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Gibbons: Communication, Radiation and Conservation Biology of the Forgotten Apes

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1. Introduction: Why gibbons?

The small apes of gibbons (Hylobatidae) occupy a key position in the phylogeny of recent apes and humans (Hominoidea): Because of their basal position in hominoid phylogeny, gibbons are a pivotal group for our understanding of the evolutionary history of living apes (Hominoidea). In addition, gibbons represent the only surviving major radition within the hominoids, as evidenced by their rich diversity (i.e. their relatively high numbers of genera, species and subspecies) as compared to the great apes. Therefore, gibbons are the best available candidates for the study of radiative processes at work in a hominoid radiation. Finally, gibbons differ not only from Old World monkeys, but also from other hominoids by several uniquely derived specialisations in their anatomy, locomotion, social structure and communication not shared by other apes. They are a unique wonder of nature.

In contrast to their sister taxon, the great apes, comparatively little research is being carried out on the small apes. In addition, media and scientists consistently portray great apes as having the highest conservation priority among apes, consistently ignoring gibbons. Therefore, the present habilitation thesis presents results of studies on three aspects of gibbon biology, which are aimed at increasing our knowledge of the gibbon radiation and in documenting the need for, and contributing to, an improvement of gibbon conservation efforts.

It is almost impossible to describe gibbons other than by describing some of their numerous specialisations, which are manifest in almost every aspect of their biology. Gibbons exhibit the most highly developed form of arboreal suspensory locomotion (Carpenter, 1969) and "are *aerialists* par excellence" (Fleagle, 1999, p. 240). Gibbon locomotor specialisations are linked to anatomical specialisations which pervade virtually every aspect of their locomotor apparatus, body proportions and trunk shape (e.g. Schultz, 1973; Fleagle, 1999). Other gibbon specialisations include their low reproductive rate (i.e. long birth intervals and long immaturity phases; Brockelman, 1975; Mitani, 1990).

Gibbons are also specialised in their social organisation. They live in small, territorial and monogamous family groups (Chivers, 2001; Leighton, 1987). Monogamy is a rare social system among mammals and is exhibited by less than 3% of species (Kleiman, 1977).

Especially early gibbon observers were impressed by the behavioural and emotional similarities between gibbons and humans and have in great detail described "the gibbon's strikingly human actions and reactions" (e.g. Forbes, 1894; Van Gulik, 1967; Yerkes & Yerkes, 1929). Although their intellectual capacities and emotions have rarely been studied, gibbons appear to be capable of self-recognition (Ujhelyi et al., 2000, see below). Their numerous specialisations also include their vocalisations: Gibbons produce long, loud and stereotyped song bouts which have been termed "the finest music uttered by a wild land mammal" (Marshall & Marshall, 1976).

In most species, mates may coordinate their song contributions to produce complex duets (Geissmann, 1999, 2000a, b; Geissmann & Orgeldinger, 2000, see below). Various aspects of gibbon communication and cognition will be discussed in section 2 of this thesis. The publications reviewed for this section will be focusing on amount, sex-specificity, syntax, variability, individuality, coordination and functions of gibbon song and duet vocalisations, and on the cognitive abilities of gibbons.

The gibbons or small apes are the most specifically diverse, and the most numerically successful of living apes (Fleagle, 1999, p. 236). The sheer number of taxa makes gibbons particularly rewarding subjects for research on the adaptive radiation of apes, as compared to the much smaller group of great apes. In section 3, I will discuss evolutionary aspects of gibbon biology and reassess the phylogeny and classification of the gibbons. The publications reviewed for this section will be focusing on genus-specific differences in body weights, the evolution of gibbon fur coloration and vocal characteristics, reconstructions of gibbon phylogeny using various data sets including fur coloration, "non-communicatory" data and vocal data and DNA sequence data, and the taxonomic implications of these results.

Gibbon specialisations such as their low reproductive rate as well as their dependence on tropical close-canopy forest makes them particularly vulnerable to changing environmental characteristics. Human induced changes of gibbon habitat and hunting have a strong negative impact on, and have lead to a marked reduction of, most or all gibbon populations, resulting in a critically endangered status of several gibbon species (Eudey, 1987; Hilton-Taylor, 2000). Section 4 will discuss aspects of gibbon conservation. The publications reviewed for this section will be focusing on the importance of gibbon vocal data for conservational and behavioural studies and the status of wild and captive gibbons in Indochina.

The high diversity of gibbons in relation to other apes strangely contrasts with the low attention they receive from scientists, media, funding agencies and conservation agencies, as compared to great apes. This long prevalent trend to prefer great apes and / or to ignore gibbons has finally ended up in additionally compromising the gibbons' chances for survival, as will be shown in section 5. Contrary to the prevalent view in the primatological literature, gibbons – not the great apes – are the real forgotten apes. This section not only documents the relevance of the gibbon studies presented in the present thesis but also the importance of continuing and increasing research on gibbon biology and conservation.

2. Gibbon communication

The male song of the silvery gibbon (*Hylobates moloch*)

Do male silvery gibbons sing?

In this thesis, a ***song*** is what fulfils the criteria set forth by Thorpe (1961, p. 15): "What is usually understood by the term song is a series of notes, generally of more than one type, uttered in succession and so related as to form a recognisable sequence or pattern in time", or, a song is a succession of phrases with non-random succession probability ("Strophenfolgen mit nicht-zufälliger Folgewahrscheinlichkeit", Tembrock, 1977, p. 33). ***Song bouts*** are separated from each other by an arbitrarily defined interval of at least 5 minutes.

All gibbon species are known to produce loud, long and well patterned morning song bouts which, among others, serve a territorial function. In mated pairs, male and female song contributions are sex-specific. The following song patterns were previously thought to occur among gibbon species:

(1) Duet song bouts only (7 species);

(2) duets and male solo songs (3 species);

(3) female solo songs and male solo songs (1 species: *H. klossii*);

(4) female solo songs only (1 species: *H. moloch*).

Only one behavioural study has previously been carried out on wild silvery gibbons (*H. moloch*). Kappeler (1984) observed the species in Ujung Kulon (the western-most tip of Java). During 130 full days of listening, he never heard any male songs of the resident groups in his study area and concluded that territorial male gibbons do not sing.

Geissmann and Nijman (2001) monitored gibbon singing activity around Linggo Asri in Dieng (central Java) on a daily basis during 19 consecutive days (October 1998). A total of 125 song bouts of at least 9 groups were heard. Most groups could be individually identified by individual-specific song characteristics. No duet songs were heard. Most of the song bouts (n=108, 86%) were female solo songs.

Geissmann and Nijman (2001) provided first evidence that male silvery gibbons regularly produce song bouts, albeit less frequently than females. In contrast to an earlier study in western Java (Kappeler, 1984), males in central Java also produced songs (n=13, 10%). The frequency distribution of the starting time of gibbon song bouts in Dieng is shown in Fig. 2.1. Males preferred to sing before dawn (05:20), whereas females sang later in the day: Most male songs (62%) started between 04:20-04:40 (pre-dawn calling). All female songs, in contrast, started after 05:00 and female singing activity peaked around 06:00 (i.e. after dawn).

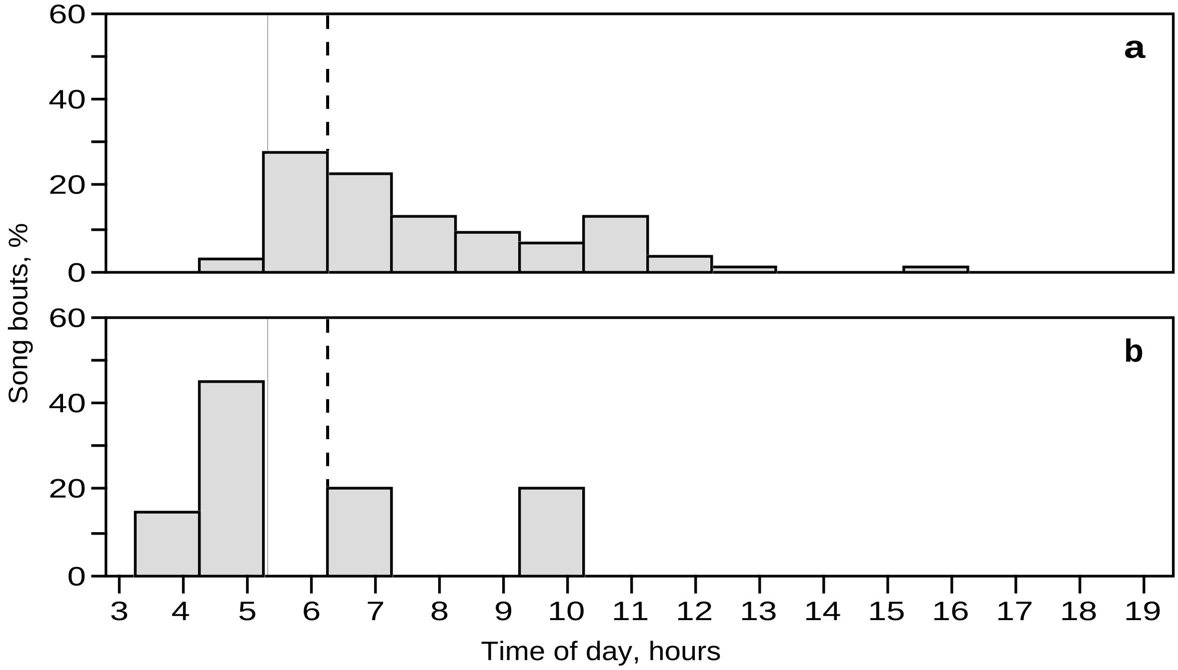


Fig. 2.1. Frequency distribution of the starting time of gibbon song bouts in Dieng, Central Java. (a) females (n = 107, this study); (b) males (n = 20, this study). Dotted line: dawn, dashed line: sunrise (from Geissmann & Nijman, 2001).

The female song of the silvery gibbon (*Hylobates moloch*)

Different levels of variability in the female song of wild silvery gibbons (Dallmann & Geissmann, 2001a)

Gibbon songs are known to include species- and sex-specific characteristics. It has been suggested frequently that these songs also exhibit a high degree of individuality, but quantifying individuality has rarely been attempted. Because the statistical methods used in earlier studies (Haimoff & Gittins, 1985; Haimoff & Tilson, 1985) were highly dependent on sample size (Kruskal-Wallis one-way analysis of variance by ranks), it was not possible to compare results among studies directly. Dallmann and Geissmann (2001a) introduced the mean pairwise difference (MPD) of scaled variables in order to quantify great-call variability and individuality. Because of its construction as simple normalised difference, the MPD is largely independent of sample size. This makes it possible to compare results directly with those of other studies on other populations or species. Even various levels of variability (intra- vs. inter-individual, intra- vs. inter-population variability) can be determined and compared with this method. In addition, the MPD can be calculated independently for any acoustic variable. This opens up a broad variety of research options in the area of comparative analysis of acoustic communication. For instance, variability in various parts of a phrase, in various parts of a song bout, in various contexts or in various seasons can be compared, and this is possible even if the variables under comparison are not the same.

As an example, Dallmann and Geissmann (2001a) analysed female great-call phrases of wild silvery gibbons (*H. moloch*) in Java (Indonesia).

The authors analysed a total of 316 great-calls from 30 different *H. moloch* females. Tape-recordings from 8 different localities were available for this study, covering most of the current distribution area of the silvery gibbon. The total sample was divided into 5 distinct populations by pooling localities of the same forest system or reserve.

The variability of pairwise differences (MPD) for intra- and inter-individual and for intra-and inter-population comparisons are shown in Fig. 2.2. Dallmann and Geissmann (2001a) found that inter-individual variability is significantly higher than intra-individual variability. This implies that females can be distinguished by their great-calls, although this was not examined during their study. Additionally, variability of female songs was found to be significantly lower within one population than among any two populations. The various sections of the great-call differ in their variability. The first half of the great-call (excluding the introductory note) shows the highest potential for individual recognition.

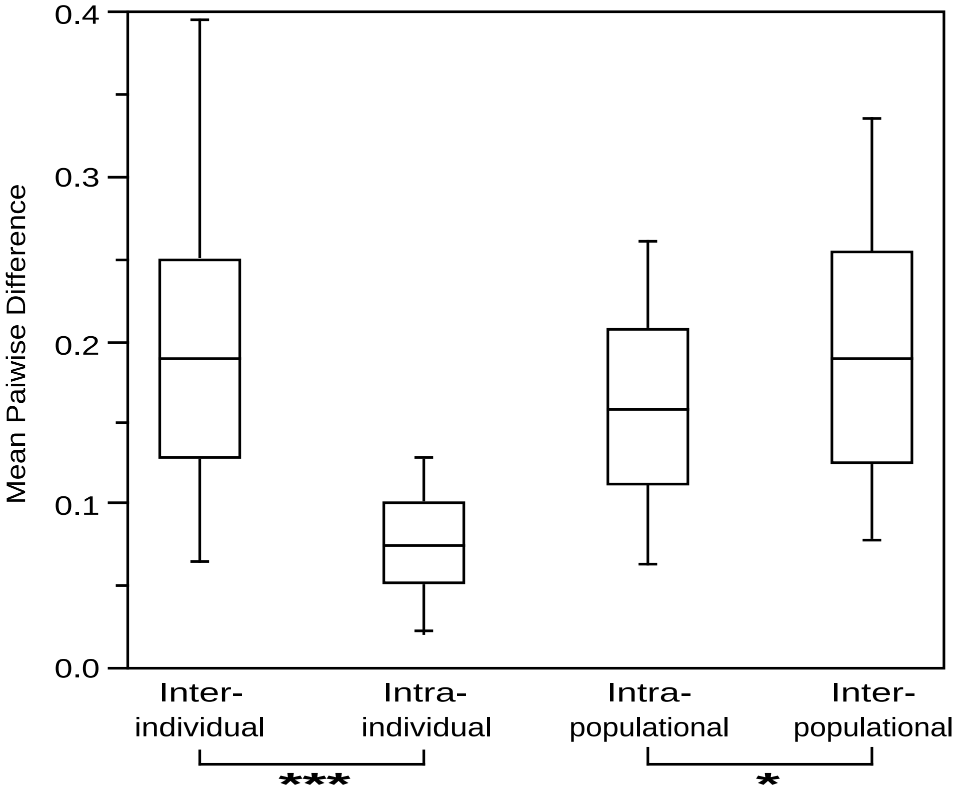


Fig. 2.2. Plot of the mean pairwise difference (MPD) for individual data and for population data, showing mean, range, and standard deviation for each sample (Mann-Whitney *U* test, *: $p < 0.05$; ***: $p < 0.001$) (from Dallmann & Geissmann, 2001a).

Because different parts of the same individual's song differ in their variability, they may also differ in their function. As a result, some functions of gibbon singing behaviour could be masked from detection, if the gibbon song is studied as a unit only. Future functional studies may benefit from approaching different song parts separately.

Comparing individual variability among gibbon species (Dallmann & Geissmann, 2001b)

All gibbon species produce loud, long and elaborate song bouts in the early morning. Silvery gibbons (*H. moloch*) differ from other hylobatids, however, in that duet song bouts are absent, male singing appears to be uncommon and most song bouts are female solo songs.

Consistent individual differences easily distinguish neighbouring females in the field, and it has been suggested that female individuality is particularly high in *H. moloch* in order to compensate for the lack of a family-labelling male song.

Dallmann and Geissmann (2001b) tested this hypothesis by quantifying individuality in *H. moloch* and comparing it with data on song individuality in two other gibbon species, *H. agilis* and *H. klossii*, available from earlier studies (Haimoff & Gittins, 1985; Haimoff & Tilson, 1985). Those studies had been focusing on the great call (i.e. the most stereotypical song phrase produced by gibbon females) and had determined individual variation of several variables (such as duration and frequency range of selected great call notes). Dallmann and Geissmann (2001b) exactly replicated each of those studies with great calls of *H. moloch* which were tape-recorded in Ujung Kulon and Gunung Pangrango (West Java, Indonesia). According to the working hypotheses, individuality should be highest in *H. moloch* lower in *H. klossii* (male singing is common) and lowest in *H. agilis* (male singing and duets are common).

The study by Dallmann and Geissmann (2001b) is the first study comparing individuality in the songs among several gibbon species. The authors found a statistically significant degree of inter-individual variability in most great call variables of *H. moloch*, which is higher than that of *H. klossii*, but lower than that of *H. agilis*. Examples of these inter-species comparisons are shown in Fig. 2.3. These results do not support the hypothesis that *H. moloch* females compensate the rarity of male song contributions with an elevated degree of individuality in their singing. Instead, these authors suggested that the amount of great call individuality may be compromised by the amount of a trill component exhibited by various species of the genus *Hylobates*.

