American Journal of Primatology 68:1–19 (2006)

RESEARCH ARTICLE

Calling in Wild Silvery Gibbons (*Hylobates moloch*) in Java (Indonesia): Behavior, Phylogeny, and Conservation

THOMAS GEISSMANN[1]* and VINCENT NIJMAN[2]
[1]*Anthropological Institute, University Zürich-Irchel, Zürich, Switzerland*
[2]*Institute for Biodiversity and Ecosystem Dynamics, Zoological Museum, University of Amsterdam, The Netherlands*

Hardly any behavioral data are available for the silvery gibbon (*Hylobates moloch*), an endangered primate that is endemic to the island of Java, Indonesia. We studied the singing behavior of the easternmost population of this species in the Dieng mountains, central Java, in 1998–1999. We aimed to document the timing of singing, quantify the amount of singing by the respective sexes, and explore the role of bioacoustics in density estimation. A total of 122 song bouts in at least 12 groups were monitored. No duet songs were heard. Most of the song bouts (91.5%) were female solo song bouts or female scream bouts. In contrast to an earlier study on the westernmost population of silvery gibbons, during which few if any male songs were heard, at least 8.5% of the song bouts in our study were male solo song bouts. They were significantly longer in duration than the female songs. All male song bouts uttered before dawn (0520 hr) were produced in a chorus fashion, with at least three individuals participating. Choruses occurred about once every 8.5 days, and lasted longer and occurred earlier than female solo song bouts. Most male songs (60%) started between 0355–0440 hr, when it was still dark. All female songs, in contrast, started after 0500 hr, and female singing activity peaked around 0600. Regular male singing, male chorusing, and regular predawn singing have not previously been reported for silvery gibbons. Similarly separated periods of male and female solo songs and the absence of duetting have been observed in Kloss's gibbons (*H. klossii*) on the Mentawai Islands, and may represent synapomorphies shared by both species. The pronounced individual-specific song characteristics of silvery gibbons allow accurate mapping of groups. The density of gibbons at our study site was established to be 1.9–3.7 groups/km^2, corresponding to 6.7–13.1 individuals/km^2. We reassess the suitability of gibbon songs as a means of estimating the density and size of gibbon populations, and

Contract grant sponsor: Netherlands Foundation for International Nature Protection; Contract grant sponsor: Society for the Advancement of Research in the Tropics; Contract grant sponsor: Stichting het Kronendak.

*Correspondence to: Thomas Geissmann, Anthropological Institute, University Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland. E-mail: thomas.geissmann@aim.unizh.ch

Received 5 October 2004; revised 23 February 2005; revision accepted 4 March 2005

DOI 10.1002/ajp.20203

discuss the proximate causes for the absence of duetting in silvery gibbons. Am. J. Primatol. 68:1–19, 2006. © 2006 Wiley-Liss, Inc.

Key words: *Hylobates moloch*; gibbon; duet; song; vocalization; population density

INTRODUCTION

All gibbon species are known to produce loud, long, and well-patterned songs. Songs are usually produced early in the morning. In mated pairs, male and female song contributions are sex-specific [e.g., Geissmann, 1993, 2003]. In virtually all species, mated males spend at least as much time singing as mated females [e.g., Gittins, 1984a, b; Haimoff, 1985; Raemaekers et al., 1984; Whitten, 1984]. The song types produced by mated gibbons differ among the species [Geissmann, 1995, 2002a] (nomenclature and classification follow Geissmann [2002b]): 1) duet song bouts only are typical of six species (all species of the genera *Bunopithecus*, *Nomascus*, and *Symphalangus*); 2) duets and male solo songs are typical of four species (*Hylobates agilis*, *H. lar*, *H. muelleri*, and *H. pileatus*); and 3) female solo songs and male solo songs (but no duet songs) are typical of two species (*H. klossii* and *H. moloch*).

