

# Duet-splitting and the evolution of gibbon songs

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## ABSTRACT

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 disagree on whether duetting or the absence of duetting represented the primitive condition in gibbons. The present study compares 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 suggest the following scenario for the evolution of gibbon songs: (1) The last common ancestor of recent gibbons produced duet songs. (2) 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 (song-splitting theory). (3) 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 can be shown to be derived from a duetting form. (4) The return to exclusive solo singing may be related to the isolated island distribution of the non-duetting species.

*Key words:* Hylobatidae, gibbon, song, duet, call, vocalisation, evolution, *Hylobates*, *Nomascus*, *Symphalangus*, *Bunopithecus*.

## CONTENTS

I. Introduction .....	58
II. Materials and methods.....	59
(1) General methods.....	59
(2) Bioacoustic terms and definitions.....	59
III. Results.....	62
(1) Degree of repertoire overlap in males and females.....	62
(a) Phrase repertoire .....	62
(b) Note type repertoire .....	63
(c) Repertoire overlap: synthesis .....	65
(2) Occurrence of male solo song bouts.....	66
(3) Occurrence of female solo song bouts.....	66
(4) Occurrence of duet song bouts .....	66
(5) Time of day of duet/female song bouts .....	67
(6) Time of day of male song bouts .....	67

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IV. Discussion .....	68
(1) Song-splitting .....	68
(2) Duet-splitting .....	70
(3) Phylogenetic implications .....	72
V. Conclusions.....	73
VI. Acknowledgments.....	73
VII. References .....	73

## I. INTRODUCTION

Although duet songs are known for many species of birds and several species of primates (e.g. Farabaugh, 1982; Geissmann, 2000*b*; Haimoff, 1986; Thorpe, 1961, 1972), previous studies have mainly been interested in analysing the structure, variability, context, systematical relevance and functional significance of duet songs. The evolution of duet songs has only rarely been studied (Geissmann, 1993, 2000*b*; Wickler & Seibt, 1982). Duet singing appears to occur mainly in monogamous species living in dense tropical forests (Thorpe, 1972) and evolved several times independently, probably four times in primates alone (Geissmann, 2000*b*). A comparative survey of, and attempts to reconstruct the essential stages which occurred during the evolution of, duet songs in gibbons or lesser apes (Hylobatidae) is presented here.

Gibbons are distributed throughout the tropical rain forests of South-east Asia (Chivers, 1977; Geissmann, 1995*a*; Marshall & Sugardjito, 1986) and live in monogamous, territorial family groups (Brockelman & Srikosamatara, 1984; Chivers, 1984; Leighton, 1987). All species of gibbons are known to produce elaborate, loud, long, stereotyped patterns of vocalisation often referred to as “songs” (Geissmann, 1993, 1995*a*; Haimoff, 1984*a*; Marshall & Marshall, 1976). Songs are mainly uttered at specifically established times of day. In most species, mated pairs may characteristically combine their songs in a relatively rigid pattern to produce coordinated duet songs. Several functions have been attributed to gibbon songs, most of which emphasise a role in territorial advertisement, mate attraction and maintenance of pair and family bonds (Geissmann, 1999; Geissmann & Orgeldinger, 2000; Haimoff, 1984*a*; Leighton, 1987).

Gibbon songs are characterised by being species-specific and, at least in part, sex-specific (Geissmann, 1993, 1995*a*; Haimoff, 1983, 1984*a*; Marler & Tenaza, 1977; Marshall & Marshall, 1976; Marshall & Sugardjito, 1986). When travelling in the Sunda region at the beginning of the last century, Volz

(1904) already noted that he needed not even leave his ship in order to recognise, just by listening to the songs which carried over from the nearest forest, which gibbon species occurred in that particular area.

In recent years, vocal characteristics have been used to assess systematic relationships among hylobatids and to reconstruct their phylogeny (Creel & Preuschoft, 1984; Geissmann, 1993, in press; Haimoff, 1983; Haimoff *et al.*, 1982, 1984; Marshall, Sugardjito & Markaya, 1984). Species-specific characteristics of gibbon songs are largely inherited (Brockelman & Schilling, 1984; Geissmann, 1984, 1993; Tenaza, 1985), and no differences between the singing behaviour of captive and wild gibbons have yet been discovered (e.g. Geissmann, 1993; Haimoff, 1983).

Gibbon songs probably developed from “loud calls” which are common to all great apes and many other Old World monkeys and which are preferentially or exclusively uttered by males (Geissmann, 2000*b*). In spite of the species-specific differences, a comparison of the various songs reveals similarities shared by all species, suggesting that gibbon songs are based on a single ancestral pattern, which is apparently not shared with other apes or monkeys (Geissmann, 1993). It is highly probable that the song structure common to all gibbon species may be interpreted in terms of homology, that is as a synapomorphic (derived) characteristic relative to other apes.

Previous authors disagree as to whether the absence of duetting represents the primitive condition in gibbons (Creel & Preuschoft, 1984), or whether duetting represents the primitive condition (Groves, 1984; Haimoff, 1983; Haimoff *et al.*, 1982). The former hypothesis was based on “the assumption that evolution normally proceeds from simple, unspecialized states to complex, specialized ones” (Creel & Preuschoft, 1984, p. 603), whereas the reasons supporting the latter hypothesis were either not explicitly formulated (Haimoff, 1983; Haimoff *et al.*, 1982) or explained on the basis that “it is evidently a primitive characteristic for gibbons to

duet, as all species do it except for *klossii*” (Groves, 1984, p. 558).

In the present article, the singing behaviour in all gibbon species is compared. Particular attention was paid to the following song characteristics of adult, mated gibbons: (1) the degree of repertoire overlap in males and females, (2) the occurrence of male solo song bouts, (3) the occurrence of female solo song bouts, (4) the occurrence of duet song bouts, (5) the preferred time of day for female and duet singing, and (6) the preferred time of day for male singing. Tracing these variables on the available phylogenetic trees was expected to enable the identification and reconstruction of the processes involved in the evolution of duetting in gibbons.

## II. MATERIALS AND METHODS

### (1) General methods

The gibbon classification used here follows Geissmann (in press) and Geissmann *et al.* (2000), and is summarised in Table 1.

Calls of nine gibbon species (*Hylobates agilis*, *H. lar*, *H. moloch*, *H. pileatus*, *Nomascus concolor*, *N. gabriellae*, *N. leucogenys*, *N. sp. cf. nasutus*, and *Symphalangus syndactylus*) were tape-recorded by the author during several field trips to China, Indonesia, Laos, Malaysia, Thailand and Vietnam in 1990–2001.

Songs of all gibbon species were tape-recorded from gibbons kept in zoos, primate centers and from privately owned animals in China, England, France, Germany, Indonesia, Italy, Laos, The Netherlands, Singapore, Switzerland, Thailand, the United States and Vietnam (Table 2) in 1980–2001. Additional tape-recordings of gibbon songs were kindly made available to the author by more people than can be listed here. Particularly important to the present study were tape-recordings made by Dr Lan Daoying (*Bunopithecus hoolock*), Mr. Vincent Nijman (*H. muelleri*), Dr M. Schwarz (duet *H. lar* male and *H. moloch* female), and Dr R. R. Tenaza (*H. klossii*).

Descriptions and sonograms of wild gibbon vocalisations have appeared in a large number of publications. Many of these data were used to supplement those collected during this study. The sources for those data are listed in Table 3, arranged by species.

Most tape-recordings carried out by the author (and all gibbon songs recorded in the field) were made with a Sony TC-D5M tape recorder equipped with a Sennheiser ME 80 (+K3U) directional microphone. Sonograms of tape-recorded vocalisations were generated with SoundEdit 2.0.1 software (see Schmidt, Radin & Brodie, 1989) on an Apple Macintosh IIfx personal computer using a Sound Recorder device (Farallon). These sounds were sampled at 11 kHz, and sonograms were created with a Fast-Fourier transformation (FFT) size of 1024 points.