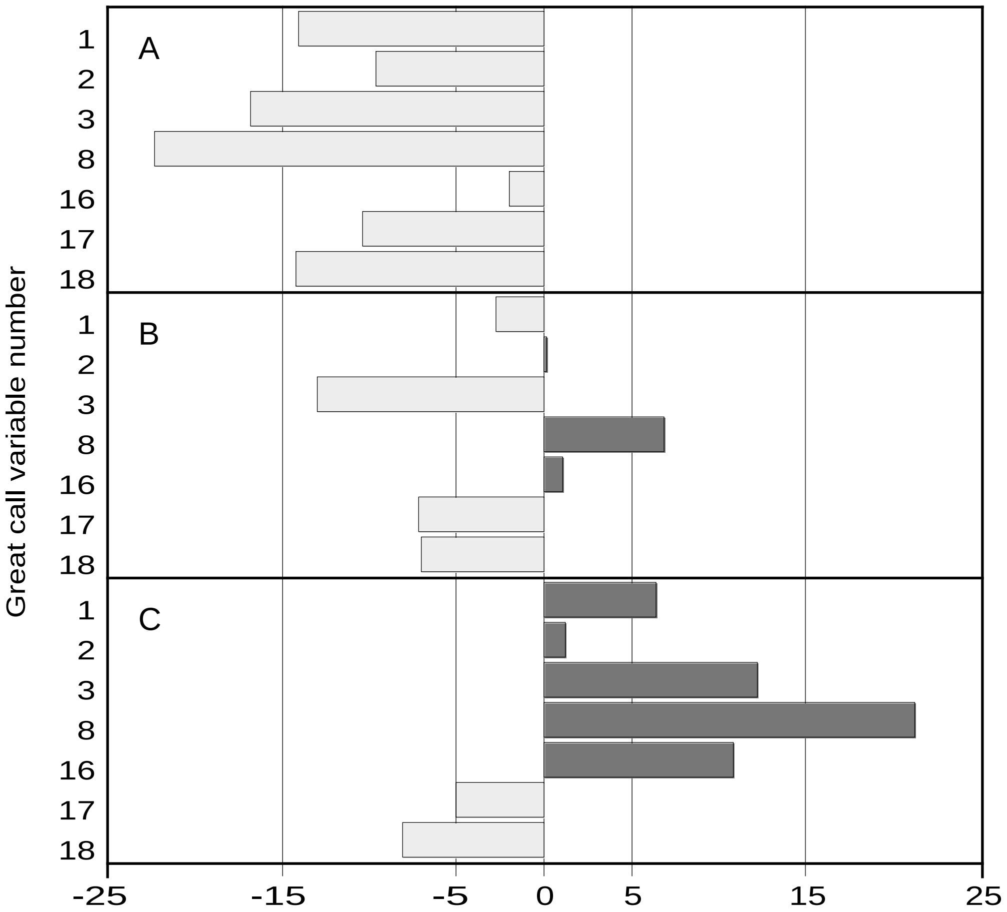


Fig. 2.3. Comparison of the H-values (from Kruskal-Wallis tests) between gibbon species for seven selected great call variables. The horizontal axis shows the difference between the H-value of *H. moloch* minus the corresponding H-value of A) *H. agilis* from Sungai Dal; B) *H. agilis* from Ulu Muda; and C) *H. klossii.* Positive bars indicate a higher individuality in *H. moloch*, whereas negative bars indicate a higher individuality in *H. agilis* and *H. klossii*, respectively. Great call variables (vertical axis) appear in the same order in A, B and C, respectively (from Dallmann and Geissmann, 2001b).

The duet song of the siamang (*Symphalangus syndactylus*)

Structure and organisation of the siamang duet

Siamangs produce loud and long song bouts which are mostly exhibited by mated pairs. Typically, mates combine their partially sex-specific repertoire in relatively rigid, precisely timed and complex vocal interactions to produce well-patterned duets. Previously, there were two published quantitative analyses of the siamang duet structure and organisation (Lamprecht, 1970; Haimoff 1981), each based on singing behaviour of two pairs.

Geissmann (2000a) presented a detailed description of singing behaviour, repertoire, and song and duet organisation of 9 adult siamangs in 10 different group constellations.

Geissmann's study revealed that previous authors have been using different terms when referring to the same vocal elements, while others have applied the same names to completely different elements.

The note repertoire of the siamang song was found to consist of 4 distinct note classes and 9 different note types (Table 2.1). There are no strict borders between types of the same note class, and vocalising animals may gradually switch from one type to another. On the other hand, no intermediate forms were found between different note classes.

Table 2.1. Note classes and types used in siamang song bouts (from Geissmann, 2000a).

Class	**Type**	**Adult song repertoire** [a)]	
		Male	Female
Booms	Grunts	+	+
	Short booms	+	+
	Long booms	+	+
	Ascending booms	+	(+)
Barks	Short fast barks	+	–
	Short slow barks	+	–
	Long barks	–	+
Ululating scream	Ululating scream	+	(+)
Bitonal scream		+	–

[a)] + = present, – = absent, (+) = produced by some females only.

Of the nine note types, only two are sex-specific in the typical duet song of adult siamangs: long barks are typically produced by females, and bitonal screams by males.

Geissmann's (2000a) study revealed that the organisation of both the song bout as a whole, as well as the great call sequence in particular, is more complex than has been believed previously

The composition of a typical siamang song bout is organised according to relatively strict rules. At the highest level of subdivision, the song bout consists of 4 different types of sequences which occur in a predetermined order, as shown in Fig. 2.4. The first of these sequences is called the grunting sequence and has not previously been recognised to be part of the siamang song bout. No homologue structure to the grunting sequence appears to exist in other gibbon species.

The great call sequence represent both the most stereotyped as well as the most complex part of the siamang duet song bout. It consists of an ordered chain of interactions between the mates: At certain predictable points in the sequence, each animal utters certain types of vocalisations in a particular temporal pattern, and exhibits particular types of locomotion.

(Fig. 2.5). In other duetting gibbon species (with the possible exception of the hoolock gibbon, *B. hoolock*), the duet structure of the great call sequence is much more simple and consists of the female interrupting the singing male with her great call phrase which, in turn, is answered by a coda phrase of male.

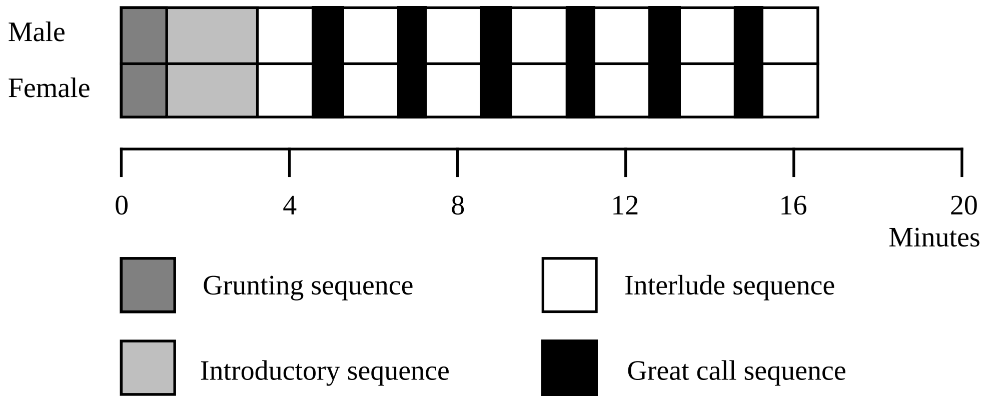


Fig. 2.4. Stylised diagram illustrating the sequential nature of the duet song bout produced by adult siamang pairs (after Haimoff, 1984, and Geissmann, 2000a).

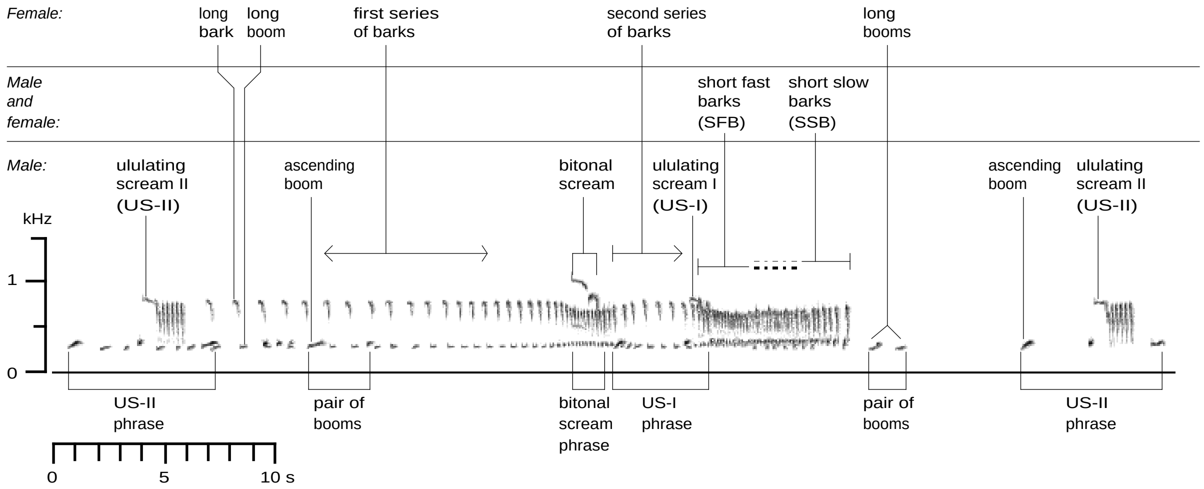


Fig. 2.5. Organisation of a typical great call sequence of a siamang pair. Selected notes or groups of notes are individually indicated (from Geissmann, 2000a).

Geissmann's (2000a) study revealed, the siamang duet song represents the most complicated duet structure among gibbons, as is evident from the richness of the partly sex-specific vocal repertoire, the number of different types of vocal interactions necessary to produce a typical great call sequence (i.e. the most spectacular and longest recurrent vocal pattern within gibbon songs), and the strict rules that regulate the sequence of, and the intervals between, these vocal interactions.

Function of the siamang duet: Testing the pair-bonding hypothesis during a partner exchange (Geissmann, 1999)

One of the most commonly cited functional explanations for animal duet songs is strengthening of the pair bond. However, the evidence to support this view is, at best, limited. A possible mechanism how duetting could might act as a reinforcement of the pair bond has been proposed by Wickler (1980). It has, however, not been demonstrated that the premises underlying the pair-bonding hypothesis are met by any duetting species.

Geissmann (1999) analysed the changes in duet structure in two pairs of captive siamangs during a forced partner exchange. The duet songs of the siamangs underwent many notable changes during partner exchange. As an example, the frequency of some selected variants of the great call sequence in various stages of one of two observed partner exchanges is shown in Fig. 2.6. Of 33 different variants of the great call sequence, 29% in one pair and 21% in the other were restricted to the first stage just after the partner exchange. Some of these changes were certainly due to individualistic traits of the new partner, and for some other changes, this possibility was not reliably excluded. At least two changes, however, could only be interpreted in terms of a learning effort by which one partner adapts his duetting behaviour to that of its new mate.

The two newly formed pairs of this report appear to be the first and only documented cases to fulfil the requirements underlying Wickler's (1980) pair-bonding hypothesis: The animals under study were showing a stable song pattern with pair-specific traits. After the partner exchange, new pair-specific traits occurred, some of them obviously achieved through a partner-directed effort of one or both individual(s).

Moreover, the pair-bonding hypothesis appears to be one of the few biological functions suggested so far which could explain a high degree of duet-complexity as adaptive. However, the loudness of the siamang song alone suggests that other functions are also involved. These are most probably related to territorial advertisement, pair bond advertisement and (possibly) mate attraction.

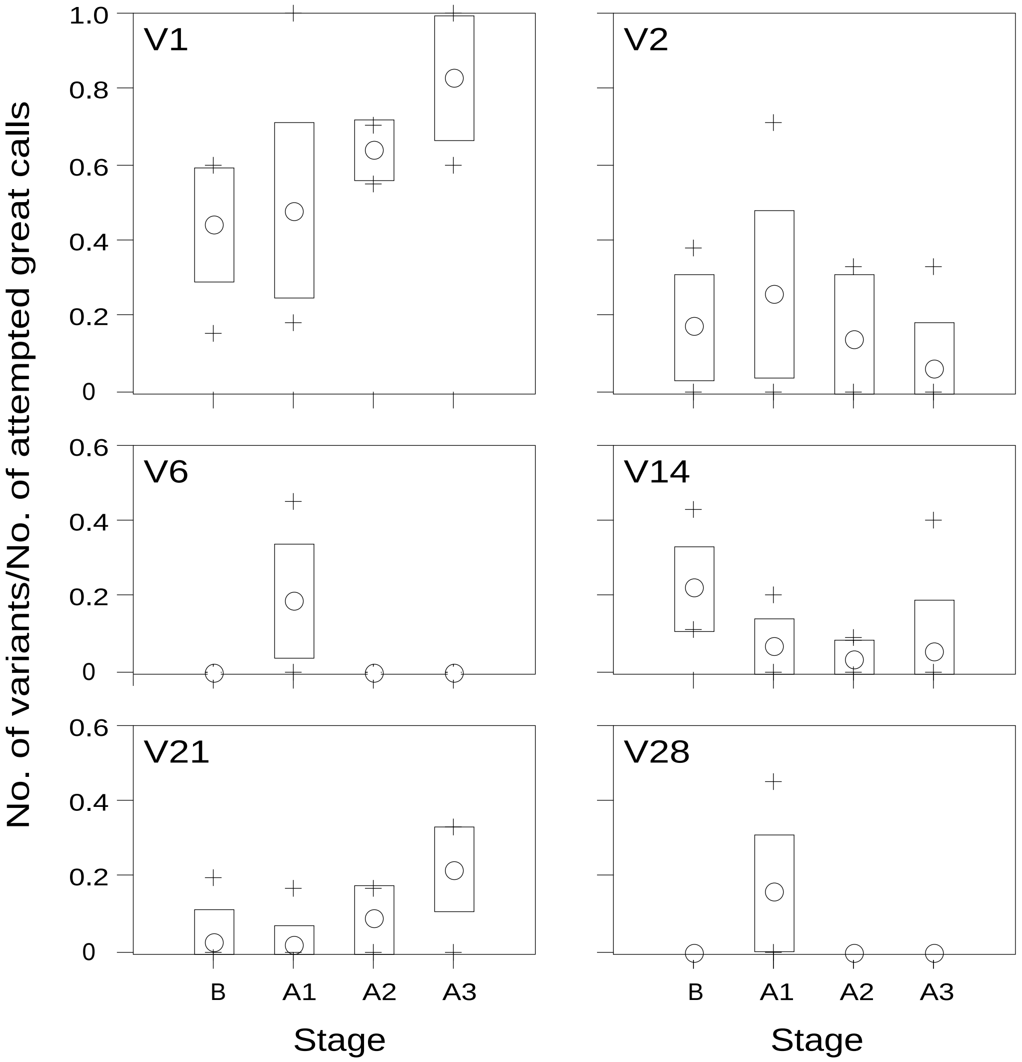


Fig. 2.6. Relative proportion of selected variants of the great call sequence during various stages of a partner exchange. In this case, the focal male was first observed with an established partner, then with a new partner. B = stage before the partner exchange; A1 - A3 = stages after the partner exchange. Symbols: circles = mean values, boxes = standard deviations, crosses = minimum and maximum values (from Geissmann, 1999).

Function of the siamang duet: The relationship between duet songs and pair bonds (Geissmann & Orgeldinger, 2000)

A study by Geissmann and Orgeldinger (2000) provided further support to the pair-bonding hypothesis by documenting that a relationship exists between pair bonds and duet singing in siamangs. As a working hypothesis, the authors assumed that if duetting were related to pair bonding, one might expect to see a relationship between duetting intensity and indicators of pair bond strength.

The authors recorded daily frequency and duration of duetting and three generally accepted indicators of pair bond strength (mutual grooming, behavioural synchronisation and distance between mates) in 10 siamang groups in zoos.

Duetting activity was positively correlated with grooming activity and behavioural synchronisation, and negatively correlated with distance between mates (Table 2.2). These results suggest that the production of coordinated duets by siamang pairs is related to pair bonding.

Table 2.2. Kendall rank order correlations among the five variables used in this study (from Geissmann & Orgeldinger 2000). [a]

Pair bond strength	**Duetting**			
	Mean no. of songs / day		Song activity (%)	
	Kendall's tau corrected for ties	*P*	Kendall's tau corrected for ties	*P*
Grooming (sessions / h)	0.491	0.036	0.527	0.024
Behavioural synchronisation between mates (%)	0.455	0.052	0.491	0.036
Distance between mates (%)	–0.587	0.012	–0.624	0.008

[a] Song activity: time spent singing per observation time; behavioural synchronisation between mates: occurrence of synchronised behaviour between mates per number of observation scans; distance between mates: mean inter-individual distance in relation to the maximal possible distance in the pair's given environment (cage or island).