Gibbon songs probably have several functions. These may include spacing among groups, defense of resources (such as territories, food sources or mates), mate attraction, and strengthening and/or advertisement of the pair bond [Cowlishaw, 1992; Geissmann, 1999; Geissmann & Orgeldinger, 2000; Geissmann et al., in press; Leighton, 1987; Mitani, 1984, 1985a,b, 1987; Raemaekers & Raemaekers, 1985a, b].

The silvery gibbon (*Hylobates moloch*) is endemic to the western half of Java, Indonesia. Most populations can be found in the western province [Asquith et al., 1995; Kappeler, 1984b], but a few populations remain in the central Javan province [Nijman, 1995, 2004]. The most recent population estimates, based on extrapolation of the available habitat, range from 2,000 [Supriatna et al., 1994] or 3,000 [Asquith et al., 1995] animals to 4,000–4,500 animals [Nijman, 2004]. The species has lost some 96–98% of its habitat [MacKinnon, 1984, 1987] and has been given the highest conservation priority rating for Asian primates [Eudey, 1987a,b]. The silvery gibbon is included in the Critically Endangered category according to the IUCN threat criteria [Eudey, 1997; IUCN, 2003] (but see Nijman [2004]), is protected by Indonesian law, and is listed in Appendix I of the CITES convention.

To date, the only comprehensive study on the behavioral ecology of wild silvery gibbons (including calling behavior) was conducted by Kappeler in 1975–1976 and 1978 [Kappeler, 1981, 1984a–c]. Because the males of the resident groups in his study area (Ujung Kulon, West Java (6°45′S, 105°20′E; see Fig. 1)) did not sing, Kappeler concluded that territorial male gibbons do not sing. Two other short studies conducted in other parts of Ujung Kulon provided some data on calling behavior, but did not specify the sex of the calling animals [Gurmaya et al., 1995; Rinaldi, 1999].

Considering the silvery gibbon's threatened status and the small amount of detailed information available on its behavioral ecology (all of which was collected from the westernmost population in Ujung Kulon), we set out to collect data on the species' calling behavior at the opposite end of its distribution area, i.e., the Dieng mountains in central Java (Fig. 1).

The aims of the present study were threefold: 1) to provide a repertoire description of silvery gibbon call and song bouts, 2) to document the timing of