Table 1. *Main divisions of the gibbons (Hylobatidae) (modified after Geissmann, 1995a)*

Genus	Diploid number of chromosomes	Other group names	Species	Common name
<i>Hylobates</i>	44	<i>Lar</i> group	<i>H. agilis</i> <sup>a</sup>	Agile gibbon
			<i>H. klossii</i>	Kloss's gibbon
			<i>H. lar</i>	White-handed gibbon
			<i>H. moloch</i>	Silvery gibbon
			<i>H. muelleri</i>	Grey gibbon
			<i>H. pileatus</i>	Pileated gibbon
<i>Bunopithecus</i>	38		<i>B. hoolock</i>	Hoolock
<i>Nomascus</i>	52	<i>Concolor</i> group, crested gibbons	<i>N. concolor</i>	Western black crested gibbon
			<i>N. sp. cf. nasutus</i>	Eastern black crested gibbon
			<i>N. gabriellae</i>	Yellow-cheeked crested gibbon
			<i>N. leucogenys</i> <sup>b</sup>	White-cheeked crested gibbon
<i>Symphalangus</i>	50		<i>S. syndactylus</i>	Siamang

<sup>a</sup> including *H. agilis albibarbis*.

<sup>b</sup> including *N. leucogenys siki*.

Table 2. Number of institutions where songs of captive gibbons were tape-recorded for this study

Location	Species <sup>a</sup>										
	ag	kl	la	mo	mu	pi	ho	co	ga	le	sy
China (6): Beijing Zoo; Gejiu Zoo; Guangzhou Zoo; Hong Kong Zoo; Shanghai Zoo; Kunming Zoo	1		1				5	1	2	2	1
England (5): Banham Zoo; Bekesbourne, Howletts Zoo; Paignton Zoo; Southport Zoo; Twycross Zoo	2	1	4	2	3	1		1		1	3
France (8): Asson Zoo; Clères Zoo; Doué-la-Fontaine Zoo; La Flèche Zoo; Mazé, Mr. J. Bauné; Mulhouse Zoo; Paris, Jardin des Plantes; Paris, Vincennes Zoo	1		4		2	2			3	6	1
Germany (15): Berlin, Tierpark Berlin; Berlin Zoo; Cottbus Zoo; Dortmund Zoo; Duisburg Zoo; Eberswalde Zoo; Frankfurt Zoo; Hannover Zoo; Kronberg, Opel Zoo; Leipzig Zoo; Munich, Zoo Hellabunn; Münster Zoo; Nordhorn Zoo; Rheine Zoo; Rostock Zoo	1		4	2	4	2			1	5	5
Indonesia (2): Cisarua, Taman Safari; Jakarta Zoo	2	1		2	2						2
Italy (1): Rome Zoo				1		1					
Laos (1): Vat Si Muong Temple				1					1	1	
The Netherlands (2): Apenheul, Beekse Bergen	1									1	
Singapore (1): Singapore Zoo	1		1		1						
Switzerland (4): Al Maglio Zoo; Rapperswil, Knie's Kinderzoo; Seeteufel Zoo, Studen; Zürich Zoo		3				1					2
Thailand (2): Bangkok Zoo; Khao Kheow Open Zoo, Chonburi			1			2				1	
United States (4): Atlanta, Yerkes Regional Research Primate Center; Miami, Metro Zoo; New York, LEMSIP Primate Center; West Palm Beach, Lion Country Safari Park				4							2
Vietnam (1): Saigon Zoo									1		
Total number of institutions (50)	9	2	24	6	12	9	5	2	8	17	16

<sup>a</sup> Abbreviations: ag – *H. agilis*; kl – *H. klossii*; la – *H. lar*; mo – *H. moloch*; mu – *H. muelleri*; pi – *H. pileatus*; ho – *B. hoolock*; co – *N. conolor*; ga – *N. gabriellae*; le – *N. leucogenys*; sy – *S. syndactylus*.

## (2) Bioacoustic terms and definitions

The acoustic terminology used here largely follows that proposed by Haimoff (1984a). 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 min. A duet occurs when one individual coordinates its vocal-

isations in time or type of vocalisation with those of another individual (Seibt & Wickler, 1982; Wickler, 1974). Accordingly, a duet song is a song jointly uttered by two individuals and coordinated in time or phrases.

Within a gibbon song, a note is any single continuous sound of any distinct frequency or frequency modulation, which may be produced during either inhalation or exhalation. A phrase identifies a single vocal activity consisting of a succession of notes which are produced together in a characteristic manner, but which also may be produced independently. Gibbon song bouts consist of phrases and occasional single notes. Great-calls are the most stereotyped and most easily identifiable

Table 3. References for information on vocalisations of wild gibbons used for the present study

Species	Own observation (this study)	References
<i>Hylobates agilis</i>	+	Brockelman & Gittins (1984); Gittins (1978, 1984 <i>b</i> ); Gittins & Raemaekers (1980); Haimoff (1984 <i>b</i> ); Haimoff & Gittins (1985); Marshall (1981); Mather (1992); Mitani (1987 <i>a, b</i> , 1988, 1990); Mitani & Marler (1989)
<i>H. klossii</i>		Haimoff & Tilson (1985); Tenaza (1976); Whitten (1982, 1984)
<i>H. lar</i>	+	Brockelman & Schilling (1984); Caldecott & Haimoff (1983); Chivers (1974); Marshall (1981); Mather (1992); Raemaekers & Raemaekers (1984 <i>a, b</i> , 1985 <i>a, b</i> ); Raemaekers <i>et al.</i> (1984); Tenaza (1985)
<i>H. moloch</i>	+	Dallmann & Geissmann (2001, in press); Geissmann & Nijman (2000); Kappeler (1984)
<i>H. muelleri</i>		Haimoff (1985 <i>b</i> ); Mitani (1984, 1985 <i>a, b, c</i> , 1987 <i>a</i> ); MacKinnon, 1974; Mather (1992); Tenaza (1985)
<i>H. pileatus</i>	+	Brockelman & Schilling (1984); Mather (1992); Srikosamatara (1980); Srikosamatara & Brockelman (1983, 1987)
<i>Bunopithecus hoolock</i>		Choudhury (1989); Feeroz & Islam (1992); Gittins & Tilson (1984); Haimoff (1985 <i>a</i> )
<i>Nomascus concolor</i>	+	Geissmann <i>et al.</i> (2000); Haimoff <i>et al.</i> (1987); Jiang & Wang (1997); Lan (1993)
<i>N. sp. cf. nasutus</i>	+	Geissmann (1997); Geissmann <i>et al.</i> (2000)
<i>N. gabriellae</i>	+	Adler (1991); Geissmann (1995 <i>b</i> )
<i>N. leucogenys</i>	+	Hu <i>et al.</i> (1989)
<i>Symphalangus syndactylus</i>	+	Chivers (1974, 1976); MacKinnon, 1974; West (1982)
Various species		Chivers (1978); Gittins (1984 <i>a</i> ); Haimoff (1983, 1984 <i>a</i> ); Haimoff <i>et al.</i> (1982, 1984); Marler & Tenaza (1977); Marshall & Marshall (1976, 1978); Marshall & Sugardjito (1986); Marshall <i>et al.</i> (1972, 1984)

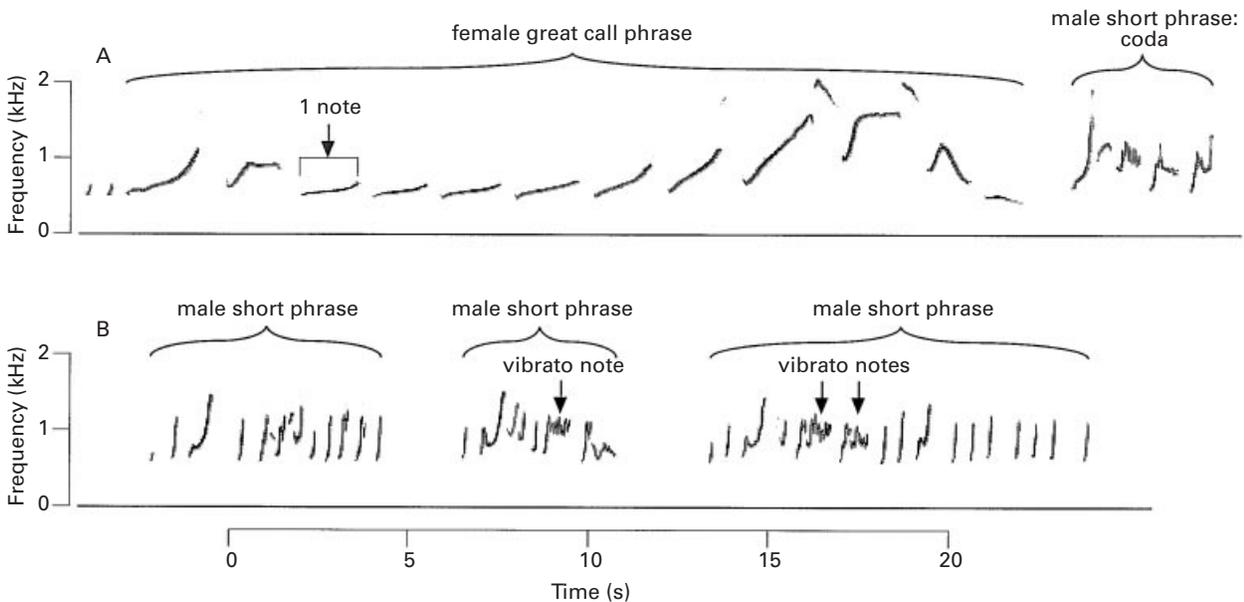


Fig. 1. Sonograms of (A) an excerpt of a duet song of *H. lar* (Mulhouse Zoo, France, 15 September 1988) and (B) an excerpt of a male solo song of the same species (Twycross Zoo, United Kingdom, 3 October 1988), illustrating the terms “phrase”, “note”, “great-call” and “coda”.