Self-recognition in gibbons

Behaviour of gibbons in the presence of mirrors (Ujhelyi et al., 2000)

Especially early observers of gibbons were struck by the behavioural and emotional similarities between gibbons and humans and have in great detail described "the gibbon's strikingly human actions and reactions" (e.g. Forbes, 1894; Van Gulik, 1967; Yerkes & Yerkes, 1929). However, their intellectual capacities and emotions have rarely been studied.

The introduction of a novel testing method, the mark test, for assessment of mirror self-recognition (MSR) in animals and humans (Amsterdam, 1972; Gallup, 1970) stimulated a number of experiments designed to examine MSR in a variety of primates. Whereas numerous series of MSR tests were carried out with great apes (see references in Ujhelyi et al., 2000), only few gibbons were studied (Hyatt 1998; Inoue-Nakamura, 1997; Lethmate & Dücker, 1973). On the basis of these studies, it has been suggested that a phylogenetic discontinuity in MSR capacity separates the great apes and humans from other primates (Anderson, 1994; Gallup 1977b; Povinelli & Cant, 1995). In view of the close phylogenetic relationship of gibbons to the great apes and in view of the paucity of descriptive information concerning the behaviour of gibbons in mirror situations provided by the studies cited above, more data on the mirror performance of the lesser apes were desirable.

Ujhelyi et al. (2000) therefore studied the behaviour of captive gibbons in a variety of mirror situations designed to provide information about their reactions to mirror exposure and the extent to which they might recognise themselves in a mirror.

Three captive gibbons (*N. leucogenys*, *N. gabriellae*, and *H. lar*) were videotaped in the course of longitudinal exposure to mirrors introduced into their familiar cage or island housing situation. Additional information on the mirror competence of gibbons was provided by modified mark tests and a hidden object task. In addition, a modified mark test was also carried out with a fourth individual, a juvenile siamang (*S. symphalangus*).

The gibbons, which differed in age, sex, species and rearing condition, exhibited great individual differences in their behavioural reactions to mirrors, spanning from a minimal reaction dominated by social responses (*H. lar*), to a dramatic sequence of progressive behavioural change that featured a variety of contingency testing behaviours (movements performed in front of the mirror and not normally part of the animal's habitual repertoire of spontaneous movements, but capable of providing information about the contingency between the animal's own movements and their mirror image) and included mirror-mediated, self-exploratory behaviour (*N. leucogenys*).

Of the four study animals, only the siamang passed the mark test. However, both males of the genus *Nomascus* provided increased amounts of contingency testing and self exploratory behaviours which can be used as indirect evidence of MSR capability (Fig. 2.7). Given that three of the four animals provided evidence of mirror competence beyond what has so far been reported for gibbons, this study suggests that gibbons may need to be included among species capable of providing evidence for recognising the image in the mirror as that of their own body and that any phylogenetic discontinuity in MSR capacity does not separate great apes and humans from other primates, but all apes from other primates. Further studies of gibbons exposed to mirrors are needed to define in greater detail their capacities in this respect, and to clarify factors involved in individual differences among animals.

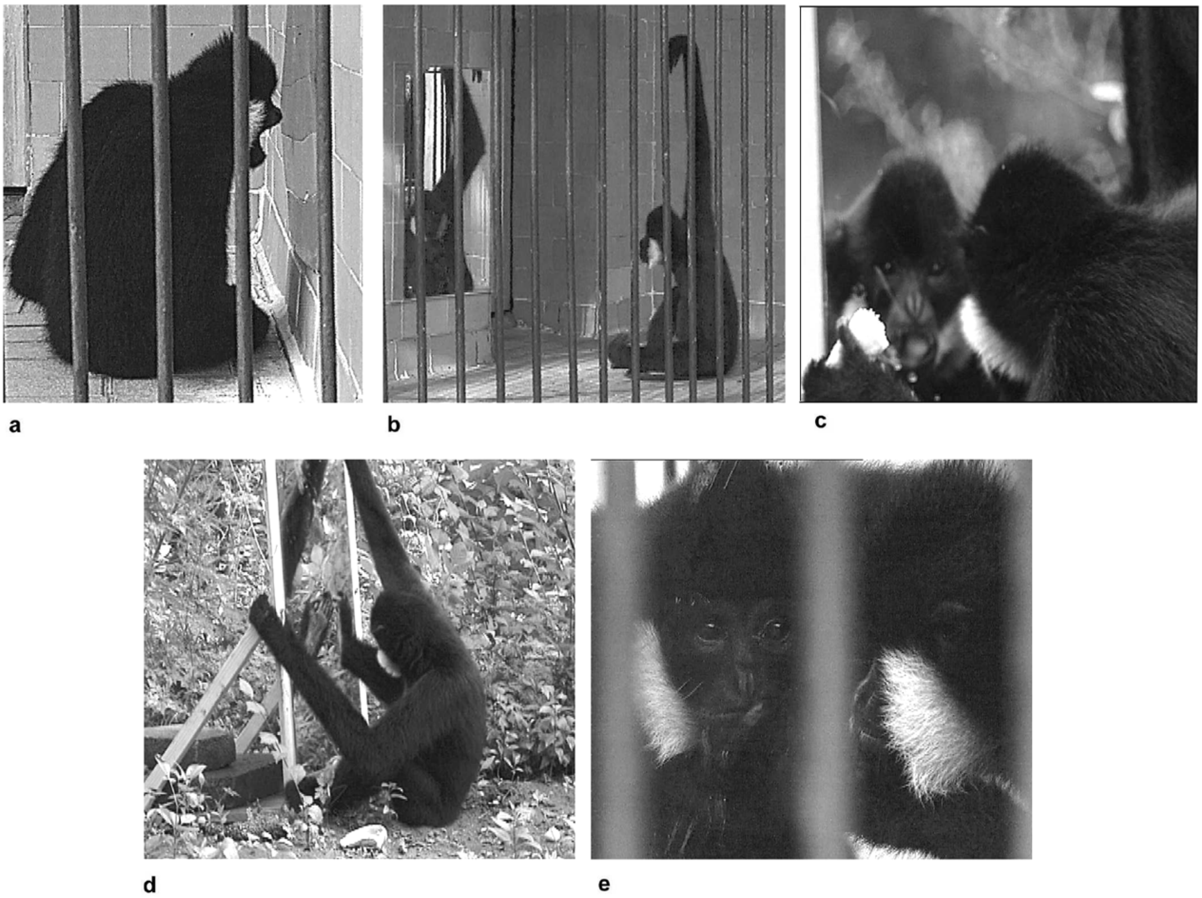


Fig. 2.7. Self exploratory movements produced by to two gibbon males, Dodo (*N. leucogenys*) and Todi (*N. gabriellae*) during mirror exposure: a. Dodo, mouth opening in front of the chrome mirror; b. Dodo, e.g. lifting in front of the mirror; c. Todi, banana eating in front of the mirror; d. Todi, leg lifting in front of the mirror; e. Dodo, manual self-inspection of his lips by his thumb (from Ujhelyi et al., 2000).

3. Gibbon radiation

Body weight in gibbons

Body weight and neonatal weight in gibbons (Geissmann & Orgeldinger, 1995)

According to the traditional view, gibbon body weights fall into two size classes, with the siamang on one side (about 11 kg) and the gibbons on the other (about 5 kg). During a world-wide survey of museum collections, Geissmann (1998) compiled body weights of wild shot gibbons directly from the collectors' original records or from the specimens' labels. These data revealed that sexual dimorphism in body weight is low and not statistically significant in most populations. Relatively large samples of body weights of wild-shot *N. concolor*, *N. leucogenys* and *B. hoolock* were made available for the first time. In these three species, body weights average around 8 kg, 7 kg and 7 kg, respectively, and are distinctly higher than mean body weights of the various species of the genus *Hylobates*. The results demonstrate that gibbons of the genera *Bunopithecus* and *Nomascus* are of distinctly higher body weight than gibbons of the genus *Hylobates* and that a trichotomy may better describe the weight distribution in gibbons than a dichotomy.

Neonatal and birth weights of gibbons have mostly been reported for single individuals, and larger samples (n=2-8) have apparently been published for only two species of gibbons (*H. lar* and *S. syndactylus*). In addition, a critical examination of the few published neonatal weights of gibbons shows that several of them should not be used, because they are based on specimens preserved in formalin, because the weights were simply wrong (printing error) or because the infants were to old when weighed.

Geissmann and Orgeldinger (1995) defined neonatal weights as weights taken on infants up to seven days old, whereas birth weights include only those taken on the day of birth. The authors presented neonatal weights for 6 representative species of gibbons (*H. lar*, *H. moloch*, *H. muelleri*, *H. pileatus*, *N. leucogenys*, *S. syndactylus*) and some of their hybrids (Fig. 3.1). Most of their data stem from surviving animals that were subsequently hand-reared and included 80 infants, thus making the previously available data set 5 times larger. Their neonatal weights fall roughly into 3 different classes: neonates of the genus *Hylobates* (about 390 g, n = 27), the genus *Nomascus* (about 510 g, n = 7), and the siamang, genus *Symphalangus* (about 540 g, n = 46). This grouping corresponds not only to taxonomic units within the hylobatids, but also to grouping of gibbons by adult body weight. No weight difference between males and females was evident in the sample, and hybrids of the genus *Hylobates* did not appear to differ in weight from pure species.

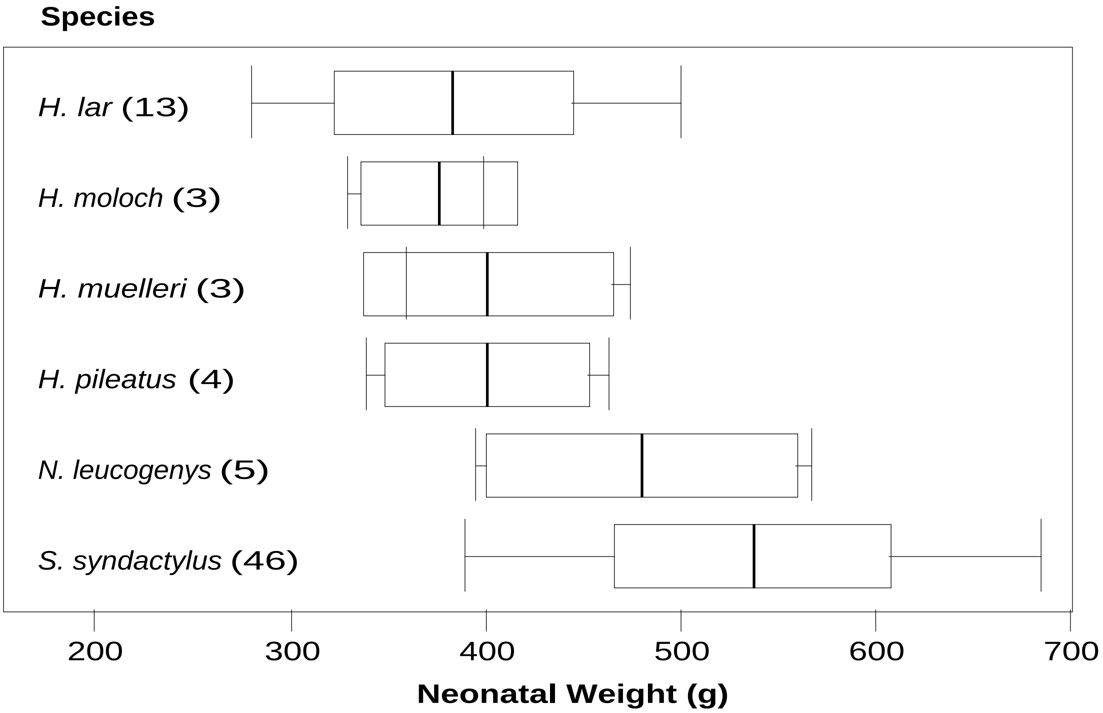


Fig. 3.1. Average neonatal weights (g) for 6 different gibbon species (excluding hybrids), showing standard deviations (boxes) and upper and lower limits. Sample size for each species is given in parentheses.

True birth weights (i.e. weights recorded on the day of birth) were available for only a few individuals. These weights were, on average, 7% higher than neonatal weights, but the difference was not statistically significant. Additional samples of neonatal weights suggested that infants that die on the day of birth weigh, on average, 17% less, twins weigh 29% less, and infants born by Cesarean section weigh 19% more than the reference sample of neonates. All these differences were statistically significant (Student's t-tests; P > 0.05).

Evolution of circumfacial markings in gibbons

Circumfacial markings in siamangs and evolution of the face ring in gibbons (Geissmann, in press b)

One of the most conspicuous and well-known characteristics of the fur coloration of many gibbons (Hylobatidae) is the white, or at least bright, circumfacial pattern (Geissmann, 1994, 1995b). In some species, this pattern consists of a closed band bordering the whole contour of the dark and almost naked facial area. It is then usually called a face ring (Fig. 3.2a). In other species, the circumfacial pattern may be reduced to a brow band (Fig. 3.2b), and in yet other species the pattern may be reduced to the cheek region (Fig. 3.2c). In the black crested gibbons (*Nomascus concolor* and *N.* sp. cf. *nasutus*), the circumfacial pattern is absent in adult males, but traces of it sometimes occur in adult females. In two species, the facial pattern is completely absent in both sexes: in the Kloss's gibbon (*Hylobates klossii*) and in the siamang (*Symphalangus syndactylus*) (Fig. 3.2d).

Geissmann (in press b) documented the occurrence of a white brow band in siamangs for the first time (Fig. 3.3). The characteristic occurs in 4.4% of the 250 siamangs examined for this study. Among adult siamangs, the characteristic was found more often in females than in males (11.3% of 71 females vs. 1.4% of 73 males, respectively). In a particular family lineage of captive siamangs (not included in the numbers above), the characteristic was unusually frequent (42.9% of 14). The trait appears to be inherited (possibly an autosomal dominant inheritance). Additional white markings occur in at least one of the study animals on hands, feet, and in a corona above the ears. These results suggest that the presence of white facial markings, and possibly also of white hands and feet and of a bright corona are primitive gibbon traits, in contrast to previous studies, which labelled the absence of a facial pattern as a primitive character state in their analyses of gibbon phylogeny and systematics (Creel & Preuschoft, 1984; Haimoff, 1983; Haimoff *et al.*, 1982, 1984). In addition, the findings of Geissmann (in press b) suggests that some degree of sexual dichromatism in the circumfacial markings appears to have occurred in the common ancestor of all gibbons.

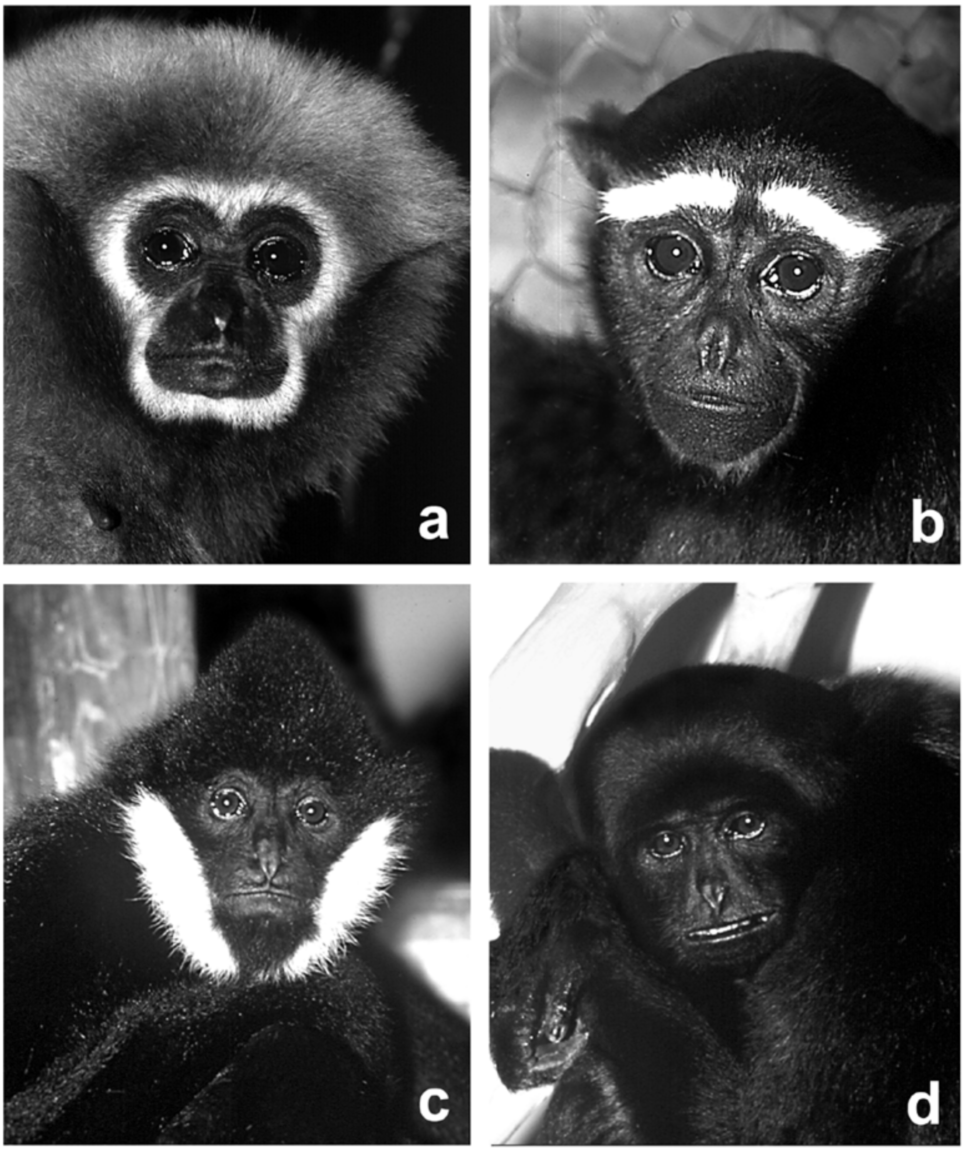


Fig. 3.2. Various circumfacial patterns in gibbons: (a) *Hylobates lar*, ad. female; (b) *Bunopithecus hoolock*, juv. male; (c) *Nomascus leucogenys*, ad. male; (d) *Hylobates klossii*, ad. male (from Geissmann, in press b).