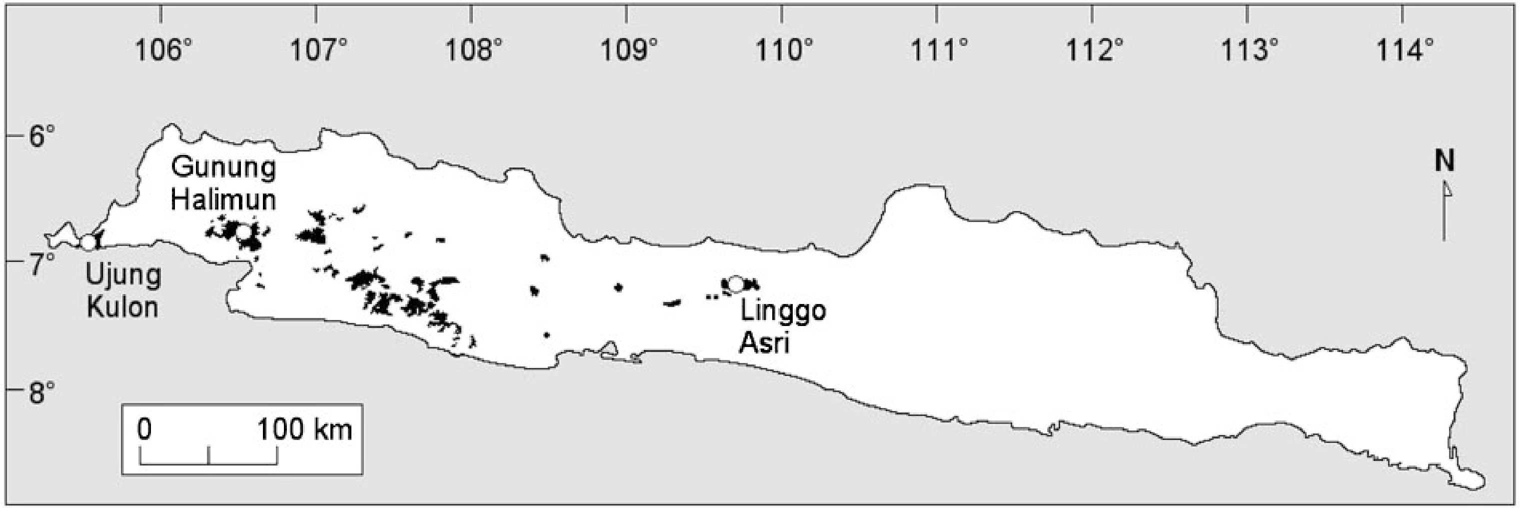

Fig. 1. Map of Java showing the remaining forest areas inhabited by gibbons, and the localities of Ujung Kulon, Gunung Halimun, and Linggo Asri, Dieng (gibbon distribution after Andayani et al. [1998], Asquith et al. [1995], Kappeler [1984a], and Nijman [1995, 2004]).

silvery gibbon songs, and 3) to quantify the amount of singing by the respective sexes and individual gibbons. In addition, we compare our results with those from previous studies in Ujung Kulon, discuss our findings in relation to current knowledge on gibbon phylogeny, and explore the role of bioacoustics in conservation-monitoring studies of gibbons (particularly for density estimation). Detailed quantitative analyses of syntax and variability of male and female songs of silvery gibbons, as well as a discussion of their functions, are presented in separate publications [Dallmann & Geissmann, 2001a,b; Geissmann et al., in press].

MATERIALS AND METHODS

Study Area and Data Acquisition

The Dieng mountains harbor the largest population of silvery gibbons in central Java, which is estimated at >500 individuals [Nijman, 2004; Nijman & van Balen, 1998]. Although central Java is largely deforested, the Dieng mountains are still extensively covered with forest ranging from about 300 m a.s.l. in the area north of Linggo to 2,565 m a.s.l. at Mt. Prahu. The vegetation of the Dieng mountains is of the wettest type, and, roughly below 1,000 m, consists of mixed lowland and hill rain forest, and, up to about 2,400 m, consists of montane everwet rain forest (for a more complete description of the study area, see Nijman and van Balen [1998]).

The study area proper was at the Linggo Asri resort [7°06′S, 109°35′E], near the village of Linggo in the western part of the Dieng mountains, central Java. The area is covered by a patchwork of old secondary forest mixed with more primary forest, and cultivated land. Its altitudinal range is between ~450 and 650 m a.s.l. The climate is perhumid with daily maximum temperatures ranging between 27–31°C, and an annual rainfall of about 6,000–7,000 mm. Less rainfall is recorded during the months of July–September, but the monthly average remains above 100 mm (climatic data from the weather stations of Sumigih and Pagilaran [RePPProT, 1990]).

We monitored gibbon singing activity around Linggo Asri, Dieng, on a daily basis during 19 consecutive days from 23 September to 11 October 1998. During the first 11 days, gibbon singing activity was monitored from predawn to dusk; the remaining 8 days covered the predawn-dawn period only (i.e., from about 1.5 hr prior to dawn to 0.5 hr after dawn). Subsequently, male predawn singing was monitored again for an additional 15 days over the period of 31 July to 25 August 1999. Dawn was defined as the time when color was first discernible in the forest canopy [Gittins, 1984a], and it occurred at ~0520 hr local time. Sunrise was determined by the time the sun was first seen at the study site, and it occurred at ~0615 hr. During each observation period, we recorded the location and sex of the singer, as well as the starting and ending time (to the next minute) of all song bouts heard.