phrases of gibbon song bouts and are produced by females of all gibbon species. All other phrases are termed short phrases here. A particularly characteristic short phrase in gibbon duet songs is the male's coda, which is produced at or near the end of the female's great-call. The combination of a female great-call and the corresponding coda is called a "great-call sequence". The short phrases occurring between the great-call sequences are termed "interlude sequences". A typical cycle of events occurring several times in a gibbon duet call bout begins with male short phrases (with or without female short phrases), followed by the onset of a female great-call. The male falls silent during the build-up phase of the great-call and adds a coda at the climax. After that, he resumes producing short phrases (again, with or without female short phrases). Fig. 1 shows two sonograms illustrating some of the terms used in this paper: note, great-call, short phrase, and coda.

### III. RESULTS

#### (1) Degree of repertoire overlap in males and females

##### (a) *Phrase repertoire*

Sex-specificity in gibbon songs can occur in at least two different respects: (1) in the repertoire of note types used by either sex, and (2) in the repertoire of phrases built up from these note types by either sex. Neither of these two aspects have apparently been quantified for any gibbon species so far. The reason for this lies in the difficulty of identifying the number of different note types which make up a gibbon's song repertoire, especially when looking at notes which gradually change their aspect (e.g. during a great-call, see below). Similarly, it is problematic to identify the number of different short phrases used by a gibbon, because these phrases are highly variable in structure. Thus, the following assessment of repertoire overlap in males and females must remain preliminary. I will briefly discuss first repertoire overlap of phrases and then repertoire overlap of note types.

The following comparison between male and female vocalisations covers each sex's entire song repertoire. Figs 2 and 3 present typical song phrases of male and female gibbons. The phrase repertoire of gibbons may, using a very simplified approach, be divided into great-call phrases and short phrases. All gibbon females exhibit a spectacular, stereotyped

and readily recognisable phrase known as the great-call (Fig. 2). In all species, the great-call consists of a series of notes, uttered with increasing speed (although the acceleration is barely noticeable in *H. agilis* and *H. lar*). In all species except *B. hoolock* and *S. syndactylus*, an increase in the maximum frequency of the notes also occurs during the great-call. During their song bouts, females repeat great-calls at quite regular intervals of approximately one to a few minutes. Adult, mated males are not known to produce great-calls. Instead, they produce short phrases only. In most species, females are also known to produce short phrases. The only exception is the crested gibbons (genus *Nomascus*): adult female crested gibbons contribute only great-calls or great-call fragments to the duet song. As a result, songs of male and female crested gibbons exhibit no overlap in their phrase repertoire and show the highest degree of sex specificity in this respect.

The short phrases of males (and females) are usually less stereotypic than the great-calls (Fig. 3). Whereas female great-calls remain essentially unchanged throughout a song bout, successive short phrases are rarely identical. Instead, males gradually build up their phrases during a song bout, beginning with single, simple notes. As less simple notes are introduced, these notes are combined to form increasingly complex phrases, reaching the fully developed form only after several minutes of singing. In all but two species, males tend to reply to female great-calls with special variants of their short phrases, the so-called codas (shown in Fig. 2). Males of *H. klossii* and *H. moloch* are unusual in that they are not known to produce codas. Usually, male and female song bouts do not even overlap in mated pairs of these two species (see Section III.4).

Interestingly, gibbons appear to recognise, and may respond to, great-calls of other species. In zoos with several gibbon cages in close proximity, neighbouring pairs of different species may engage in synchronous call bouts with great-calls of several species uttered in concert. In captivity, typical great-call sequences with male codas are produced by pairs of mixed-species combinations such as, for instance: *H. pileatus* – *H. lar*, *H. agilis* – *H. muelleri*, *H. pileatus* – *N. gabriellae*, and a *H. lar* male and a *H. moloch* female. An excerpt of a duet song bout of the latter pair is shown in Fig. 4. In this sonogram, the male produces short phrases during the interlude sequence, interrupted by the introductory notes of the female's great-call. The male falls silent during the great-call and adds a coda at its end. This example is of particular interest when discussing the

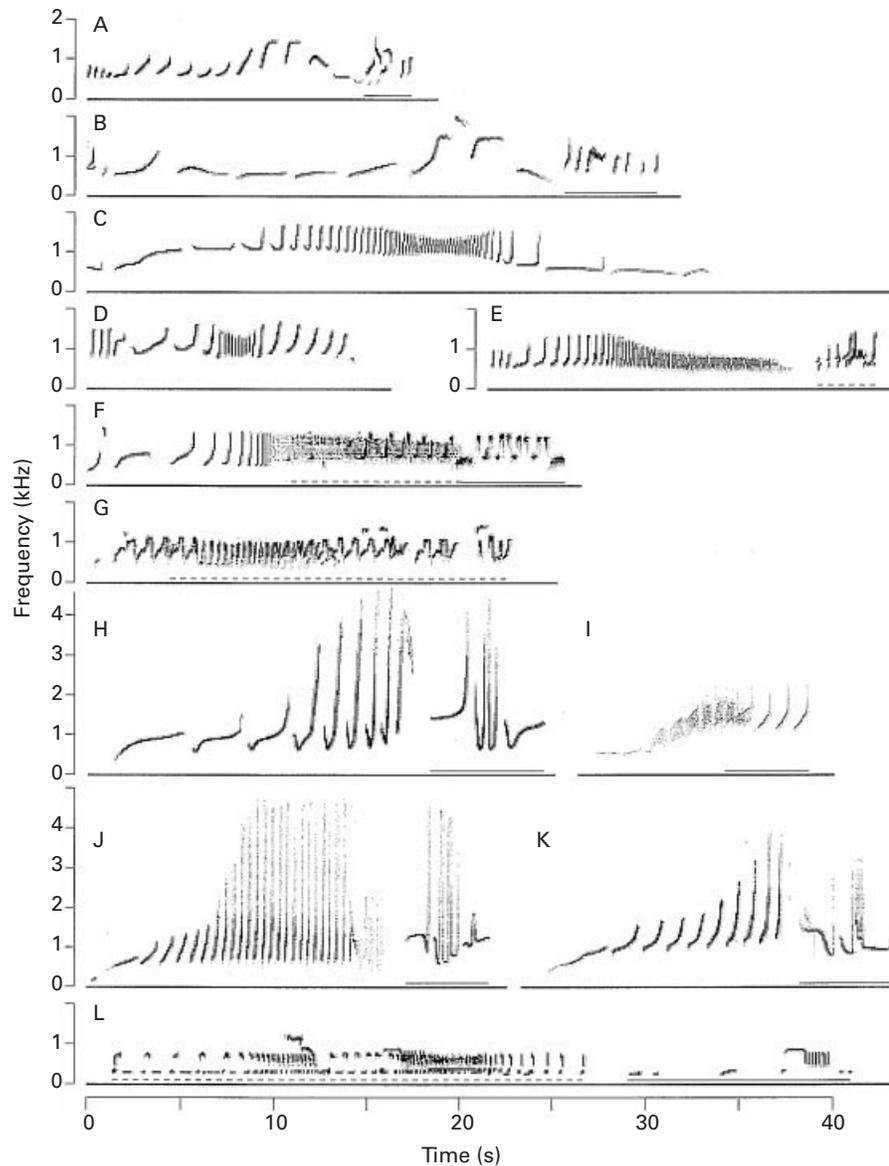


Fig. 2. Sonograms of great-call sequences of all gibbon species. C and D are excerpts from female solo song bouts; all other sonograms show duets. Male solo contributions to duets are underlined with a solid line, synchronous male and female vocalisations are underlined with a dashed line. (A) *H. agilis* (Asson Zoo, 31 May 1988); (B) *H. lar* (Paignton Zoo, 20 October 1988); (C) *H. klossii* (South Pagai, 27 November 1987, recorded by Dr R. R. Tenaza); (D) *H. moloch* (Munich Zoo, 16 July 1987), (E) *H. muelleri* (Paignton Zoo, 22 October 1988); (F) *H. pileatus* (Zürich Zoo, 5 May 1988); (G) *B. hoolock* (Kunming Zoo, 27 July 1990); (H) *N. concolor* (Xujiaba, Ailao Mountains, China, 1 August 1990); (I) *N. sp. cf. nasutus* (Bawangling Nature Reserve, Hainan, China, 15 October 1993); (J) *N. leucogenys* (Paris, Ménagerie, 17 May 1988); (K) *N. gabriellae* (Mulhouse Zoo, 13 September 1988); (L) *S. syndactylus* (Metro Zoo, Miami, 31 July 1988).

evolution of duetting in gibbons. It documents that great-calls of *H. moloch* females may elicit a coda response from males of other species, although they do not have this effect on males of their own species and that typical gibbon duets with *H. moloch* females are possible, although pure pairs of *H. moloch* do not duet.