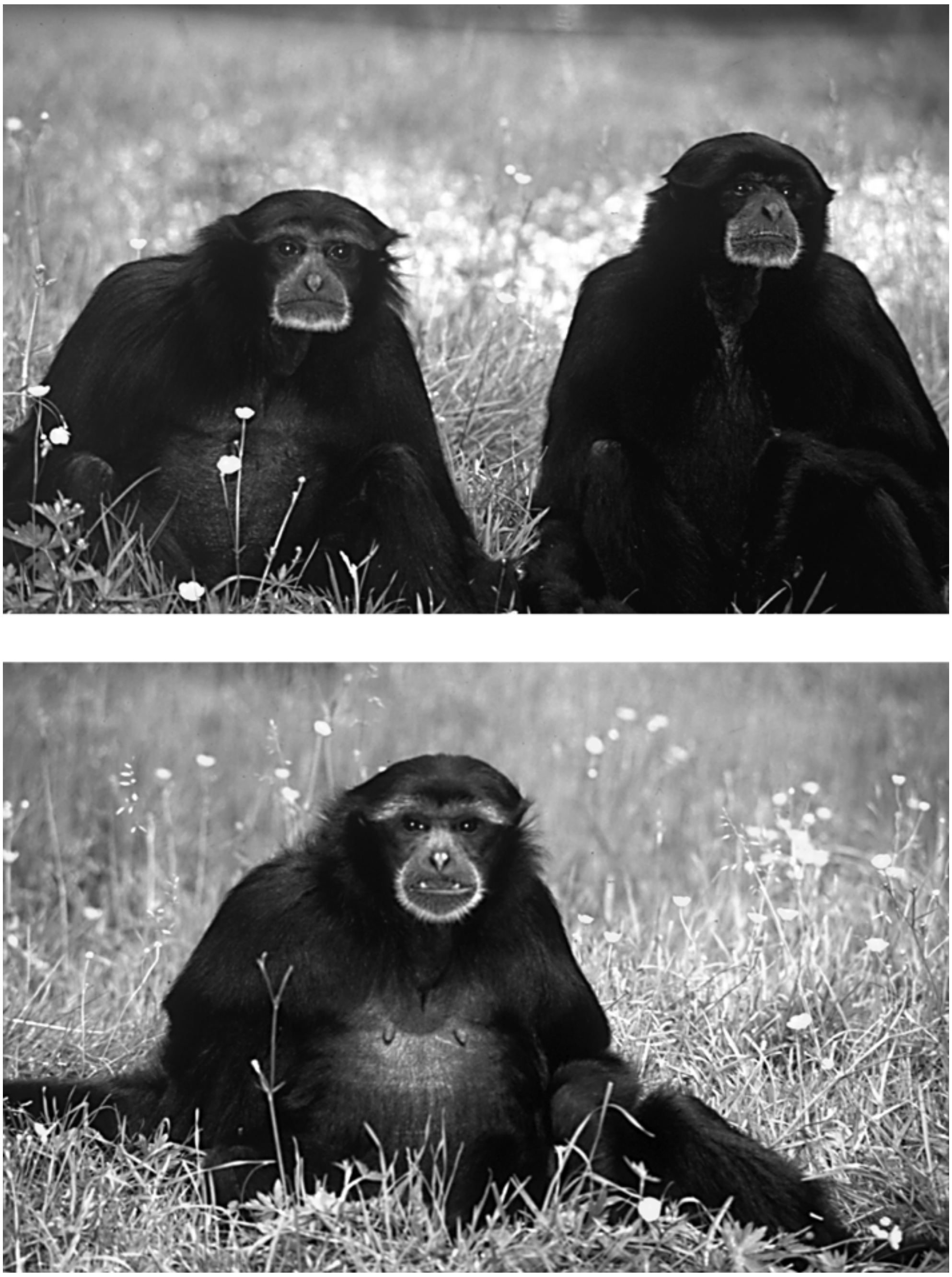


Fig. 3.3. Siamangs at the Duisburg Zoo. Above: Adult female ("Püppi II", left) and adult male siamang ("Piet", right). Note the conspicuous white brow band in the female, and the absence of the characteristic in her father. Below: Adult female siamang "Hexe". The distinct white brow band of this female is slightly broader at the lateral ends than the brow band of her daughter in the upper photograph (from Geissmann, in press b).

Relevance of gibbon songs for gibbon systematics

*Geographical variability in the female song of wild silvery gibbons (*H. moloch*) (Dallmann & Geissmann, 2001a)*

Recent molecular data appear to support a split of *H. moloch* into two distinct populations (possibly subspecies), one in western Java and one in central Java (Andayani *et al*., 1998; Supriatna *et al.*, 1999; Supriatna & Wahyono, 2000). Indeed, the possible existence of two subspecies was previously proposed by Sody (1949) based on fur coloration, but rejected Groves (1972) and Kappeler (1981). Interestingly, molecular data suggest that the border between the two subspecies should be located in West Java, between the Gunung Halimun and the Gunung Pangrango mountain complexes. In contrast, Sody (1949) suggested that the subspecies border was located much more to the east, between West Java and Central Java.

Gibbon songs provide particularly suitable characteristics for taxonomic classifications (Geissmann, in press c, Haimoff *et al.*, 1982). Dallmann and Geissmann (2001a) compared female song characteristics among 4 populations of wild silvery gibbons. These populations were 1) Ujung Kulon (westernmost Java), 2) Gunung Pangrango complex (West Java), and 3) Dieng (Central Java). If there were two subspecies on Java, one should expect more pronounced differences in singing behaviour between populations belonging to different subspecies than between populations of the same subspecies. In order to correspond to the molecular findings of Andayani *et al.* (1998), one should find higher vocal differences between populations 1 and 2 than between 2 and 3, but Dallmann and Geissmann (2001a) found exactly the opposite. Their data do not disprove the occurrence of subspecies, but if there were two subspecies in *H. moloch*, the common distribution border between them should not be located in West Java between populations 1 and 2, as indicated by the results of Andayani *et al.* (1998), but somewhere between populations 2 and 3, i.e. between West Java and Central Java, as suggested by Sody (1949).

Further investigations are necessary in order to resolve these contradicting results and to determine whether these vocal and/or molecular differences between populations identify different subspecies in the first place.

A previously unrecognised gibbon species

The crested gibbons (genus *Nomascus*) have traditionally been regarded as consisting of a single species, *N. concolor*, containing 6 subspecies (*concolor*, *hainanus*, *lu*, *leucogenys*, *siki*, *gabriellae*) (e.g. Simonetta, 1957; Groves, 1972; Chivers, 1977; Marshall & Sugardjito, 1986). More recent studies suggested that this group should be split into two species, *N. concolor* and *N. leucogenys*, with *concolor*, *hainanus* and *lu* being subspecies of the former (Dao Van Tien, 1983; Ma & Wang, 1986). Additional anatomical evidence (penis bone differences) appeared to support recognition of a third species, *N. gabriellae*, with some debate as to whether *siki* is a subspecies of *N. leucogenys* (Geissmann, 1995b) or of *N. gabriellae* (Groves, 1993b; Groves & Wang, 1990), or whether *siki* should be recognised as a distinct species as well (Groves, 2001). In addition, Ma and Wang (1986) described two new black gibbon subspecies from the Chinese Province of Yunnan (*N. c. furvogaster* and *N. c. jingdongensis*).

Geissmann (1997) and Geissmann et al. (2000) described and compared crested gibbon vocalisations and fur characteristics. Tape-recordings were carried out in a large number of European, Asian and American zoos and in the wild in southern Vietnam and in southwestern China, including Yunnan Province and Hainan Island. In addition, virtually all known wild-shot museum specimens world-wide were examined.

Results by Geissmann (1997) and Geissmann et al. (2000) based on museum skins and vocalisations of captive gibbons clearly support the recognition of the species *N. concolor*, *N. leucogenys* and *N. gabriellae*, with *siki* being more closely related to *N. leucogenys* than to *N. gabriellae.*

Research results also suggest that the diversity of Indochinese gibbons is larger than previously assumed. The affinities of populations in central Vietnam and southern Laos appear to be particularly complex. Tape-recorded songs of wild populations suggest the existence of an intermediate population between *siki* and *gabriellae*, as indicated in Fig. 3.4.

No clear vocal or fur coloration differences were found among Chinese populations of *N. c. concolor*, *N. c. jingdongensis* and *N. c. furvogaster*, making the recognition of the latter two taxa questionable.

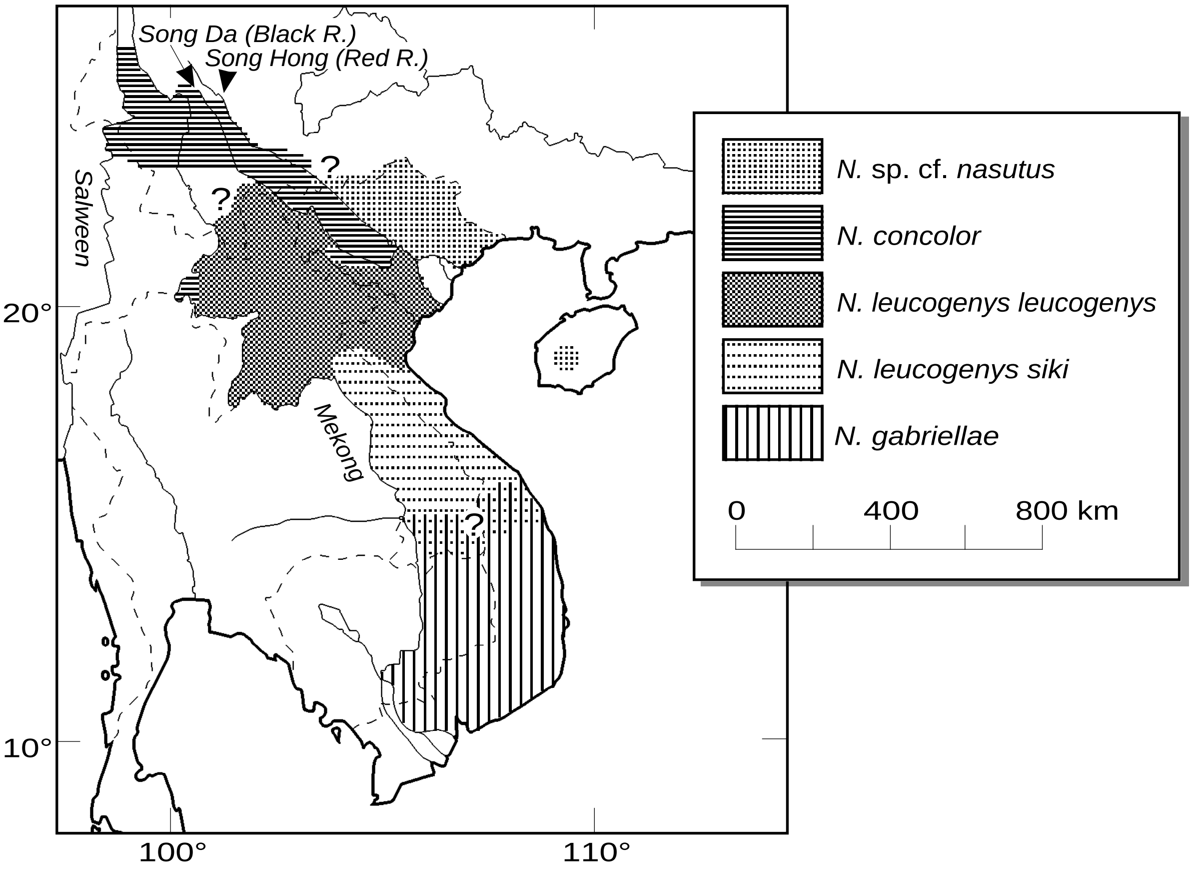


Fig. 3.4. Distribution of the species of the genus *Nomascus* (from Geissmann et al., 2000). Question marks refer to, from north to south, (1.) the unknown survival (and identity) of Chinese gibbons east of the red river in Yunnan Province; (2.) a large apparent gap in the distribution area of gibbons in Yunnan Province; and (3.) the unknown identity of gibbons in a large area between the distribution areas of *N. leucogenys* and *N. gabriellae*, respectively.

Geissmann (1997) and Geissmann et al. (2000) identified two unnamed forms of crested gibbon based on Zoo and Museum specimens from northeastern Vietnam. At least one of these forms, tape-recorded at the Tierpark Berlin, produced a radically distinct song, and the same type of song was found later in the population from Hainan island (Fig. 3.5). Although both northeastern populations and the Hainan population have been previously attributed to *N. concolor,* they should be recognised as three subspecies of a distinct species, tentatively identified here as *Nomascus* sp. cf. *nasutus*. The estimated original distribution area of the species is shown in Fig. 3.4.

Chances that the species will survive the next 50 years are very low. First, it is unclear whether the two mainland subspecies still survive in the wild. The Berlin female was caught in 1962, and the most recently shot Museum specimen stems from 1965. No recent sightings of gibbons have been reported from northeastern Vietnam. Second, the author's own survey on Hainan revealed that the island form is probably down to less than 20 individuals, suggesting that this may be one of the rarest primate species world-wide.

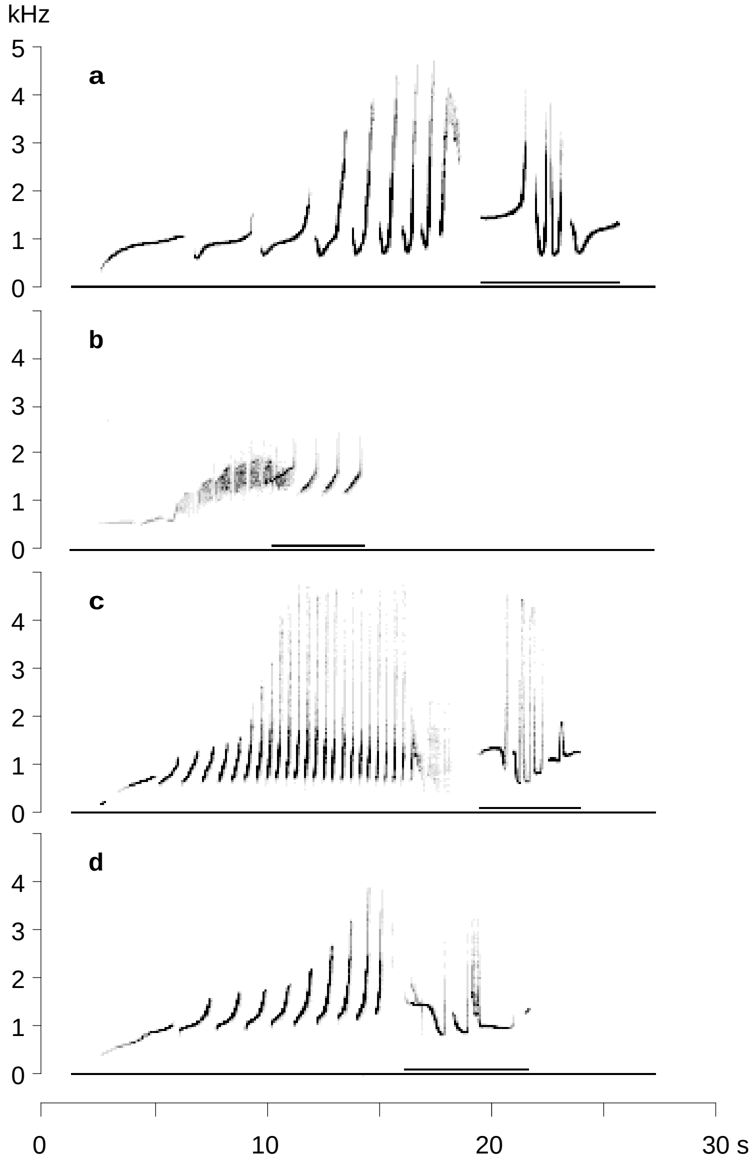


Fig. 3.5. Great call phrases, uttered as a duet by mated pairs, of four species of crested gibbons. Male contributions are underlined. a. *Nomascus concolor* (Ailao mountains, Yunnan Prov., China), b. *N.* sp. cf. *nasutus hainanus* (Bawangling Nature Reserve, Hainan, China), c. *N. leucogenys leucogenys* (Paris, Ménagerie, France), d. *N. gabriellae* (Mulhouse Zoo, France) (from Geissmann, 1997).