We estimated the density of gibbons by mapping the localities in which the gibbons were vocalizing (as detectable from one single listening post), as described by Brockelman and Ali [1987]. From this fixed point count, density estimates were calculated with the use of the following equation:

$$D = n/(p \cdot A) = n/(p \cdot \phi \cdot \pi r^2),$$

where D is density (mated pairs/km^2); n is the average number of different groups heard calling per day, as determined over a 10-day period; p is the estimated proportion of days on which the gibbons sang, as established by monitoring the complete song output of two individually recognizable groups (AS-9 and AS-2);

ϕ is the section of a circle from which the gibbons could be heard; and r is the radius within which the gibbons could be heard.

We made a calculation for a smaller area within which all groups could be identified by their song ($r = 1.0$–1.4 km; $\phi = 135^\circ$), and for a larger area, which also included unknown groups within hearing distance ($r = 1.4$–1.8 km; $\phi = 180^\circ$). Because there was more intact forest in the larger area, the section of the circle from which the gibbons could be heard was broader there.

Supplementary observations on the singing behavior of captive silvery gibbons were carried out between 1984 and 2002 by one of the authors (T.G.) during various short visits to the following zoos: Berlin Zoo and Munich Zoo (Germany); Jakarta Zoo and Taman Safari, Cisarua (Indonesia); and Howletts Zoo and Paington Zoo (United Kingdom). The data collection method used was the same as that described above for wild silvery gibbons.

Bioacoustic Methods and Definitions of Bioacoustic Terms

All tape-recordings were made with a Sony TC-D5M tape-recorder equipped with a Sennheiser ME80 (+K3U) directional microphone or a Sony WM-D6C tape-recorder equipped with a JVC directional microphone.

Sonagrams of song sequences were made with the use of Canary 1.2.4 software [Charif et al., 1995] on an Apple personal computer (PowerMacintosh). The recording parameters included an 11 kHz sampling rate and 16 bit sampling. The analysis parameters were as follows: FFT (Fast Fourier Transformation), Hamming analysis window; analysis resolution: filter bandwidth=43.7 Hz; frame length=1,024 points; grid resolution: time=23.1 ms; overlap=75%; frequency=5.4 Hz; and FFT size=2,048 points. Duration and frequency measurements of vocalizations were also carried out with the use of Canary 1.2.4 software.

The acoustic terminology used in this study largely follows that proposed by Haimoff [1984]. A "song" is what fulfills 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 recognizable sequence or pattern in time," or, a song is a succession of phrases with nonrandom succession probability ("Strophenfolgen mit nicht-zufälliger Folgewahrscheinlichkeit" [Tembrock, 1977, p. 33]). Song bouts are separated from each other by an arbitrarily defined interval of >5 min. A "duet" occurs when one individual coordinates its vocalizations in time or type of vocalization with those of another individual [Seibt & Wickler, 1982; Wickler, 1974], and a "duet song" is a song jointly uttered by two individuals and coordinated in time and/or phrases.

Gibbon song bouts consist of phrases, and phrases consist of notes. A "phrase" identifies a single vocal activity consisting of a succession of notes that are produced together in a characteristic manner, but may also be produced independently. A "note" is any single continuous sound of any distinct frequency or frequency modulation, which may be produced during either inhalation or exhalation. "Great calls" are the most stereotyped and most easily identifiable phrases of gibbon song bouts, and are produced by females of all gibbon species. Another characteristic phrase in many gibbon songs is the male's "coda," a phrase that is produced at or near the end of the female's great call. A "chorus" is defined as the temporal overlap of song bouts of several individuals during a continuous time period, which normally exceeds the duration of any single participant's song bout [Tenaza, 1976].

RESULTS

Description of Female Song Bouts

To facilitate a comparison among the various types of song bouts described below, a short identification guide is presented in Table I.