#### (b) Note type repertoire

All gibbon species use a variety of different note types. The hoolock, *Bunopithecus hoolock*, is unique in that its note repertoire does not appear to include sex-specific note types. This has been mentioned in virtually every study on the vocal repertoire of this

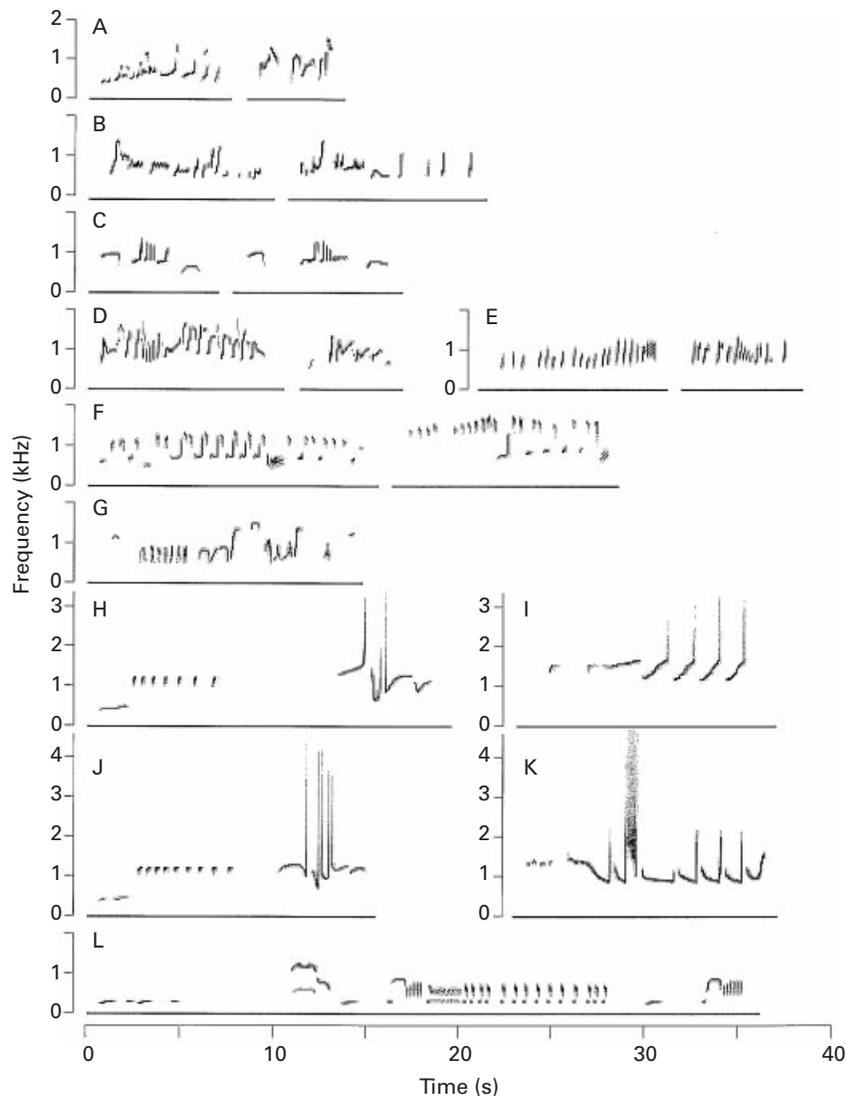


Fig. 3. Sonograms of fully developed male phrases of all gibbon species. In order to show variability, sonograms of two different phrases are provided for species A–F. In *H. klossii* (F), these stem from the same male; in all other cases, two different individuals are shown. (A) *H. agilis* (Twycross Zoo, 2 October 1988; and Guangzhou Zoo, 7 September 1990); (B) *H. lar* (Rheine Zoo, 5 July 1987; and Twycross Zoo, 3 October 1988); (C) *H. klossii* (both phrases from Twycross Zoo, 2 October 1988); (D) *H. moloch* (Munich Zoo, 16 July 1987; and Howletts Zoo, 17 October 1988), (E) *H. muelleri* (Doué-la-Fontaine Zoo, 25 May 1988; and Banham Zoo, 14 October 1988); (F) *H. pileatus* (Zürich Zoo, 5 May 1988; and Berlin Zoo, 29 June 1988); (G) *B. hoolock* (Kunming Institute of Zoology, October 1988, recorded by Dr Lan Daoying); (H) *N. concolor* (Gejiu Zoo, 2 August 1990); (I) *N. sp. cf. nasutus* (Bawangling Nature Reserve, Hainan, China, 21 October 1993); (J) *N. leucogenys* (Paris, Ménagerie, 17 May 1988); (K) *N. gabriellae* (La Flèche Zoo, 29 May 1988); (L) *S. syndactylus* (Howletts Zoo, 16 October 1988).

species, starting with Marshall and Marshall (1976) and Marler and Tenaza (1977), and was confirmed during the present study. Although the adult male does not produce great-call phrases, all great-call note types *per se* occur in the short phrases of both males and females. In all other gibbon species, great-call notes are sex-specific.

Crested gibbons (genus *Nomascus*), represent the other extreme of the spectrum: they show the highest

degree of sex-specificity in their note type repertoire. Males and females both produce several note types, each of which is not normally produced by adult conspecifics of the opposite sex. This has been repeatedly documented in earlier studies (e.g. Deputte, 1982; Schilling, 1984) and was confirmed during the present study in all species of the genus, either in the wild or in captivity.

In all remaining gibbon species (genera *Hylobates*

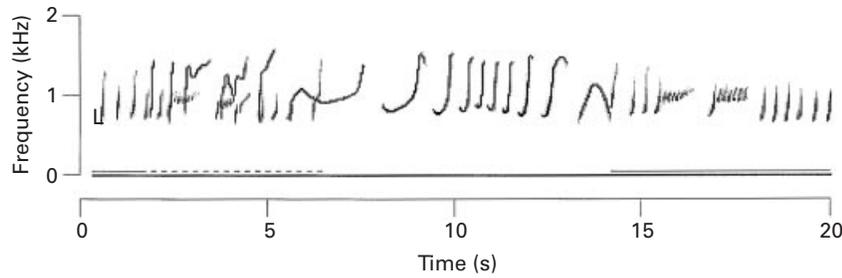


Fig. 4. Sonogram of great-call sequence of a mixed pair: *H. lar* (male) and *H. moloch* (female). Knie’s Kinderzoo, Rapperswil, 30 April 1979 (recorded by Dr M. Schwarz). Male solo contributions are underlined with a thin solid line, synchronous male and female vocalisations are underlined with a thin dashed line.