Evolution of gibbon songs

Duet-splitting and the evolution of gibbon songs (Geissmann, in press a)

Unlike the great apes and most other primates, all species of gibbons are known to produce elaborate, species-specific and sex-specific patterns of vocalisation usually referred to as "songs". In most, but not all, species, mated pairs may characteristically combine their songs in a relatively rigid pattern to produce coordinated duet songs. Previous studies disagreed on whether duetting or the absence of duetting represented the primitive condition in gibbons.

Geissmann (in press a) compared singing behaviour in all gibbon species. Various vocal characteristics were subjected to a phylogenetic analysis using previously published phylogenetic trees of the gibbon radiation as a framework. Variables included the degree of sex-specificity of the vocal repertoire, the occurrence of solo songs, and the preference for a specific time of day for song-production.

The results suggested the following scenario for the evolution of gibbon songs, as illustrated in Fig. 3.6:

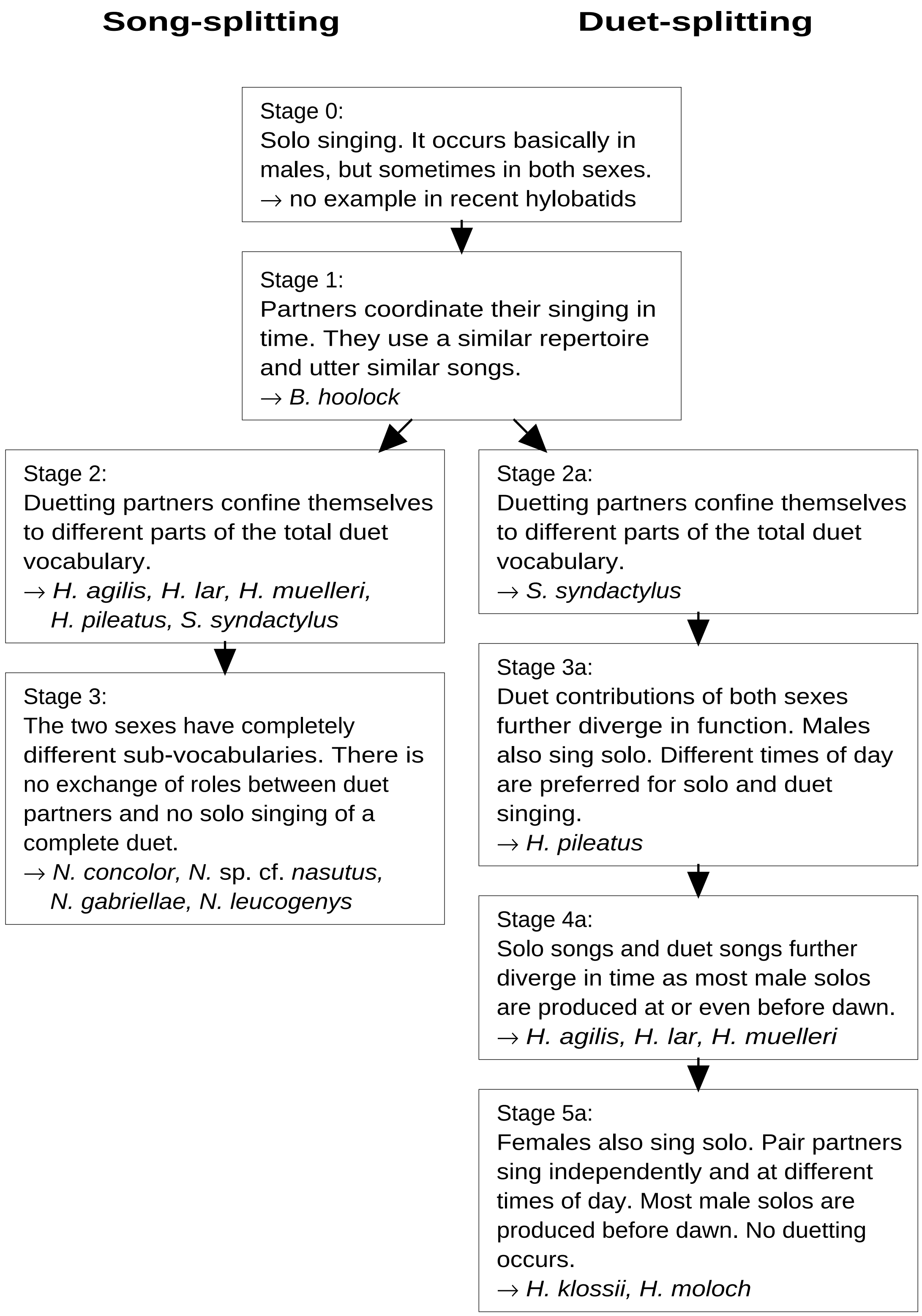
(1) The recent hylobatids represent a monophyletic group, whose common ancestor produced duet songs, although not all recent species are known to do so.

(2) Duet songs of recent gibbon species are likely to have evolved according to the song-splitting theory: gibbon duets probably evolved from a song which was common to both sexes and which only later became separated into male-specific and female-specific parts.

(3) In the evolution of gibbon songs, a process tentatively called "duet-splitting" is suggested to have led secondarily from a duetting species to a non-duetting species, in that the contributions of the pair partners split into temporally segregated solo songs. This appears to be the first time that a non-duetting animal was shown to be derived from a duetting form.

(4) The final stage of the duet-splitting process is represented by two species, *H. klossii* and *H. moloch*, which probably represent a monophyletic group.

(5) The return to exclusive solo singing may be related to the isolated island distribution of the non-duetting species.



Song-splitting

Duet-splitting

Stage 0:
Solo singing. It occurs basically in males, but sometimes in both sexes.
→ no example in recent hylobatids

Stage 1:
Partners coordinate their singing in time. They use a similar repertoire and utter similar songs.
→ *B. hoolock*

Stage 2:
Duetting partners confine themselves to different parts of the total duet vocabulary.
→ *H. agilis, H. lar, H. muelleri, H. pileatus, S. syndactylus*

Stage 3:
The two sexes have completely different sub-vocabularies. There is no exchange of roles between duet partners and no solo singing of a complete duet.
→ *N. concolor, N.* sp. cf. *nasutus, N. gabriellae, N. leucogenys*

Stage 2a:
Duetting partners confine themselves to different parts of the total duet vocabulary.
→ *S. syndactylus*

Stage 3a:
Duet contributions of both sexes further diverge in function. Males also sing solo. Different times of day are preferred for solo and duet singing.
→ *H. pileatus*

Stage 4a:
Solo songs and duet songs further diverge in time as most male solos are produced at or even before dawn.
→ *H. agilis, H. lar, H. muelleri*

Stage 5a:
Females also sing solo. Pair partners sing independently and at different times of day. Most male solos are produced before dawn. No duetting occurs.
→ *H. klossii, H. moloch*

Fig. 3.6. Gibbon species arranged according to the song-splitting hypothesis (gibbon duets probably evolved from a song which was common to both sexes and which only later became separated into male-specific and female-specific parts) and the duet-splitting hypothesis (a process tentatively called "duet-splitting" is suggested to have led secondarily from a duetting species to a non-duetting species, in that the contributions of the pair partners split into temporally segregated solo songs) (from Geissmann, in press a).

A link to human music?

Gibbon songs and human music in an evolutionary perspective

The interesting questions, when comparing gibbon and human singing, are: do similarities between gibbon and human singing help us to reconstruct the evolution of human music (especially singing)? and are these similarities pure coincidence, analogous features developed through convergent evolution under similar selective pressures, or the result of evolution from common ancestral characteristics? Geissmann (2000b) provided the first study assessing these questions.

Music may be one of the most ancient and universal forms of human communication. Song is one of the most prominent features in most forms of popular music, and the human voice has often be identified as the most ancestral instrument used in music (Ewens, 1995).

In contrast to birds, singing behaviour is rare in mammals and, among nonhuman primates, is known only for members of the following four groups – the genera *Indri*, *Tarsius*, *Callicebus*, and the gibbons (Hylobatidae) (Robinson 1979, 1981; MacKinnon & MacKinnon, 1980; Haimoff, 1986; Niemitz et al., 1991; Geissmann, 1993; Thalmann et al., 1993; Müller, 1994, 1995; Nietsch & Kopp, 1998). These singing primates comprise about twenty-six species (depending on the currently accepted taxonomy), amounting to about 11% of primate species or 6% of primate genera.

In all singing primates, males and females both sing, and in most singing primates, duet singing occurs. It is interesting to note that all primate species that are known to sing are also thought to have a monogamous social structure. In birds, too, duet songs mainly occur in monogamous species. This suggests that the evolution of singing behaviour in primates and of duet singing behaviour in general are somehow related to the evolution of monogamy.

Since the four species groups of primates that exhibit singing (and duet singing) behaviour are not closely related, it is likely that singing (and duet singing) evolved four times independently within the order of primates (Fig. 3.7).

As pointed out by Geissmann (2000b), both the context in which singing occurs in nonhuman primates and the structure of some song contributions show similarities to territorial calls or alarm calls in non-singing species. This suggests that singing in primates evolved each time from loud calls used in a territorial or alarm context. It makes sense to assume that the same applies to the evolution of human singing behaviour, and that loud calls of early hominids may have been the substrate from which human singing and, ultimately, music evolved.

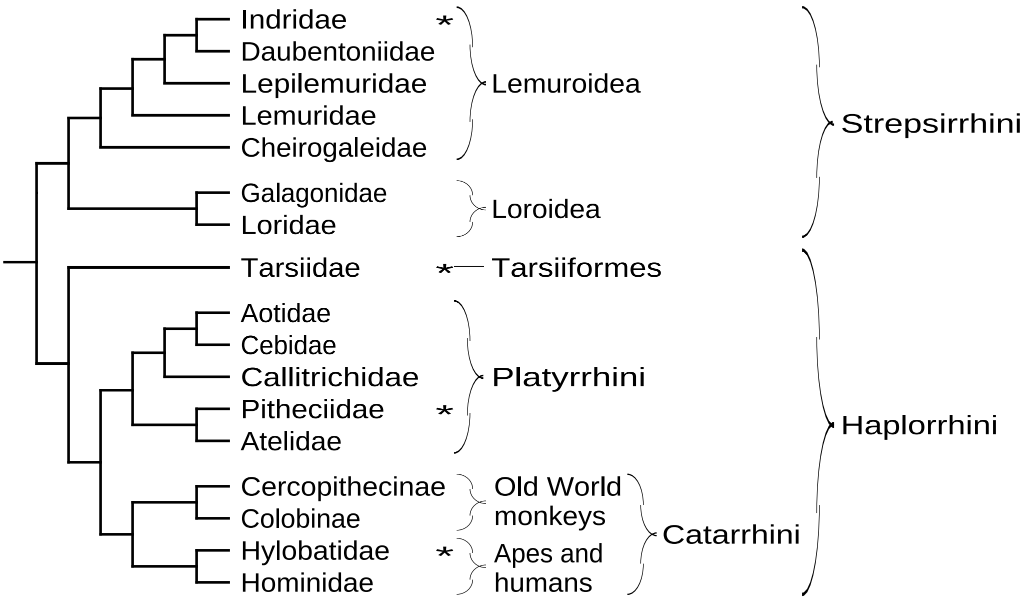


Fig. 3.7. Phylogenetic tree of extant primate families and some subfamilies (phylogeny adapted from Purvis, 1995; nomenclature after Groves, 1993a). Stars indicate singing and duet singing behaviour which is known of only four primate genera (*Indri*, *Tarsius*, *Callicebus*, *Hylobates*) representing four only distantly related species groups (from Geissmann, 2000b).

Most forms of music are tied to emotionality and have a powerful effect on both the audience and the performer, compelling them to shake body parts to the rhythm, beat the rhythm by clapping or stomping, or locomote (dance) to the rhythm. Often, dancing appears to be inseparably linked with music (Ewens, 1995; McNeill, 1995). The almost universal, almost hypnotic effect of music on most humans suggests that this is an ancestral characteristic that may have a strong inherited component. In addition, this behaviour bears an obvious similarity to the ritualised locomotor displays (drumming, stomping, branch shaking) associated with loud calls of many Old World primates, providing additional support that music is derived from loud calls.

It is tempting to assume that early hominid singing shared many characteristics with loud calls of modern Old World monkeys and especially apes, such as loudness for long distance communication, pure tonal quality of notes, use of stereotyped phrases, use of biphasic notes, accelerando in note-rhythm and possibly a slow down near the end of the phrase, a locomotor display, and a strong inherited component.

After the divergence between early humans and some forms of African apes from a common ancestor, several characteristics of human music evolved that are not found in loud calls of modern monkeys and apes. The most conspicuous of these are a steady rhythm (pulse, beat), reduction of inherited stereotypy in favour of increased importance of learning phrases and sequence rules, and the option to invent new signal patterns (improvisation) and new conventions (exact repetition of improvised units) spontaneously. Universals of human music are difficult to identify but probably include a steady, accentuated beat (see Arom, 2000;

Nettl, 2000; Mâche, 2000). Although some primates are able to produce short, monosyllabic calls for several seconds at a relatively steady pulse (e.g. some galagos [Galagonidae, E. Zimmermann, personal communication], mouse lemurs [Cheirogaleidae] and gibbons [Geissmann, unpublished observations]), nonhuman primates, unlike humans, do not seem to be able to keep a steady pulse in their song vocalisations (Williams, 1967).

What fitness advantage is there to add a steady beat to a song vocalisation? The beat may help larger social groups to participate in a song, to coordinate it. A well-coordinated song may be a more effective display than a cacophony of voices, and other social groups are less likely to attack or threaten well coordinated groups. In addition, introduction of a steady beat may make it easier to assess a group's cohesiveness and therefore its strength based on the group display.

The main message of Geissmann's (2000b) paper is that loud calls in modern apes and music in modern humans are derived from a common ancestral form of loud call. If this interpretation is correct, early hominid music may also have served functions resembling those of ape loud calls. Loud calls are believed to serve a variety of functions, including territorial advertisement; inter-group intimidation and spacing; announcing the precise locality of specific individuals, food sources, or danger; and strengthening intra-group cohesion. The most widely distributed (albeit not universal) function, and probably the most likely function of early hominid music, is to display and possibly reinforce the unity of a social group toward other groups. In humans, this function is still evident today whenever groups of people, be they united by political, religious, age, or other factors, define themselves by their music. National anthems, military music, battle songs of fans and cheerleaders encouraging their favourite sports teams, or the strict musical preferences of youth gangs may serve as examples of this phenomenon, whose origin may go back to the very beginning of human evolution.

Reconstructing gibbon phylogeny

Taxonomy and evolution of gibbons

Because the fossil history of gibbons is virtually unknown (Fleagle, 1999; Geissmann, 1993), gibbon evolution can only be reconstructed from a comparative analysis of evolutionarily informative characteristics of modern gibbons and, to some degree, of related primate taxa that can be used as outgroups.

Several studies tried to reconstruct gibbon phylogeny, using fur coloration, morphological, vocal or molecular data (e.g., Groves, 1972; Chivers, 1977; Haimoff at al., 1982; Creel & Preuschoft, 1984; Garza & Woodruff, 1992; Hayashi et al., 1995; Purvis, 1995). Each study produced a different result. As a result, the relationships among the various hylobatids are under debate and even the evolutionary relationships among the major groups of gibbons remain unresolved (Hall et al., 1998).