Females typically produce two types of vocalizations during their song bouts: 1) simple *wa* notes or phrases of *wa* notes, and 2) great calls or aborted great calls. A female song bout is usually introduced by a variable but simple series of notes, termed the ''introductory sequence.'' It consists of single *wa* notes uttered at irregular intervals and a series of *wa* notes. Thereafter, great calls are produced at intervals of about 1–2 min. Between great calls, females usually produce so-called ''interlude sequences.'' Similarly to the introductory sequence, the interlude sequences consist of single *wa* notes uttered at irregular intervals and variable series of *wa* notes. Series that

TABLE I. Various Types of Call Bouts Produced by Silvery Gibbons

Call bout	Note and phrase types	Comments	Participants
Female song bout	Simple *wa* notes. Short phrases of mostly *wa* notes. Great calls of various notes types uttered in highly stereotypic order.	Climax of great call may or may not be accompanied by a locomotor display. Neighboring groups tend to avoid overlapping great calls. Bout duration relatively short (3–18 min).	Adult female. Immature group members may join in during great calls.
Scream bout	Simple *wa* notes. Short phrases of screams and *wa* notes.	May include great calls and may develop into a female song bout. Possibly identical to ''border conflict'' [Kappeler, 1984c]. Bout duration like female song bout.	Adult female. Other group members may or may not join it during scream phrases, possibly including adult male (but not verified during this study).
Harassing call bout	Short loud screams.	Screams emitted by all group members mixed with bursts of agitated movement [Kappeler, 1984c].	This type of call bout was not reliably identified during the present study.
Communal call bout	Simple *wa* notes. Bursts of *wa* notes.	May include great calls. Bout duration like female song bout.	All group members join in during bursts of *wa* notes.
Male song bout	Simple *wa* notes.Short phrases of various notes types, including complex hoots. Note types not uttered in stereotypic order (vs. great call).	Several males of a population may join in to produce their song bouts in a chorus bout. Song bout often begins with a long sequence of soft hoots. Bout duration longer than female song bout (8–42 min).	Adult male.
Disturbance hoot bout	Hoots (= soft *wa* notes of narrow frequency range).	Disturbance hoots may be produced during several minutes and may or may not develop into a male song bout.	Adult male (whether adult females also produce disturbance hoots was not verified during the present study).

are separated from other notes by an interval of at least 5 sec are termed "female short phrases."

Female great calls (Fig. 2a–c) are announced by a particularly regularly paced series of *wa*'s. The great call itself consists of eight to 22 notes and often begins with a special inflected note, followed by one or several long notes of slowly increasing frequency. Through a steady shortening of both note duration and

Fig. 2. Sonagrams of representative phrases of female songs (**a–c**), female scream calls (**d**), communal group calls (**e**), and male phrases (**f–i**), tape-recorded from captive and wild silvery gibbons. **a:** Female *wa* notes and great call from Ujung Kulon, west Java. **b:** Female *wa* notes and great call from Pelabuhanratu, west Java. **c:** Female *wa* notes and great call from Linggo Asri, Dieng, central Java. **d:** Screams and *wa* notes of two neighboring females at the common territorial border in Linggo Asri, Dieng, central Java. **e:** Communal *wa* phrases of family group (adult pair and juvenile) at Berlin Zoo, Germany. **f:** Male phrases from Gunung Lawet, central Java. **g:** Male phrases ("Omar") from Howletts Zoo, United Kingdom. **h:** Male phrases ("Hilo") from Howletts Zoo, United Kingdom. **i:** Male phrases ("Paul") from Munich Zoo, Germany.

intervals, the great call develops into a series of accelerated *wa* notes that build up to a trill-like climax, after which the speed of note delivery becomes slower again at the end of the great call [Geissmann, 1993, 1995]. As previously noted by Kappeler [1981, 1984c], great calls are not only highly stereotypic, but often exhibit distinct individual characteristics. Among the females of our study site, one individual (AS1) had a particularly short pretrill phase, another female (AS3) produced a particularly long trill, and another one (AS9) produced the transition between notes 2 and 3 at lowered intensity, which enabled us to recognize individuals after a few days.