Table 4. Combined summary of literature data and data resulting from this study

Species	Character					
	1. Degree of sex-specificity of song repertoire	2. Male solo song bouts	3. Female solo song bouts	4. Duet song bouts	5. Time of day for duet/female songs	6. Time of day for male songs
<i>H. agilis</i>	intermediate	present	absent	present	dawn	pre-dawn/dawn
<i>H. klossii</i>	intermediate	present	present	absent	dawn	pre-dawn/dawn
<i>H. lar</i>	intermediate	present	absent	present	dawn	pre-dawn/dawn
<i>H. moloch</i>	intermediate	rare	present	absent	dawn	pre-dawn/dawn
<i>H. muelleri</i>	intermediate	present	absent	present	dawn	pre-dawn/dawn
<i>H. pileatus</i>	intermediate	present	absent	present	later	later
<i>B. hoolock</i>	small	absent	absent	present	later	n.a.
<i>N. concolor</i>	large	absent	absent	present	dawn	n.a.
<i>N. sp. cf. nasutus</i>	large	absent	absent	present	dawn	n.a.
<i>N. gabriellae</i>	large	absent	absent	present	dawn	n.a.
<i>N. leucogenys</i>	large	absent	absent	present	dawn	n.a.
<i>S. syndactylus</i>	intermediate	absent	absent	present	later	n.a.

n.a. = not applicable, because mated males do not usually sing solo songs.

and *Symphalangus*), adult males and females share a certain part of the note type repertoire, but also use some sex-specific notes. In gibbons of the genus *Hylobates*, the shared notes include various variants of *wa*-notes which make up a large proportion of the song repertoire, whereas the great-call notes are female-specific, and some other notes are male specific, like the vibrato notes in *H. lar* (visible in Fig. 1). In *Symphalangus syndactylus*, the part of the repertoire shared by males and females includes various barks and booms, whereas the long barks of the great-call are female-specific, and the bitonal scream is male-specific (Geissmann, 2000a).

(c) *Repertoire overlap: Synthesis*

In summary, roughly three classes of sex-specificity can be differentiated (Table 4). The genus *Nomascus*

exhibits the largest specificity: there is no overlap between the sexes in note repertoire and no overlap in the phrase repertoire. Female song contributions consist of great-calls only which consist of female-specific notes, whereas males produce short phrases only, and these consist of male-specific notes. The genus *Bunopithecus*, on the other hand, exhibits the smallest degree of vocal sex specificity: although only females produce great-call phrases, both sexes use the same note repertoire and produce the same types of short phrases.

All other gibbons are intermediate in their degree of vocal sex specificity: only females produce great-calls, which include female-specific note types. Both males and females produce short phrases, which may, however, include sex-specific notes in males (exceptions: *H. pileatus*, and, possibly, *H. agilis* and *H. muelleri*).

Although all gibbon species show at least some degree of sex-specific repertoire, as shown above, it should be noted that typical male and typical female duet parts can be sung by individuals of the opposite sex. This has been observed in immature animals (Geissmann, 1993), unmated or freshly mated animals (Geissmann, 1983; Srikosamatara, 1982) or gibbons in other unusual situations (Schilling, 1984).

## (2) Occurrence of male solo song bouts

Mated males of most gibbon species may engage in uninterrupted solo song bouts of considerable length, sometimes lasting more than 2 h, but mated males of *B. hoolock*, *S. syndactylus* and of all crested gibbons (genus *Nomascus*) usually sing in duet with their females only (duet songs are described below).

Evidence on *H. pileatus* is somewhat contradictory. Srikosamatara and Brockelman (1983) mention solo songs of unmated males only, but Brockelman (personal communication cited in Haimoff, 1983, p. 225) observed that males produced solo songs in a chorus, like other species of the *lar* group. During a brief survey at Khao Soi Dao Wildlife Sanctuary (NE Thailand), I recorded 51 song bouts in five days, 14 (27%) of which were male solo song bouts (T. Geissmann, unpublished data). Unless there was an unusually high proportion of unmated males in our study area, some of the solo-singing males were mated. I observed seven captive pairs of *H. pileatus* (Berlin Zoo, Twycross Zoo, Zürich Zoo), five of which regularly produced male solo song bouts. These observations suggest that solo songs of mated males are not uncommon in *H. pileatus*.

It has been questioned whether mated males of *H. moloch* sing at all. During 130 full days of listening scattered over the whole year, none of the five resident mated males in Kappeler's study area ever performed a song bout, suggesting "that territorial male moloch gibbons do not sing" (Kappeler, 1984). Only two male song bouts were heard during that study, one by an unmated individual on the border between two territories and one by an unidentified individual singing outside the study area. During a short study in Central Java, however, male solo songs appeared to be more common, amounting to approximately 10% of all song bouts heard (N = 125, Geissmann & Nijman, 2000; T. Geissmann + V. Nijman, in preparation). In conclusion, it appears that solo songs of mated males do occur, but may be relatively rare in this species.

## (3) Occurrence of female solo song bouts

Mated females of most gibbon species do not normally produce solo song bouts, with two exceptions: females of *H. klossii* and *H. moloch*, as a rule, produce solo songs only. Female solo song bouts are of shorter duration than male solo song bouts (usually less than 30 minutes).

There has been some uncertainty as to whether female solo songs occur in mated *H. muelleri*. One early description of *H. muelleri* songs identified male solo songs and female solo songs only (Marshall & Marshall, 1976). Another early report described song bouts of this species as duet songs during which the male does not contribute to the interlude sequences, but simply adds a brief coda to the end of the female's great-call (Marler & Tenaza, 1977). Later, singing behaviour of this species was described as including male solo songs and duet song bouts, and occasional solo songs of females (Mitani, 1984). More recent reports on songs of Mueller's gibbon fail to mention female solo songs altogether (Haimoff, 1985b; Marshall & Sugardjito, 1986) or explicitly state that they do not occur in this species (Leighton, 1987). Although some female solo songs are included in a collection of tape-recordings made by Vincent Nijman in the Balikpapan area (SE-Kalimantan), it is not known whether these songs were produced by mated or unmated individuals. Only two pure pairs of *H. muelleri* were available during the present study. One of them produced several duet song bouts. The female of the second pair uttered three solo song bouts. The male contributed a few single *wa*-notes to the female songs, but no song phrases at all. The same male produced one solo song bout. With the information available at present, it appears reasonable to assume that female solo songs may occasionally occur in *H. muelleri*, but are not customary.

## (4) Occurrence of duet song bouts

Whereas mated females of *H. klossii* and *H. moloch* have been reported to produce solo song bouts, mated females of other species usually confine their singing behaviour to duet song bouts only. Duet song bouts, like female song bouts, usually have a duration of less than 30 min. All gibbon species produce duet song bouts with two exceptions: *H. moloch* and *H. klossii*. Although it is generally accepted that males of *H. moloch* and *H. klossii* do not contribute vocally to the great-calls of the females, there has been some controversy about whether these two species produce

duet song bouts at all. In his paper on vocalisations of *H. klossii*, Tenaza (1976) mentions that “males utter short, soft whistles during 25–50% of the intervals between successive female songs” and explains later in the same paper: “Unlike other gibbons that have been studied, in which mated males and females sing duets with their mates, Kloss’ gibbons sing in all-male and all-female choruses.”

In contrast to this view, other authors have since reported that mated *H. klossii* perform duets in a substantial proportion of their interlude sequences (Cowlshaw, 1992; Haimoff, 1983, 1984a; and Whitten, 1980, cited as evidence in all three publications). Subsequent to his publication (Tenaza, 1976) on the singing behaviour of *H. klossii* on Siberut Island, R. R. Tenaza (personal communication, November 1992) was able to supplement the results of his earlier study by additional observations made on *H. klossii* in the Pagai islands. These more recent observations apparently confirmed that this species does not duet. On occasion, a late-morning male chorus would overlap a female chorus, but a male and a female from the same pair were never heard to participate in these overlapping choruses. The short, soft, monosyllabic whistle often produced by males between great-calls of their mates does not necessarily represent a song contribution. “Rarely if ever did a male whistle more than once between songs [i.e. great-calls] of his mate” (R. R. Tenaza, personal communication, November 1992). Similar whistles precede male song (Tenaza, 1976), but also occur when undisturbed gibbons are simply travelling or foraging (R. R. Tenaza, personal communication, November 1992).

The same authors who recognise duetting in the songs of *H. klossii* also recognise it in the songs of *H. moloch*, in contrast to Kappeler (1981, 1984), who never heard duet songs during his field study. I had the opportunity to listen to all of Kappeler’s many original tape-recordings, and found no evidence for duetting. There was no vocal contribution of the males to the female songs. Similar to Kappeler’s observation, no duet songs were heard among 125 call bouts heard in Central Java (Geissmann & Nijman, 2000; T. Geissmann + V. Nijman, in preparation). Males appear actively to avoid singing together with their mates: I repeatedly observed males of *H. moloch*, both in the wild and in captivity, to abort an ongoing song bout as soon as a female song bout started.

As evidence for duetting in *H. moloch*, Haimoff (1983) cites tape-recordings he made of a captive gibbon pair at Bristol Zoo, and Cowlshaw (1992)

cites a tape-recording made by Marshall and Marshall (1976) in Java. Duetting of the pair at Bristol Zoo should not be cited for this purpose, however, because the male of this pair was not *H. moloch* but *H. muelleri abbotti* (as identified by Geissmann, 1993, p. 182).