Geissmann (in press c) collected three different data sets of about equal size in order to assess their relevance for a reconstruction of gibbon phylogeny with cladistic methods: Set 1 used characteristics of fur coloration, set 2 consisted of mainly morphological and anatomical data, and set 3 consisted of vocal data.

The suitability of each data set for the reconstruction of a gibbon phylogeny was judged by criteria such as (among others) the number of bootstrap values above 50, the number of shortest trees, the consistency index of the trees, and the degree by which pairwise distances between taxa of different subspecies, species and genera, respectively, were overlapping.

Trees calculated with each data set are shown in Fig. 3.8, whereas various parameters used to assess the quality of the trees (and, therefore, the data sets) are shown in Table 3.1 and Fig. 3.9.

The cladistic analysis suggested that the tempo of evolutionary change differed among the data sets under study, similar to DNA sequences derived from different parts of the genome. Fur coloration characters appeared to change considerably faster than each "non-communicatory" and vocal characters.

The three data sets produced different results and each set appeared to be suited to the analysis of different levels of resolution within the hylobatid radiation. Fur coloration characteristics appeared to provide little information for a gibbon phylogeny, but appeared be valuable tools for subspecies identification, in contrast to most characters of the other two data sets. In addition, many fur coloration characters differed among individuals of the same taxon (polymorphisms).

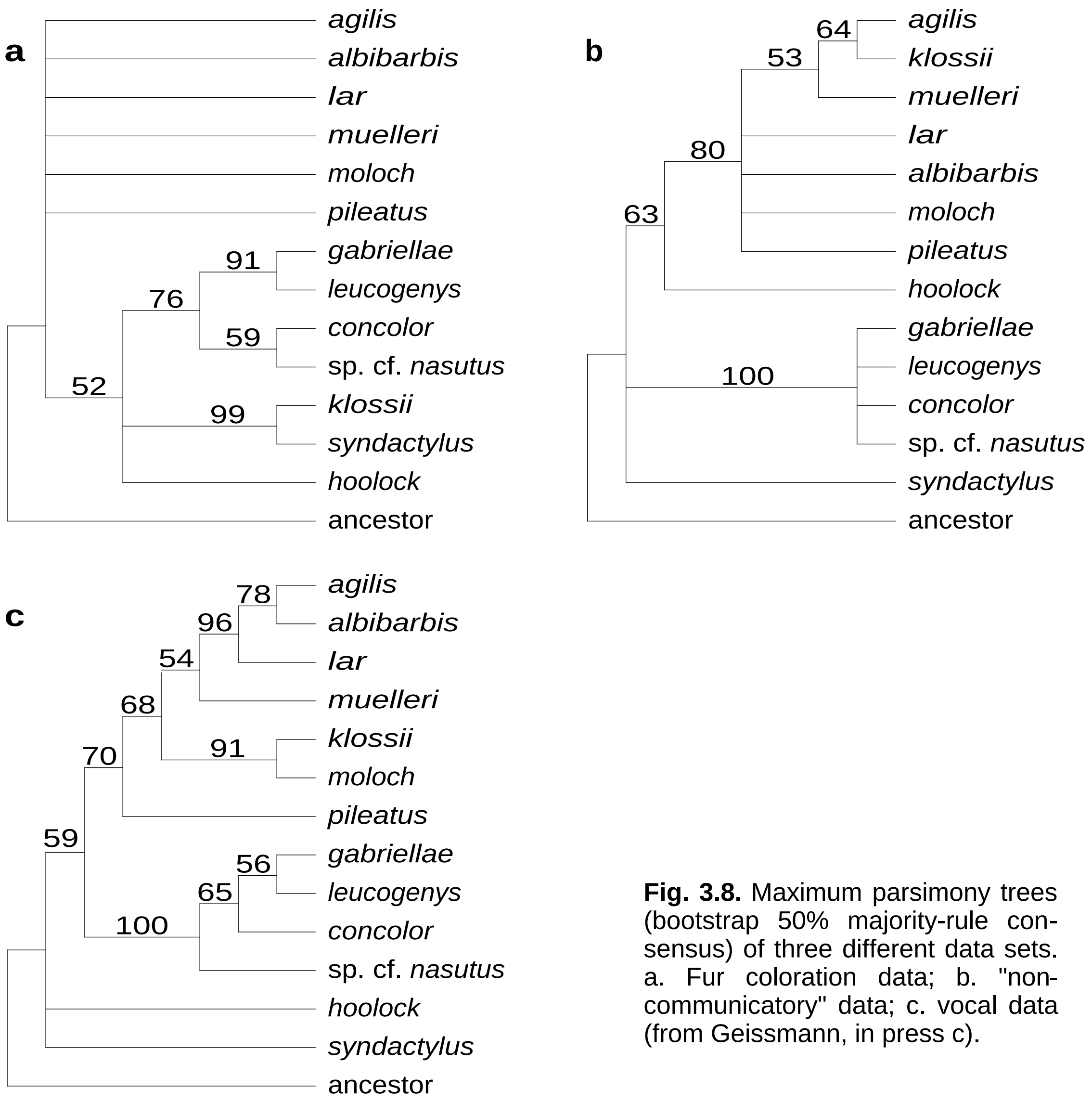


Fig. 3.8. Maximum parsimony trees (bootstrap 50% majority-rule consensus) of three different data sets. a. Fur coloration data; b. "non-communicatory" data; c. vocal data (from Geissmann, in press c).

Table 3.1. Various parameters of the trees in Figure 3.8 (from Geissmann, in press c).

Data set	**Set 1:** Fur coloration data	**Set 2:** "Non-communicatory" data	**Set 3:** Vocal data
Number of characters	37	34	34
Tree length of shortest tree	158	73	88
Number of bootstrap values above 50	5	5	10
Number of shortest trees	2	117	1
Consistency Index CI	0.41	0.62	0.66

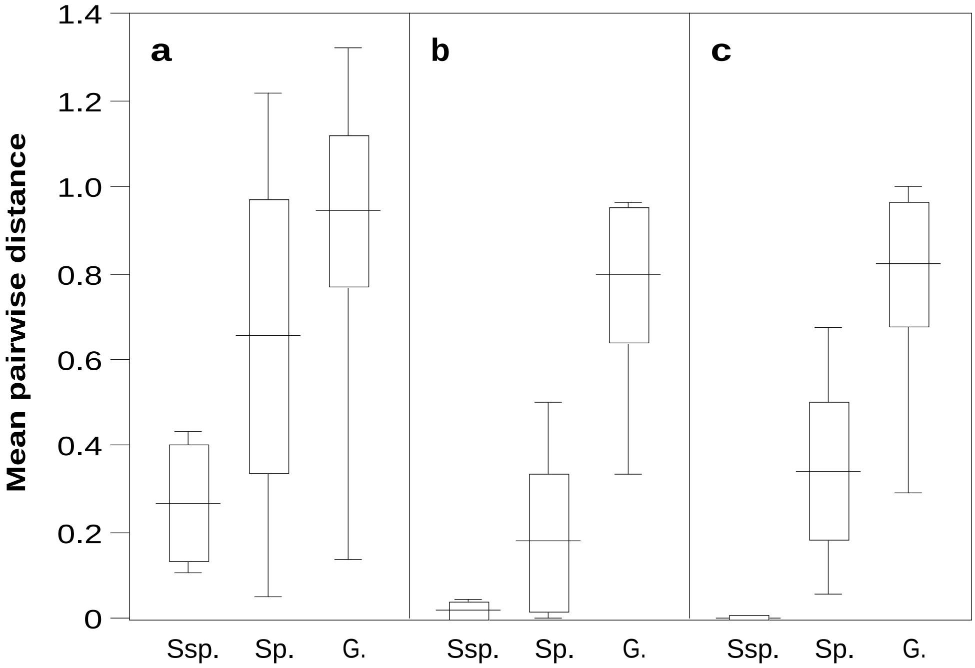


Fig. 3.9. Pairwise character differences between (from left to right) different subspecies (Ssp.) of the same species, species (Sp.) of the same genus, and genera (G.) of the same genus. a. Fur coloration data; b. "non-communicatory" data; c. vocal data. Each box plot shows the mean value (horizontal line through box), standard deviation (box) and range ("whiskers") (from Geissmann, in press c).

"Non-communicatory" data appeared to be much better suited for reconstructing the gibbon phylogeny, but it was vocal data which produced the most reliable phylogeny of the three data sets (Fig. 3.9).

The trees generated with vocal data (Fig. 3.8c) suggest:

– The gibbons of the genus *Hylobates* (*lar* group) and the genus *Nomascus* (crested gibbons or *concolor* group) each are monophyletic groups. There is weak support for a sister group relationship between the *concolor* and *lar* groups.

– *Hylobates klossii* is neither the sister taxon of the siamang (*S. syndactylus*) as suggested by some early studies (Elliott, 1913; Miller, 1903), nor the sister taxon or the most basal group of the *lar* group, in contrast to many previous studies (Chivers, 1977; Haimoff at al., 1982; Creel & Preuschoft, 1984; Purvis, 1995; Schultz, 1933). This species is a fully integrated member of the genus *Hylobates* (Garza & Woodruff, 1992), and apparently the sister taxon of *H. moloch*. The same conclusion was independently reached by a study using a much smaller set of vocal characteristics (including the degree of sex-specificity of the vocal repertoire, the occurrence of solo songs and the preference for a specific time of day for song production) (Geissmann, in press a).

– *Bunopithecus hoolock* may be more basal than previously believed. Most earlier studies recognised this species as the sister taxon to the genus *Hylobates* (Chivers, 1977; Haimoff at al., 1982; Purvis, 1995), whereas a more basal position has only rarely been suggested (Creel & Preuschoft, 1984; Geissmann, in press a).

The radiation of the four genera is not reliably resolved with these preliminary results. A better resolution could possibly be obtained with larger data sets. DNA sequence data appeared particularly promising in this respect. This possibility was evaluated on the following study.

Molecular phylogeny of the major hylobatid divisions (Roos & Geissmann, 2001)

Although the monophyly of the gibbons (family Hylobatidae) is widely accepted, this is not the case for the taxonomy adopted within the family. In early studies on gibbon systematics, the Hylobatidae were grouped into two distinct genera including the siamang (*Symphalangus*) on one hand, and all the remaining gibbons (*Hylobates*) on the other (e.g. Napier and Napier, 1967; Schultz, 1933; Simonetta, 1957). When gibbons were studied in more detail, however, it became clear that four, not two, major hylobatid divisions needed to be recognised. These groups have generally been accepted as four distinct subgenera (i.e. *Symphalangus*, *Nomascus*, *Bunopithecus*, and *Hylobates*, respectively) (Geissmann, 1994, 1995b; Marshall and Sugardjito, 1986; Nowak, 1999; Prouty et al., 1983; Rowe, 1996).

The phylogenetic relationship between these four major groups is still unknown. Most previous studies were based on morphology, vocalisation, electrophoretic protein evidence and karotyping and have differed in their conclusions (Bruce and Ayala, 1979; Creel and Preuschoft, 1984; Geissmann, 1993, in press c; Groves, 1972; Haimoff et al., 1982; Liu et al., 1987; Shafer, 1986). Even the use of molecular techniques mainly based on mitochondrial DNA sequences was not able to resolve the evolutionary relationship between the gibbon subgenera (Garza and Woodruff, 1992; Hall et al., 1998; Hayashi et al., 1995; Zehr, 1999; Zhang, 1997). Furthermore, most molecular studies did not include the subgenus *Bunopithecus* and therefore presented an incomplete view on gibbon evolution (Garza and Woodruff, 1992; Hayashi et al., 1995).

Roos and Geissmann (2001) described DNA sequences for the mitochondrial control region and phenylalanine-tRNA from the four extant gibbon subgenera. The mitochondrial control region is known to evolve faster than other parts of mtDNA and may therefore be more suited to resolve a radiation which evolved over a short time-span than sequences used in previous studies (Garza and Woodruff, 1992; Hall et al., 1998; Hayashi et al., 1995; Zehr, 1999; Zhang, 1997).

To determine the phylogenetic affiliations among the gibbon subgenera and the hominids, sequences of all the gibbons, human, common and pygmy chimpanzee were aligned. The complete alignment of the control region and adjacent Phe-tRNA was 1238 bp in length. After the exclusion of gaps and poorly aligned positions, the final alignment was 857bp in length with 574 (67%) constant sites.

In contrast to earlier studies on gibbon phylogeny that used other parts of the mtDNA, the control region depicts the crested gibbons (*Nomascus*) as the most basal group of the Hylobatidae, followed by *Symphalangus*, with *Bunopithecus* and *Hylobates* as the last to diverge (Fig. 3.10).

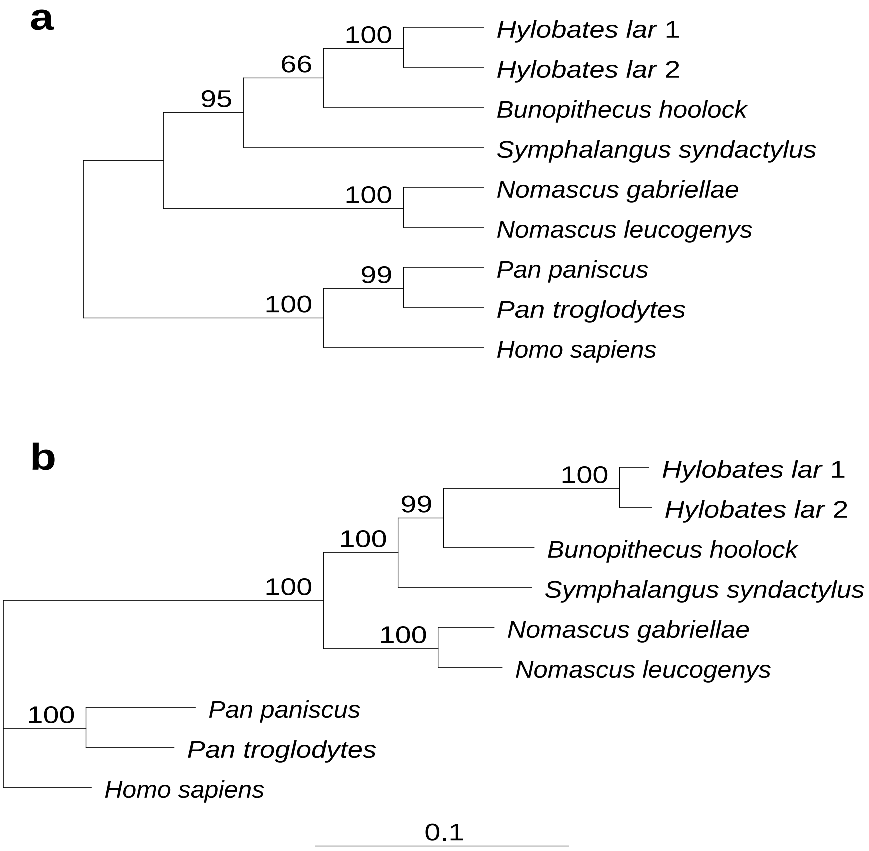


Fig. 3.10. 50%-majority-rule consensus trees the for neighbour-joining (b) and maximum likelihood (c) methods. The maximum likelihood tree is unrooted. Branch lengths are drawn according to the number of substitutions per position with the bar indicating 0.1 substitutions per site (from Roos & Geissmann, 2001).

By considering the pure observed sequence distances and not taking different generation times into account, it was obvious that the distances between the four gibbon subgenera were in the same range as those between *Homo* and *Pan*, or even higher. The uncorrected average distances were 10.3% between *Hylobates* and *Bunopithecus*, 10.6% between *Symphalangus* and the *Bunopithecus*-*Hylobates* clade, and 12.8% between *Nomascus* and the other three subgenera. In contrast, the distance between *Homo* and *Pan* was only 9.6%. Based on these findings, Roos and Geissmann (2001) propose to raise all four gibbon subgenera to genus rank.

4. Gibbon conservation

Estimating population size and density based on gibbon vocalisations

Density estimation by use of song bouts

Geissmann and Nijman (2001) documented that gibbon songs are an appropriate mean to estimate gibbon density. Their study on silvery gibbons (*H. moloch*) was carried out in the hill rain forest of the Dieng mountains (Central Java, Indonesia).

