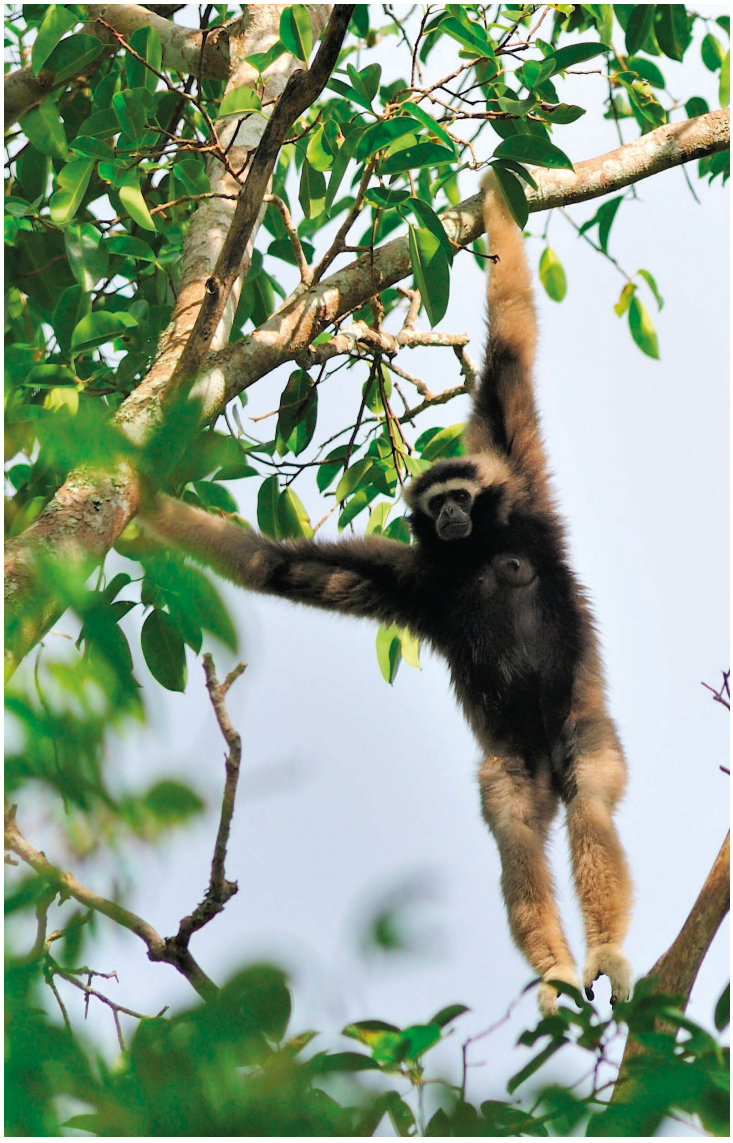

Figure 7. A hybrid adult female gibbon in Khao Yai National Park. The rather irregular color patterns of hybrids depend on sex and on the genetic composition of the parents. This individual resembles *H. pileatus* more than *H. lar,* and may be a backcross to *pileatus.* (Photograph by Kulpat Saralamba.)

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