Some kind of communal calling appears to occur, however, in the Marshalls’ tape-recording of wild *H. moloch* (later published on a phonograph disc: Marshall & Marshall, 1978). It appears to be identical to the “border conflicts between neighbouring groups” described by Kappeler (1984). I witnessed one similar call bout spontaneously produced by the family group at the Berlin Zoo, consisting of the breeding pair and a juvenile male. All three members of the group contributed loudly to the interlude sequences, which consisted of brief outbursts of loud series of simple *wa*-notes. The males abruptly stopped calling each time the female started a great-call, but did not add a coda at its end. On the following day, this tape-recording was played back to the group. The animals reacted by producing the same communal *wa*-phrases in synchrony with those presented on the tape-recording. A few communal call bouts were also heard in Central Java; one of these was elicited by the playback of a female solo song bout presented on the common territory boundary of two neighbouring groups (T. Geissmann, personal observations).

In conclusion, it appears that *H. klossii* and *H. moloch*, as a rule, produce only solo songs. *Hylobates moloch* may occasionally engage in communal call bouts which reportedly occur in specific situations and which may include great-calls at irregular intervals. These were not considered to be duet songs, either in Kappeler’s (1984) study or in the present one.

##### (5) Time of day of duet/female song bouts

Gibbons preferentially utter their song bouts in the early morning hours. The time at which each species tends to produce the majority of duet song bouts (and female solo song bouts) can be divided into two categories: at or soon after dawn (*H. agilis*, *H. klossii*, *H. lar*, *H. moloch*, *H. muelleri*, crested gibbons), and 2–3 h later in the morning (*H. pileatus*, *B. hoolock*, *S. syndactylus*).

##### (6) Time of day of male song bouts

The time at which each species tends to produce most male solo song bouts can be divided into two

categories: in the dark before dawn (*H. agilis*, *H. klossii*, *H. moloch*, *H. muelleri*) or around dawn (*H. lar*), and about 2–3 h after dawn (*H. pileatus*). In those species where male solo song bouts occur, the solo songs tend to start approximately 1–3 h prior to the duet song bouts.

The character states found in this study are listed in Table 4.

#### IV. DISCUSSION

##### (1) Song-splitting

Wickler and Seibt (1982) outlined three alternative routes in order to explain how duet songs could have evolved: “(a) through song merging: two individuals combine their respective songs in a more or less complicated manner; or (b) through song copying: individuals copy their partner’s song; or (c) through song-splitting: a given song is divided up between the partners.”

Only routes (a) and (c) would be expected to lead to duets with mates having a sex-specific repertoire, as is typical of most gibbon species. By contrast, route (b) requires that “individuals take over the partner’s vocalisations and then join him in unisono singing” (Wickler & Seibt, 1982, p. 138). Unisono singing has not been reported for mated gibbons. All gibbon species use at least one sex-specific phrase (the great-call) in their adult song repertoire. Wickler and Seibt (1982) do not specify how individuals would take over the partner’s vocalisations during the course of evolution, but in an earlier paper, these authors describe their example (the African forest weaver *Symplectes bicolor*) in more detail suggesting that learning may be involved (Wickler & Seibt, 1980). There is no evidence of gibbons learning parts of their repertoire from other gibbons; instead, there is evidence that the gibbon song repertoire is largely inherited (Brockelman & Schilling, 1984; Geissmann, 1984, 1993; Tenaza, 1985). Thus, routes (a) and (c) are more likely candidates to explain the evolution of gibbon duets.

In route (a), mates with basically different repertoires may combine them in a duet. This is the song-merging hypothesis. At no transitional stage along this evolutionary route would one expect a mate to be able to sing the other’s repertoire. This is more likely to occur in song-splitting (c), where a basic song is divided into two sub-repertoires, each becoming increasingly confined to one sex. The observation that both typical male and typical female duet parts can be sung by individuals of the

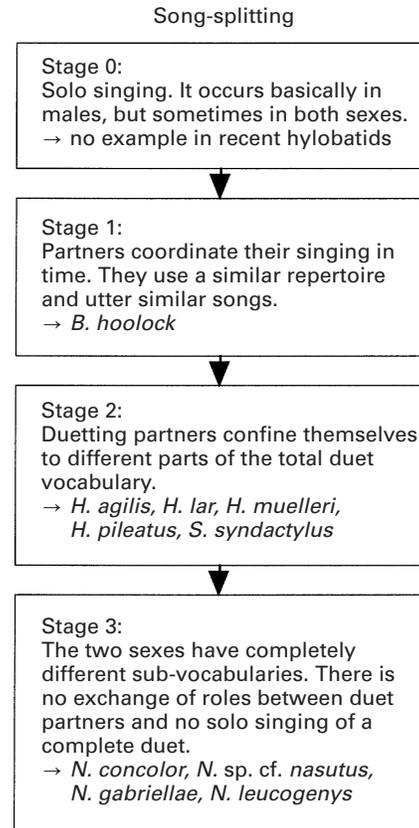


Fig. 5. Gibbon species arranged according to the song-splitting hypothesis. See text for explanation.

opposite sex (see Section III.1c) suggests that song-splitting rather than song merging occurred during the phylogeny of duetting in gibbons.

The song characteristics of the various gibbon species can be arranged linearly according to the degree of sex-specificity of the song repertoire (Fig. 5), similar to the stages of song-splitting proposed by Wickler and Seibt (1982) to document the evolution of duetting in some species of birds.

This hypothetical arrangement leads from duets in which both pair partners sing virtually identical duet contributions, through pairs in which the repertoires of both sexes overlap partially, and finally to pairs where the repertoires are completely sex-specific, because each sex confines its vocalisations to only one part of the whole song. This linear arrangement is interpreted as representing an evolutionary trend from solo singing to full partner dependence and increasing song-splitting. The direction of evolutionary change is suggested because the more complex structure is more likely to be derived. Because duet songs of recent gibbon species appear to have preserved several of the hypothetical stages of the song-splitting scenario, they are likely to

have evolved according to the song-splitting hypothesis as set out by Wickler and Seibt (1982).

The specialisation of the sexes on different parts of the whole song must probably be seen in connection with the frequently proposed possibility that the song contributions of each sex serve different functions and therefore are under different selective pressures (Cowlshaw, 1992; Geissmann, 1983; Gittins, 1978; Marshall & Marshall, 1976). It should be noted, however, that the arrangement of species presented in Fig. 5 does not necessarily represent a phylogeny. Different species could independently have reached the same stage of song-splitting.

Two species are missing from the arrangement shown in Fig. 5: *H. klossii* and *H. moloch*. Their position within the framework of the song-splitting hypothesis will be discussed below.

## (2) Duet-splitting

In some gibbons, another trend can be recognised in addition to the trend of song-splitting. In mated pairs of *H. pileatus*, male solo song bouts occur as well as duet song bouts. The majority of these solo songs are sung approximately 2 h after dawn but approximately 2 h earlier than duet songs. In *H. agilis*, *H. lar* and *H. muelleri*, however, the first peak of singing activity occurs at or even before sunrise. At this time, the males are reported to produce solo songs on their sleeping trees. The second peak is one to several hours later in the morning, after a first feeding bout. At this time, the females usually join the males in duet songs.

Two gibbon species, *H. klossii* and *H. moloch*, are exceptional in that the pair partners are reported to sing solo songs only. At first sight, the logical conclusion would be to interpret this condition as a primitive trait, which would fit perfectly into the hypothetical stage zero of Wickler and Seibt's (1982) song-splitting hypothesis (see Fig. 5). In the following discussion, however, three arguments are presented which support an alternative view, that is, solo singing in these two species is derived secondarily from duet singing.

(1) Several different phylogenies have been proposed for hylobatids; some of them are presented in Fig. 6. They are based on morphological, behavioural or molecular characters. Although differing in several details, they share basic similarities. They all agree on the following point: several duetting species, such as *N. concolor*, *S. syndactylus* and *B. hoolock*, split off from the main stem of hylobatids before the two non-duetting species

did, and several duetting species split off afterwards, such as *H. muelleri*, *H. agilis* and *H. lar*.

The conclusion of this comparison is that, if duetting is primitive and non-duetting is derived, non-duetting must have evolved at least once in gibbons, but maximally twice if the trait has been developed independently in *H. klossii* and in *H. moloch*. If non-duetting is primitive and duetting derived, however, duetting must have evolved at least twice in gibbons, or four to five times if any one of the phylogenetic trees shown in Fig. 6 is realistic. It has been shown elsewhere (Geissmann, 1993) that gibbon duets exhibit a considerable number of characteristics which are shared by all duetting gibbon species. The complexity of the duet pattern renders convergent evolution very unlikely.