Song data from a fixed point count suggested that densities in the surroundings of the study site (Linggo Asri) were in the order of 1.9-3.7 groups per km^2 based on a small area ($\leq$1.2 km^2) with individually recognisable groups, and 1.5-2.4 groups per km^2 based on a larger area ($\leq$5.1 km^2), including non-identified groups. The lower estimate for the larger area may reflect non-homogeneous densities or greater inaccuracy in estimating number of groups and distance for more remote groups. Densities reported from lowland sites on Java are in the order of 1.9-2.9 groups per km^2, with average group sizes between 3-5 individuals (Kappeler, 1981, 1984b; Gurmaya et al., 1995; Rinaldi, 1999; Supriatna et al., 1994). Geissmann and Nijman's (2001) density estimate is higher than previously reported by Nijman and van Balen (1998). Taking into account the higher densities of gibbons in the Dieng mountains, and since Nijman & van Balen (1998) followed Supriatna et al. (1994) in assuming that gibbons do not inhabit the forest edge, which they clearly do, the previous estimate of 519-577 gibbons for the Dieng mountains as a whole (Nijman & van Balen 1998) might be an under-estimate.

Primates are frequently used as indicator species in monitoring programs. Although line transects may be the most commonly employed method to establish densities (Brockelman & Ali, 1987; Whitesides et al., 1988), for species that call at predictable times of the day, like gibbons, fixed point counts are a frequently used alternative (e.g., Haimoff et al., 1986; Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993). Fixed point counts have been used previously in the study of silvery gibbons (Kappeler, 1981, 1984a; Kool, 1992; Nijman & van Balen, 1998; Nijman, 2000). Because Kappeler's (1981, 1984b) study suggested that only mated female silvery gibbons sing, it has been assumed that every vocalising individual represents a family group (e.g. Nijman & van Balen, 1998). Densities are estimated by multiplying the average group size with the number of groups per area unit. Geissmann and Nijman's (2001) findings indicate that at least 8.5% of gibbon calls heard in Central Java are male songs. Although there is little information concerning male calling in other parts of Java, Gurmaya et al. (1995) and Rinaldi (1999) report that gibbon songs are occasionally heard well before dawn in Ujung Kulon. These calls may well have been produced by males. If in other areas, as in Dieng, some 8.5% of the songs heard are in fact male songs, it may imply that densities in the past may have been over-estimated considerably. In order to accurately estimate densities a (site-specific) correction factor has to be taken into account, or, better still, male and female calls have to be separated during data collection.

With practice, silvery gibbons can be recognised individually by their song (Kappeler 1884c; Dallmann & Geissmann, 2001a, 2001b). Individual groups can thus be studied more easily without many of the difficulties involved in observing primates in tall tropical rain forest, without intruding into their habitat, without habituating groups, and without disturbing groups. As such, vocal recognition might be a more suitable tool for surveying and studying this critically endangered primate than some traditional methods. Vocal recognition furthermore facilitates longitudinal studies (Baptista & Gaunt, 1997) which otherwise often require intrusive methods.

Captive management and conservation of captive gibbons in Indochina

Captive management and conservation of gibbons in China and Vietnam

Geissmann (1995a) carried out a first census of captive gibbons in selected zoos and primate holding institutions of China and Vietnam. Gibbons are kept in 11 of the 12 visited institutions.

In Chinese institutions, *B. hoolock* was relatively common, whereas in Vietnam, *N. gabriellae* was the species most frequently seen in captivity. Some of the other gibbon forms distributed in these countries were particularly rare in captivity (*N. concolor, N. leucogenys siki*) or not seen at all (*N.* sp. cf. *nasutus, H. lar yunnanensis*). Their numbers in captivity probably reflect the status of these taxa in the wild.

The surveyed captive population is characterised by: 1. virtual absence of breeding, 2. high influx of young animals from the wild, and 3. probably low survival rate.

Although it may be possible to build up self-sustaining captive gibbon populations in China and Vietnam – at least for *B. hoolock* and perhaps *N. gabriellae* – this goal cannot be reached in the near future without an improvement of captive management. Some suggestions for improvement concern cage size, cage furniture, distance between gibbon groups, the social unit of gibbons, the coordinated exchange of gibbons between zoos, and the confiscation of gibbons from animal dealers.

Status and conservation of wild gibbons in Vietnam

*A brief survey of the yellow-cheeked gibbon (*N. gabriellae*) in Nam Bai Cat Tien (southern Vietnam) (Geissmann, 1995c)*

Geissmann (1995c) collected data concerning the status, habitat and vocalisations of yellow-cheeked crested gibbons (*N. gabriellae*) during a short field trip to the Nam Bai Cat Tien National Park (southern Vietnam). Nam Bai Cat Tien may be the southernmost locality where crested gibbons (genus *Nomascus*) still survive.

Fewer songs were heard at Nam Bai Cat Tien National Park than at other crested gibbon sites visited by the author. Geissmann revisited the territories (two forested hills) of two gibbon groups which had been observed during two previous surveys (Adler, 1990, 1991, 1993; Eames & Robson, 1993; Robson, 1990). Geissmann (1995c) found that the forest tract of one gibbon group had been cleared in the meantime whereas the forested area of the second group had been severely decimated. The first gibbon group had disappeared (probably hunted). A female solo song was heard of the second gibbon group, suggesting that at least one individual of that group was surviving in a very small isolated forest fragment. This study documents that Vietnamese gibbons are poorly protected even in National Parks.

*A survey of the eastern black crested gibbon (*N. *sp. cf.* nasutus*) in northeastern Vietnam*

The eastern black gibbon (*Hylobates* sp. cf. *nasutus*) appears to be the most critically endangered primate species. Recent reports provided some hope that the species may still survive in two areas of northeastern Vietnam (provinces of Bac Kan and Thai Nguyen). In order to investigate on these reports, Geissmann and Vu Ngoc Thanh (2001) conducted a brief survey of diurnal primates in the corresponding areas. In both areas, nonhuman primates appeared to be both heavily decimated in numbers and particularly shy. Only *Macaca arctoides* was occasionally encountered, other macaque species (*M. assamensis* or *M. mulatta*) may have disappeared from the survey areas. *Trachypithecus francoisi* appeared to be rare, and *Rhinopithecus avunculus* is probably extinct in the survey areas. Gibbons were neither sighted nor reliably heard during the survey, but evidence from interviews with numerous local hunters appeared to indicate that a small gibbon population may still exist in at least one of the surveyed areas (Kim Hi forest, Bac Kan province).

The authors identified over-utilisation of wildlife for trade and subsistence as the most immediate threat to wildlife conservation in general and of gibbon conservation in particular in the survey areas. Gibbons are not primarily hunted for food but for pharmacological products which yield very high prices and result in a high hunting pressure on gibbons and some species of monkeys.

In addition, gold mining activities were found to have a strong influence on the ecosystem in both survey areas. Not only are forests cleared in the mining location, but the miners need wood for construction works and cooking. In addition, the presence of large communities of miners also increases the hunting pressure in the adjacent forests.

The eastern black crested gibbon (*N.* sp. cf. *nasutus*) appears to be the rarest and most endangered primate species, with a global population of probably less than 50 individuals.

Vietnam gibbon conservation status review

Although several faunistic surveys have been carried out in Vietnam in recent years, survey results have rarely been published. Research results, too, are often just preliminary reports published in little-known local journals. A critical reassessment of the gibbon populations, their size and their phylogenetic affinities was urgently required.

The Vietnam Primate Conservation Status Review began implementation in July 1999 with the objective of collating a comprehensive data set for leaf monkeys and gibbons. As a first result of that project, Geissmann et al. (2000) published the "Vietnam primate conservation status review 2000 - Part 1: Gibbons". This was not only the first nation-wide status review of Vietnamese gibbons, but also the first scientific book publication on gibbons since several years.

Based on earlier reports, museum specimens or forest quality, Geissmann et al. (2000) were able to identify 87 potential gibbon areas in Vietnam. During the last 5 years, however, the occurrence of gibbons was only confirmed for 21 of these areas. In 17 additional areas, the occurrence of gibbons is probable, albeit not reliably documented. In 49 areas (56.3%), gibbons are possibly or probably extinct. The proportion of these areas is particularly high in northern Vietnam: *N. concolor* 61.1%, *N. leucogenys leucogenys* 74.1%, and *N.* sp. cf. *nasutus* 75%. The situation is particularly alarming for *N.* sp. cf. *nasutus* which has no reliably confirmed populations in Vietnam (12 localities evaluated). The only confirmed observations of this species were made on the Chinese island of Hainan (population: less than 20 individuals), and this species appears to exhibit the sad distinction of being the most critically endangered primate species world-wide. Other gibbons in the northern half of Vietnam are also critically endangered: *N. concolor* was confirmed in only 2 of 18 localities, and *N. leucogenys leucogenys* in only 4 of 27. These findings are summarised in Table 4.1.

Table 4.1. Status of Vietnamese gibbons (data from Geissmann et al., 2000). [a]

Status	*N.* sp. cf. *nasutus*	*N. concolor*	*N. l. leucogenys*	*N. l. siki*	*? / siki / gabriellae*	*N. gabriellae*
Total number of localities	12	18	27	6	9	15
Confirmed occurrence 1995-2000	0	2	4	5	3	7
Provisional occurrence 1995-2000	3	5	3	0	3	3
Possibly extinct [b]	9	11	20	1	3	5
	75%	61%	74%	17%	33%	33%

[a] N = 87 gibbon localities.

[b] The pooled value for both subspecies of *N. leucogenys* amounts to 67%.

5. Gibbons: The real neglected apes

In an ever increasing way, media and scientists alike have succeeded in making us aware of the plight of the great apes, while at the same time ignoring the gibbons or small apes. We are being taught that the great apes are "neglected apes", "forgotten apes" or "vanishing apes" (book titles on great apes: De Waal & Lanting, 1997; Nadler et al., 1995; Rijksen & Meijaard, 1999), and that our first conservation priority among primates should be directed at these species.

A simple review of research activities documents that not the great apes, but the small apes are the true neglected or forgotten apes. For instance, at the last Congress of the American Society of Primatologists, great apes were represented in numerous presentations as follows: *Gorilla* 18; *Pan* 31; *Pongo* 5. In contrast, the small apes were represented as follows: *Bunopithecus* 0, *Hylobates* 0, *Nomascus* 0, *Symphalangus* 0 (source: American Journal of Primatology 54 Supplement - 2001, pp. 200-201).

Similarly, a simple review of the population numbers suffices to show that conservation priorities should be directed at small apes (Table 5.1). Whereas even the most endangered species of great apes (*Pongo abelii*) still has populations of more than 10,000 individuals in the wild, there are at least three gibbon species (e.g. *Nomascus concolor*, *N.* sp. cf. *nasutus*, *Hylobates moloch*) with less than 3,000 individuals. Population sizes of several other gibbon species have not been estimated since the early 1980's and population numbers of several other species are simply "data deficient."

In Asia, habitat destruction is particularly severe for gibbons because they are more dependent on habitat quality than most other Asian primates. In 1987, all gibbons were estimated to have lost more than 50% of their original habitat, except Kloss's gibbons (*H. klossii*) and Bornean gibbons (*H. muelleri*) (MacKinnon, 1987; MacKinnon & MacKinnon, 1987). In all probability, the amount of habitat loss has increased since these estimates were made.

Javan silvery gibbons (*H. moloch*), for instance, have lost a drastic 96% of their original habitat (MacKinnon, 1987). Kappeler (1984a) estimated that fewer than 8,000 Javan gibbons remained in 1978. In 1994, this estimate was revised to 400-3,000 individuals (Asquith et al., 1995; Supriatna et al., 1994).

Table 5.1. Classification [a] of the Hominoidea, with estimates of the total population sizes of each species. Notice that the majority of population estimates for gibbons were published in 1987, whereas more recent estimates for great apes are available (from Geissmann, submitted).

Hylobatidae		**Population estimate** [b]	**References** [c]
Bunopithecus hoolock	Hoolock, white-browed gibbon	169,000	(1)
Hylobates agilis	Agile gibbon	850,000	(2)
Hylobates klossii	Kloss's gibbon	36,000	(2)
Hylobates lar	Lar, white-handed gibbon	233,000	(3)
Hylobates moloch	Javan gibbon, silvery gibbon	400-3,000	(4)
Hylobates muelleri	Bornean gibbon, Müller's gibbon	1,168,000	(2)
Hylobates pileatus	Pileated gibbon	33,600	(1)
Nomascus concolor	Western black crested gibbon	1,000	(5)
Nomascus gabriellae	Yellow-cheeked crested gibbon	DD	
Nomascus leucogenys	White-cheeked crested gibbon	DD	
Nomascus sp. cf. *nasutus*	Eastern black crested gibbon	50	(6)
Symphalangus syndactylus	Siamang	360,000	(2)
Hominidae			
Gorilla beringei	Eastern gorilla	17,000	(7)
Gorilla gorilla	Western gorilla	94,000	(7)
Homo sapiens	Human	6,000,000,000	(8)
Pan paniscus	Bonobo	40,000	(7)
Pan troglodytes	Chimpanzee	200,000	(7)
Pongo abelii	Sumatran orang-utan	12,000	(9)
Pongo pygmaeus	Bornean orang-utan	15,000	(9)

[a] Consensus classification reached at the Workshop "Primate Taxonomy for the New Millennium" held in Orlando, FL, U.S.A., 25-29 February 2000

[b] DD= data deficient

[c] (1) MacKinnon & MacKinnon (1987);
(2) MacKinnon (1986, 1987);
(3) pooled estimates from MacKinnon (1986, 1987) for Indonesia / Malaysia, and MacKinnon & MacKinnon (1987) for Indochina;
(4) Asquith et al. (1995), Supriatna et al. (1994, p. 2);
(5) Wang et al. (2000);
(6) Geissmann & Vu Ngoc Thanh (2001);
(7) Butyinski (2000);
(8) NCSE (1999), U.S. Bureau of the Census (1999, p. 9);
(9) Rijksen & Meijaard (1999, p. 286).

The situation in other areas is even more dramatic. The original distribution range of Chinese gibbons extended as far north as the Yellow River in historical times (Gao et al., 1981; Geissmann et al., 2000; van Gulik, 1967; Zhang et al., 1992), covering an area of approximately 2,000,000 km^2, as shown in Fig. 5.1. During the last 1,000 years, hunting and deforestation have probably heavily contributed to the extirpation of gibbons from the largest part of their former range in China. Today, Chinese gibbons are restricted to small, isolated forest fragments of southern Yunnan and Hainan (Fooden et al., 1987; Ma & Wang, 1986; Tian et al., 1996). This corresponds to an area loss of about 99%. The five gibbon species occurring in China have an estimated number of less than 1,200 individuals in total (Tian et al., 1996), whereas even the rarest one of them (*N*. sp. cf. *nasutus*) still had a population of no less than 2,000 individuals before the 1950's (Wang et al., 2000). The large scale extinction of crested gibbons from most parts of China appears to be a process which is still continuing in virtually every part of the *Nomascus* distribution area (e.g. Geissmann et al., 2000).

Whereas the research on, and conservation activities directed at, the great apes are supported by a strong lobby, gibbons tend to be overlooked whenever media, scientists, funding agencies and conservation agencies are referring to apes. Not only is the continued preference for great apes unjustified, it has in recent years contributed to divert from the increasingly critical status of many gibbon populations in the wild. Gibbons are largely ignored in current debates about ape conservation (e.g. bush meat, world heritage status for great apes etc.). If the long-standing tradition to favour great apes, or to ignore the small apes, is not consciously and actively being counteracted, it may result in the loss of several ape species.

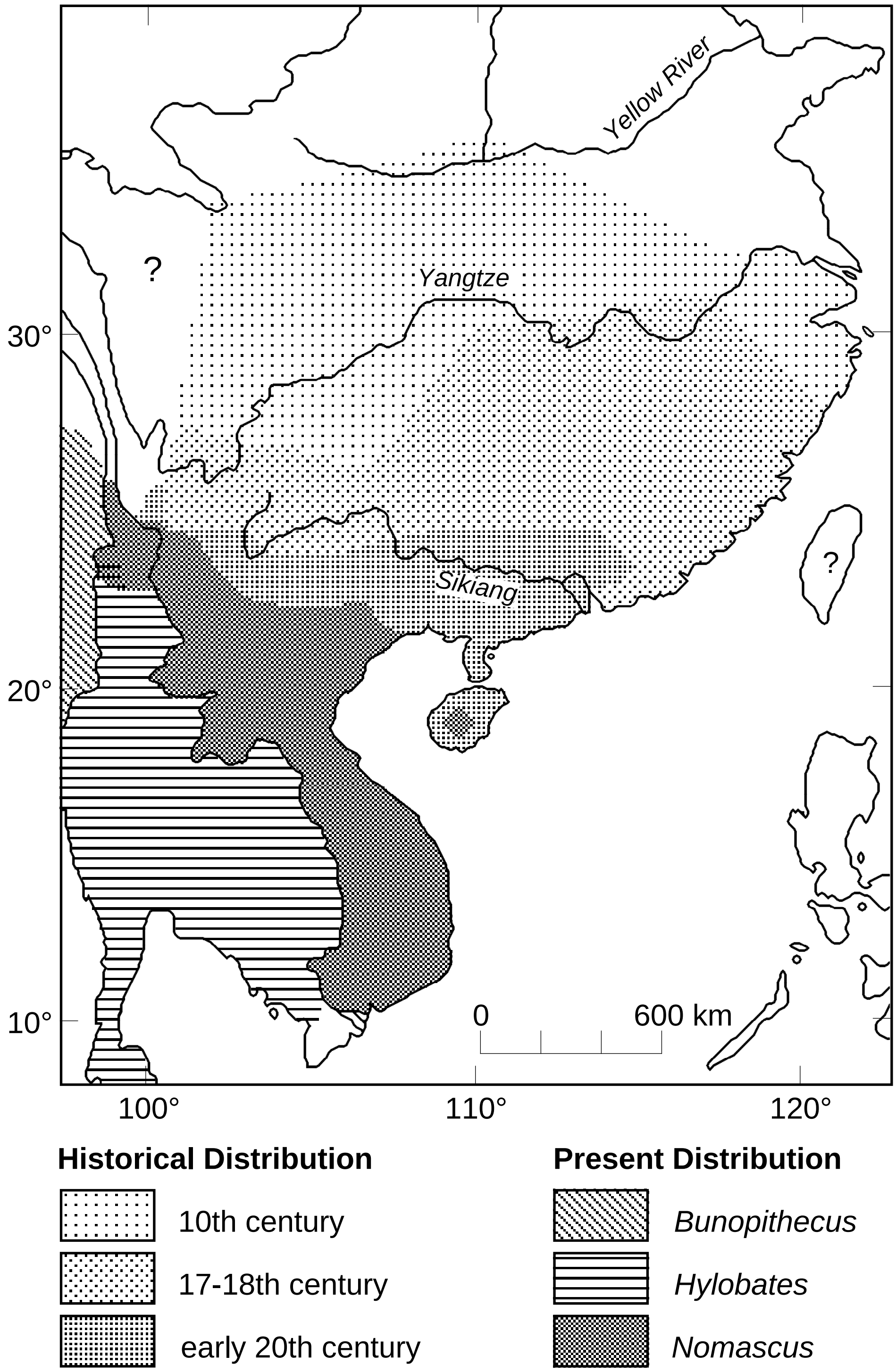


Fig. 5.1. Historical and present distribution of gibbon in China and adjacent regions (from Geissmann et al., 2001).

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Summary

Because of their basal position in the phylogeny of the recent apes and humans and because of their species diversity, the gibbons or small apes (Hylobatidae) are a key group for our understanding of the evolutionary radiation of living apes (Hominoidea). Gibbons differ not only from Old World monkeys, but also from other hominoids by several derived specialisations in their anatomy, locomotion, social structure and communication not shared by other apes. In contrast to their sister taxon, the great apes, comparatively little research is being carried out on the small apes. Therefore, the present habilitation thesis is focusing on three aspects of gibbon biology.

(1) In the first part of this thesis, various components of gibbon communication are analysed. All gibbon species produce long, loud and relatively stereotyped morning song bouts. Males and females of the silvery gibbon (*Hylobates moloch*) prefer to sing at different times of the day: Males sing more often before dawn, whereas females sing after dawn. This species is unusual among gibbons in that males rarely sing and most of the songs are female solo songs. Silvery gibbon females can easily be recognised by their songs. Female song phrases can be shown to exhibit more variability between individuals than within individuals, and more variability between populations than within populations. In spite of a previously published hypothesis, silvery gibbon females do not compensate the near absence of a family-labelling male song by an increased individuality of their female phrases. The amount of female song individuality in this species is intermediate between the variabilities exhibited by two other species (*H. klossii* and *H. agilis*), both of which exhibit more frequent male than female singing. Mated siamangs (*Symphalangus syndactylus*) produce duet songs only. These are more complex than duet songs produced by other gibbon species. Siamang duet songs may serve to strengthen the pair bond as supported by the results of two studies: (1) Upon a partner exchange, newly mated siamangs have to re-coordinate their duet contributions by a partner directed learning effort and (2) the amount of duetting siamang pairs is correlated with indicators of pair bond strength. Mirror self-recognition (MSR) has rarely been studied in gibbons. One of the studies of this thesis found first evidence for MSR capacity in a siamang and two gibbons of the genus *Nomascus*. This appears to be the first time such evidence is presented for nonhuman primates other than great apes.

(2) A second part of this thesis is focusing on gibbon diversity and evolution. Body weights of adult wild gibbons fall into three distinct size classes corresponding to the genera *Hylobates*, *Bunopithecus* and *Nomascus*, and *Symphalangus*, respectively. These differences appear to exist in neonatal body weights as well. The absence of light facial markings in the siamang has previously been regarded as a primitive characteristic. It can be demonstrated that white facial markings do occasionally occur in siamangs and that their presence is

probably a primitive feature in gibbons. Gibbon songs are shown to be useful tools in systematics. They permit to find the location of potential subspecies boundaries (e.g. in *H. moloch*), to discover previously unrecognised species (e.g. *N.* sp. cf. *nasutus*), and to reconstruct gibbon phylogeny at least on the species level. All but two species of gibbons produce duet songs. It can be shown that duetting is a primitive characteristics in gibbons and that the absence of duetting in *H. klossii* and *H. moloch* is a derived and probably synapomorphic characteristic of these two species. Singing evolved at least four times in nonhuman primates. Gibbon and human singing behaviour probably share several characteristics with, and probably evolved from, loud calls similar to those exhibited by most living Old World monkeys and apes. In contrast to previous studies, DNA sequences from the mitochondrial control region may have the potential to resolve the phylogeny of the gibbons above the species level. In addition, the distances between gibbon species groups are in the same range as those between *Pan* and *Homo*, or higher, suggesting that four distinct genera of gibbons should be recognised (previously recognised as subgenera only).

(3) The third part of this thesis is focusing on gibbon conservation. Captive gibbon populations in Vietnam and China are characterised by a virtual absence of breeding success, a high influx of young animals from the wild and a probably low survival rate. Unless these conditions are reversed, building-up of self-sustaining captive populations will not be possible. As demonstrated in the example of wild Javan silvery gibbons (*H. moloch*), song data are a valuable and non-invasive tool in estimating gibbon population size and density. Wild gibbons are still being decimated even within National Parks (as documented for Nam Bai Cat Tien, Vietnam). The eastern black crested gibbon (*N.* sp. cf. *nasutus*) appears to be the rarest and most endangered primate species with a global population of probably less than 50 individuals (distributed over Hainan and NE-Vietnam). A survey of Vietnamese gibbons reveals that gibbons probably are extinct in 56% of the areas in which they have previously been recorded or believed to occur. This proportion is particularly high in northern Vietnam, suggesting that three gibbon species are now critically endangered in Vietnam: *N. concolor* (61%), *N. leucogenys* (67%), *N.* sp. cf. *nasutus* (75%).

Media and scientists consistently portray great apes as having the highest conservation priority among apes. Unless stronger and more efficient efforts are made to conserve the more critically endangered small apes, we will, in the near future, lose several species of this radiation which is pivotal for our understanding of hominoid and human evolution. This habilitation thesis is a contribution towards the improvement of gibbon conservation.

Zusammenfassung

Aufgrund ihrer basalen Abspaltung vom Stammbaum der rezenten Menschenaffen und des Menschen sowie aufgrund ihrer hohen Artenvielfalt sind die Gibbons oder Kleinen Menschenaffen (Hylobatidae) eine Schlüsselgruppe zum Verständnis der Evolution der Menschenaffenartigen (Hominoidea). Gibbons unterscheiden sich nicht nur von den geschwänzten Altweltaffen (Cercopithecoidea), sondern auch von den anderen Menschenaffen durch viele abgeleitete Merkmale in ihrer Anatomie, Fortbewegung, Sozialstruktur und Kommunikation. Im Gegensatz zu ihrer Schwestergruppe, den Grossen Menschenaffen, wird an den Kleinen Menschenaffen jedoch kaum wissenschaftliche Forschung betrieben. Deshalb werden in der vorliegenden Habilitationsschrift drei Aspekte der Gibbonbiologie untersucht.

(1) Im ersten Teil dieser Arbeit werden vor allem verschiedene Komponenten der Gibbonkommunikation analysiert. Alle Gibbonarten produzieren lange, laute und relative stereotype Morgengesänge. Männchen und Weibchen des javanischen Silbergibbons (*Hylobates moloch*) singen bevorzugt zu verschiedenen Tageszeiten: Männchen singen öfter vor der Dämmerung, Weibchen öfter danach. Diese Gibbonart ist ungewöhnlich, weil Männchen selten singen und die meisten Gesänge Weibchensoli sind. Die Weibchen können an ihren Gesängen leicht individuell erkannt werden. Ihre Strophen weisen mehr Variabilität zwischen den Individuen auf als innerhalb der Individuen, und auch mehr Variabilität zwischen den Populationen als innerhalb der Populationen. Im Gegensatz zu einer früher publizierten Hypothese kompensieren Silbergibbonweibchen nicht die Abwesenheit von gruppen-spezifischen Männchenstrophen durch eine erhöhte Individualität ihres Gesangs. Das Ausmass ihrer Individualität liegt vielmehr intermediär zwischen den Werten für zwei andere Arten (*H. klossii* und *H. agilis*), in welchen die Männchen deutlich mehr singen als die Weibchen. Verpaarte Siamangs (*Symphalangus syndactylus*) produzieren nur Duettgesänge. Diese sind komplexer als die Duette anderer Gibbonarten. Siamang-Duette könnten eine Rolle bei der Stärkung der Paarbindung spielen. Diese Hypothese wird unterstützt durch die Resultate zweier Studien: (1) Nach einem Partnertausch müssen neuverpaarte Siamangs lernen, ihrer Duettbeiträge mit denen ihrer neuen Partner zu koordinieren, und (2) die Häufigkeit und der Zeitanteil des Duettierens korrelieren mit Indikatoren der Paarbindung. Selbsterkennung im Spiegel wurde bei Gibbons nur selten untersucht. Eine im Rahmen dieser Habilitationsarbeit durchgeführte Studie erbrachte erste Hinweise für die Selbsterkennung bei einem Siamang (Gattung *Symphalangus*) und zwei Schopfgibbons (Gattung *Nomascus*). Es handelt sich dabei vermutlich um die ersten derartigen Resultate für nichtmenschliche Primaten ausserhalb der grossen Menschenaffen.

(2) In einem zweiten Teil dieser Habilitationsschrift werden Diversität und Evolution der Gibbons untersucht. Körpergewichte adulter Gibbons fallen in drei unterschiedliche

Gewichtsklassen, welche den Gattungen *Hylobates*, *Bunopithecus* und *Nomascus*, und *Symphalangus* entsprechen. Diese Unterschiede zeichnen sich bereits bei den Körpergewichten neonataler Gibbons ab. Das Fehlen einer hellen Gesichtszeichnung beim Siamang wurde bisher als ursprüngliches Gibbonmerkmal interpretiert. Tatsächlich tritt das Merkmal, wenn auch selten, in Form einer weissen Überaugenbinde auf. Diese Entdeckung lässt annehmen, dass nicht das Fehlen, sondern die Präsenz der Merkmals ein ursprüngliches Gibbonmerkmal ist. Gibbongesänge sind nützliche Hilfsmittel für die Systematik. Mit ihrer Hilfe lassen sich vermutete Unterartgrenzen lokalisieren (z.B. bei *H. moloch*), bisher unerkannte Arten entdecken (z.B. *N.* sp. cf. *nasutus*), und – zumindest auf dem Artniveau – Phylogenien rekonstruieren. Alle ausser zwei Gibbonarten produzieren Duettgesänge. Es lässt sich zeigen, das Duettieren ein ursprüngliches Gibbonmerkmal ist und dass das Fehlen von Duetten bei *H. klossii* und *H. moloch* vermutlich ein gemeinsam abgeleitetes Merkmal dieser beiden Arten ist. Gesang entstand mindestens vier Mal unabhängig bei nichtmenschlichen Primaten. Gibbon- und Menschengesänge weisen mehrere Gemeinsamkeiten mit den *loud calls* von Altweltaffen und Grossen Menschenaffen auf und dürften sich wohl aus ähnlichen Rufen entwickelt haben. Die Phylogenie der Gibbons lässt – auch über dem Artniveau – mit Hilfe von mitochondrialen DNS-Sequenzen rekonstruieren. Sequenzen der Kontrollregion zeigen Distanzen zwischen den Artengruppen, die der Distanz zwischen *Pan* und *Homo* entsprechen oder noch darüber liegen. Dies weist darauf hin, dass die Artengruppen der Gibbons vier unterschiedlichen Gattungen entsprechen, obwohl bisher nur Untergattungen anerkannt wurden.

(3) Im dritten Teil dieser Habilitationsschrift wird die Erhaltungsbiologie der Gibbons untersucht. Die Gefangenschaftspopulationen der Gibbons in Vietnam und China zeichnen sich durch einen praktisch fehlenden Fortpflanzungserfolg, einen hohen Zustrom von Jungtieren aus dem Freiland und eine vermutlich niedrige Überlebenswahrscheinlichkeit aus. Solange diese Verhältnisse nicht umgekehrt werden, wird es nicht gelingen, sich selbst erhaltende Gefangenschaftspopulationen aufzubauen. Am Beispiel der javanischen Silbergibbons wird aufgezeigt, dass die Gibbongesänge ein wichtiges Hilfsmittel für die Schätzung der Populationsgrösse und die Bestandesdichte sind. Wilde Gibbons werden selbst in Nationalparks dezimiert (wie am Beispiel des vietnamesischen Nam Bai Cat Tien Nationalparks aufgezeigt). Der Östliche Schwarze Schopfgibbon (*N.* sp. cf. *nasutus*) scheint heute die seltenste und am kritischsten bedrohte Primatenart der Welt zu sein, mit einer geschätzten Population von weniger als 50 Tieren (verteilt über Hainan und NO-Vietnam). Ein *survey* der vietnamesischen Gibbons zeigt, dass die Tiere in 56% der Gebiete, in denen sie früher gefunden oder zumindest vermutet wurden, vermutlich ausgerottet sind. Dieser Anteil ist in Nordvietnam besonders hoch und lässt annehmen, dass drei Gibbonarten in Vietnam als kritisch bedroht eingestuft werden müssen: *N. concolor* (61%), *N. leucogenys* (67%), und *N.* sp. cf. *nasutus* (75%).

Sowohl Medien wie Wissenschaftler streichen konsistent die Grossen Menschenaffen als die Affenarten heraus, welche die höchste Schutzpriorität erhalten sollten. Wenn nicht sofort effizientere Massnahmen für die deutlich bedrohteren Kleinen Menschenaffen konzipiert werden, werden wir in nächster Zukunft mehrere Arten dieser für das Verständnis der menschlichen Evolution wichtigen Primatenreihe verlieren. Diese Habilitationsschrift soll dazu beitragen, die Grundlagen für die Erhaltung der Gibbons zu schaffen.

List of refereed publications which are part of this habilitation thesis

Publication numbers correspond to those in the curriculum vitae (separate item).

19. Geissmann, T., 1995: The yellow-cheeked gibbons (*Hylobates gabriellae*) in Nam Bai Cat Tien (southern Vietnam) revisited. *Primates* **36:** 447-455.
20. Geissmann, T. & Orgeldinger, M., 1995: Neonatal weight in gibbons (*Hylobates* spp.). *American Journal of Primatology* **36**: 179-189.
22. Geissmann, T., 1999: Duet songs of the siamang, *Hylobates syndactylus*: II. Testing the pair-bonding hypothesis during a partner exchange. *Behaviour* **136:** 1005-1039.
23. Geissmann, T. & Orgeldinger, M., 2000: The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus. Animal Behaviour* **60:** 805-809.
25. Ujhelyi, M.; Merker, B.; Buk, P. & Geissmann, T., 2000: Observations on the behavior of gibbons (*Hylobates leucogenys*, *H. gabriellae*, and *H. lar*) in the presence of mirrors. *Journal of Comparative Psychology* **114:** 253–262.
26. Dallmann, R. & Geissmann T., 2001a: Individuality in the female songs of wild silvery gibbons (*Hylobates moloch*) on Java, Indonesia. *Contributions to Zoology* **70:** 41-50.
27. Dallmann, R. & Geissmann T., 2001b: Different levels of variability in the female song of wild silvery gibbons (*Hylobates moloch*). *Behaviour* **138:** 629-648.
28. Roos, C. & Geissmann, T., 2001: Molecular phylogeny of the major hylobatid divisions. *Molecular Phylogenetics and Evolution* **19:** 486-494.
29. Geissmann, T., in press: Circumfacial markings in siamangs and evolution of the face ring in the Hylobatidae. *International Journal of Primatology*.
30. Geissmann, T., in press: Duet-splitting and the evolution of gibbon songs. *Biological Reviews.*