(2) In both *H. klossii* and *H. moloch*, only the males sing before dawn in the sleeping trees, whereas the females sing their solos later in the morning. These completely separated singing periods of males and females appear to be the logical consequence of the previously mentioned trend of *H. agilis*, *H. lar* and *H. muelleri* to produce male solo songs before or around dawn, 1–3 h earlier in the morning than duet song bouts. The gibbon species whose pair partners always duet and those species which do not duet can be linked with these intermediate stages, in which duets are usually separated in time from solo songs. The occurrence of the intermediate stages 3a and 4a (see Fig. 7) supports the view that the non-duetting species should be placed in a new, derived position in the evolutionary framework of the song-splitting hypothesis, as shown in Fig. 7. The term “duet-splitting” which is used in Fig. 7 will be explained below.

(3) A final argument results from the observation that the male of a duetting species (*H. lar*) was able to produce a typical duet with the female of a non-duetting species, *H. moloch* (Fig. 4). The two gibbons produced a well-coordinated duet; the organisation of their interaction in the great-call sequence is virtually identical to that of duetting gibbon species. Apparently, the female song of *H. moloch* fulfils all the requirements for duetting, although this species is not known to duet during the great-call sequence. Moreover, this is not simply a male *H. lar* which follows the female great call with a coda and thus creates the duet, but it is also the female *H. moloch* following the male's short phrases with her great call. The female, too, chooses to duet with this male and to insert great calls in his song. This does not normally occur in pure pairs of *H. moloch*. This observation provides additional support for the

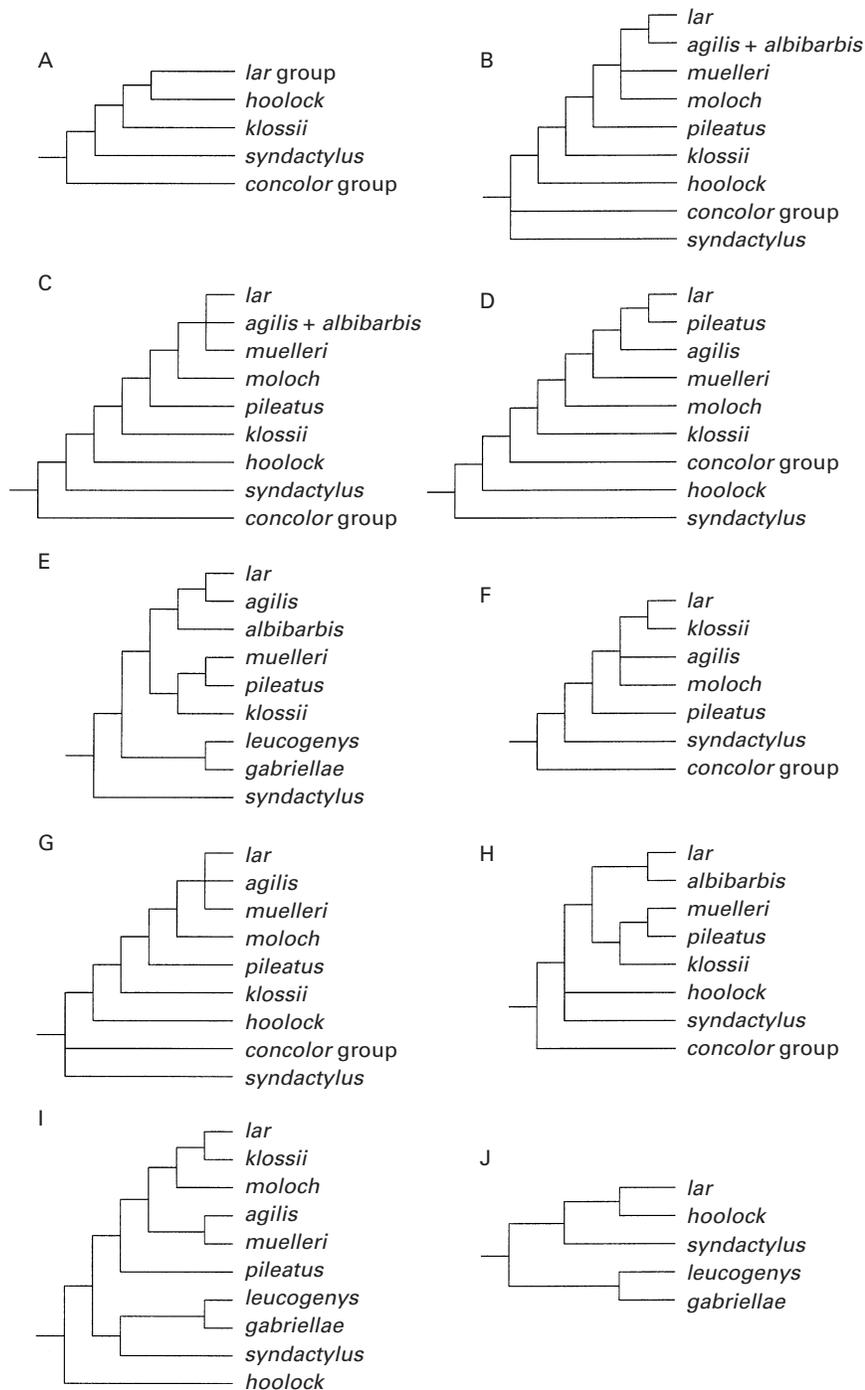


Fig. 6. Published representations of the phylogenetic relationships among gibbon taxa. (A) Chivers (1977); (B) Creel & Preuschoft (1984); (C) Garza & Woodruff (1992); (D) Groves (1972); (E) Haimoff *et al.* (1982); (F) Hayashi *et al.* (1995); (G) Purvis (1995); (H) Zhang (1997); (I) Zehr (1999); (J) Roos & Geissmann (2001).

hypothesis that this non-duetting species has evolved from a duetting one. It would be even more impressive if a male *H. moloch* was producing a duet with a female *H. lar*, but such an example was not observed.

The arguments presented in this study suggest that *H. moloch* and *H. klossii* have secondarily

abandoned duetting behaviour, and that the common ancestor of all recent hylobatids did produce duet songs. Only subsequently did the duet contributions of each sex become increasingly independent (stages 2a–5a in Fig. 7). This appears to be the first time that a non-duetting animal can be shown to be derived from a duetting form. This process is

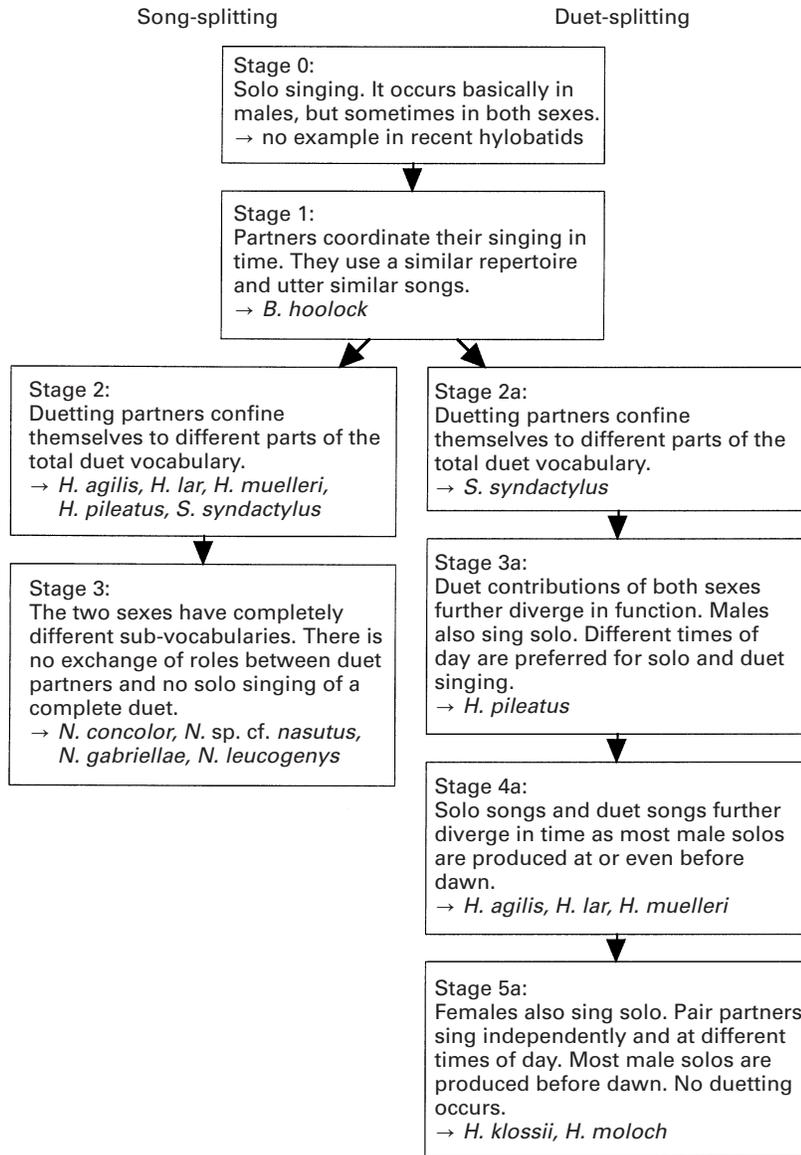


Fig. 7. Gibbon species arranged according to the song-splitting hypothesis and the duet-splitting hypothesis. See text for explanation.

tentatively called “duet-splitting”, in analogy to the term song-splitting of Wickler and Seibt (1982), and is summarised in Fig. 7.

If mated females of *H. muelleri* do occasionally produce solo songs, as the currently available evidence appears to indicate (see above), this would represent an intermediate strategy between mated females which sing duet song bouts only and mated females which sing solo song bouts only. As a result, *H. muelleri* would occupy an additional intermediate stage between stages 4a and 5a in Fig. 7.

Of course, it would be interesting to know which evolutionary constraints may have favoured the occurrence of duet-splitting. One obvious approach

to this problem is to scan all gibbon taxa for other characteristics shared by the non-duetting species but absent in duetting gibbons, or *vice-versa*. Aspects from ecology, geography and ethology of the various species were taken into consideration. As a result, it appeared that the non-duetting gibbons are unique in having no common border with other gibbon species. Whereas *H. moloch* is restricted to the western half of Java, and *H. klossii* occurs only on the small Mentawai islands, all duetting gibbon species are in contact with at least one other species, and all presently occupy larger areas of distribution than both non-duetting species (Chivers, 1977; Chivers & Gittins, 1978; Groves, 1972; Marshall & Sugardjito,

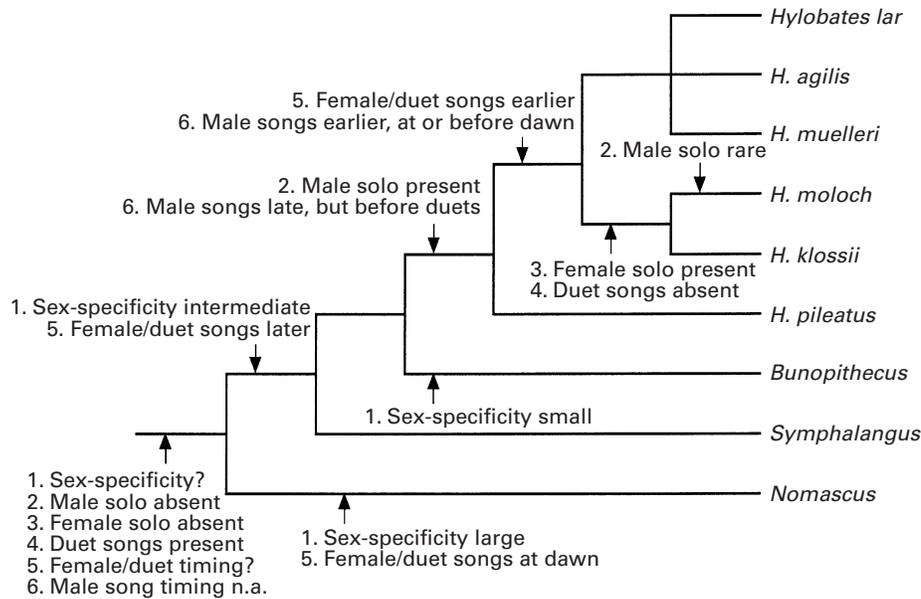


Fig. 8. Tracing the vocal character states on a hypothetical gibbon phylogeny (character state numbers as in Table 4). In this example, the tree proposed by Haimoff *et al.* (1982) was used, except that a sister taxon relationship was assumed for *H. klossii* and *H. moloch*, as explained in the text. Character 6 (“Male song timing”) is not applicable (“n.a.”) to *Nomascus*, *Bunopithecus* and *Symphalangus*, because mated males do not usually sing solo songs in these taxa.

1986). How might the benefits of duetting have diminished as a consequence of isolation?

It appears reasonable to assume that the acoustic differences between gibbon species evolved as a consequence of selection against hybridisation (Marshall & Marshall, 1976; Mitani, 1987*a*), but a causal relationship between speciation and duetting is unknown, so far. It has repeatedly been speculated on how traits that act as intrinsic barriers to inbreeding might be affected by the number of related species. Organisms released from the competitive pressure of related species could become less tightly adapted to a particular situation. It has been observed that songs of birds and crickets living on islands or in areas which are isolated from related species are less complex and less stereotyped (Catchpole & Slater, 1995; Otte, 1989). Song simplicity of isolated species may result from the lack of need for complexity as a species marker where there are few other species (Catchpole & Slater, 1995). Apparently, isolation can lead to the loss of signal elements and a return to simpler song types in birds and crickets. If isolation can lead to simpler song types and if solo singing is a simpler song type than duet singing, isolation could have reduced the necessity to produce complex composite signals by mated gibbon pairs and have freed males and females to sing independently. This purely speculative hypothesis appears plausible considering that

there has already been some selection pressure acting on males and females to sing at different times of the day in some of the duetting species, as shown above.

### (3) Phylogenetic implications

The position of *H. moloch* and *H. klossii* together at the same stage of duet-splitting suggests a synapomorphic character state. Because both species are isolated, the differences in their songs from those of other gibbons may result from convergence rather than common ancestry. Both species share a number of probably derived vocal character states, such as the presence of female solo song bouts, the absence of duet song bouts and the temporal separation of male and female singing. Because at least (the first) two of these character states are unique among gibbons, it appears more likely that they represent synapomorphies. I suspect that the two species are more closely related to each other than to other gibbons, in contrast to the various arrangements shown in previously published phylogenetic trees (Fig. 6). In Fig. 8, the vocal character states of the present study are traced on a hypothetical gibbon phylogeny. In this example, the tree proposed by Haimoff *et al.* (1982) was used, except that *H. klossii* was moved to a sister taxon position to *H. moloch*. Using the vocal characters of the present study, any other published hylobatid tree that includes these two species would

be two steps shorter if *H. klossii* were recognised as a sister taxon of *H. moloch*.

Among recent gibbons, *B. hoolock* occupies the most primitive stage of song-splitting (Fig. 5), because males and females typically use the same repertoire of note types. If the song-splitting hypothesis is correct in identifying this as a primitive character state, derived stages of song-splitting would have evolved more than once unless *B. hoolock* occupied the most basal position in the phylogenetic tree. Most previously published trees shown in Fig. 6, however, place either *S. syndactylus*, crested gibbons (*concolor* group) or both in that position, not *B. hoolock* (but see Zehr, 1999, and Fig. 6I). The results of the present study suggest that *B. hoolock* could be one of the candidates for the earliest split-off from the main stem of the gibbon radiation. Because only one variable of the present study (i.e. sex-specificity of the repertoire) supports that arrangement, this is a highly tentative conclusion which should be confirmed with a larger data set. It is important to keep in mind, however, that the main components of the gibbon phylogeny (i.e. the dichotomies among the four subgenera) are still not reliably resolved. The order of the generic splits has, so far, resisted conclusive analysis by molecular methods (Hall, Jones & Wood, 1998; Hayashi *et al.*, 1995; Zehr, 1999; Zhang, 1997; but see Roos & Geissmann, 2001), and no two of the available molecular trees are alike. When more reliable and more complete phylogenetic trees are available, it will be possible to reconstruct the evolution of gibbon singing and duetting behaviour in much more detail.

## V. CONCLUSIONS

Long and complex song bouts have been described for all gibbon species. Comparison of their singing behaviour supports the following conclusions concerning the evolution of gibbon songs:

(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.

(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 complete segregation of male and female singing may have been facilitated by isolation from other gibbon species (island distribution).

## VII. ACKNOWLEDGEMENTS

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