In some groups, two animals can be heard to produce synchronized great calls (i.e., great calls starting, accelerating, and ending in near synchrony). Because adult males are not known to sing great calls, it has been assumed that synchronized great calls are produced by subadult daughters singing along with their mothers [Kappeler, 1981, 1984c]. However, observations of captive gibbons have revealed that immature gibbons of either sex may accompany their mother during great calls (Geissmann, unpublished data).

Ongoing female song bouts were often stopped as soon as a second group started to sing. Apparently, females of neighboring groups avoid singing at the same time. Occasionally, two neighboring groups were heard singing at the same time (e.g., AS1 and AS2), in which case the females produced their great calls in alternation.

The females in Kappeler's study typically exhibited a locomotor display during the climax of their great calls (''each great call is accompanied by a burst of locomotion within the crown of the tree'' [Kappeler, 1984c, p. 381]). This kind of behavior did not occur in the two groups we directly observed singing during the present study, or in the groups one of the authors (V.N.) observed in the Dieng mountains at other times (1995–2002), or in two females observed by Björn Merker in Gunung Halimun National Park, West Java (personal communication to T.G.). Instead, these females sat still during their great calls.

Description of Scream Bouts

Scream bouts consist mainly of screams and *wa* notes (Fig. 2d). Scream notes begin like *wa* notes with rapidly increasing frequency, but have a more complex drawn-out ending of less steeply increasing frequency (''*wa-ee*'') or of several short-frequency modulations. Scream bouts tend to last longer than female song bouts. We heard one female that, at variable intervals ranging from 1 to 12 min, produced scream bursts and *wa* notes during 41 min, but no great calls. Like female song bouts, scream bouts may occasionally be interrupted by great call phrases, but these appear to occur at longer and less regular intervals than female song bouts. One scream bout had a duration of 18 min, but no great calls occurred during the first 12 min, and only three great calls were produced during the whole bout. Another scream bout with a duration of 11 min included only one great call after 9 min. In some (but not all) scream bouts, several group members were heard participating in the scream bursts. They became silent when a female sang her great call.

Scream bouts appear to be common during group encounters, and often included several groups vocalizing near each other. A particularly spectacular one occurred during a meeting between groups AS1, AS2, and AS9, which resulted in a continued exchange of scream bouts during 69 min. No individual called continuously during the entire exchange period, and each group resumed calling at least twice.

Scream bouts, as described in the present study, appear to correspond to what has previously been described as ''border conflicts between groups'' [Kappeler, 1984c]. According to Kappeler, all group members participate in producing the bursts of screams. Although males may have participated in some scream bouts, several scream bouts that included only a single individual (the adult female) were recorded, suggesting that a participation of the male in scream bouts may not be the rule.

A third category of loud calls was described by Kappeler [1984c, p. 388] as ''harassing call bouts'' emitted as a response to potential ground predators. According to Kappeler's description, ''harassing call bouts'' consist of ''loud screams emitted by all group members mixed with bursts of agitated movement.'' Although we did not observe anything fitting this description during our short study, we were not always close enough to the calling gibbons to tell whether agitated movement occurred during screaming or not. Therefore, our scream bouts may also include some ''harassing call bouts.''

While the structure of scream bouts often differs from that of female song bouts, any attempt to exclude these from the following analysis would be subjective. A female song bout may become a scream bout if the females are upset during the course of the bout, and likewise a scream bout may normalize to a female song bout as the gibbons calm down. A similar observation was previously made by Raemaekers et al. [1984] regarding the distinction between normal duet song bouts and disturbed call bouts in white-handed gibbons (*H. lar*).

There may be additional categories of call bouts produced by silvery gibbons. A communal call bout consisting of bursts of *wa* notes produced by all group members (Fig. 2e) was heard once in captivity and once at Dieng. The reasons for the occurrence of this type of calling are unknown. These call bouts also included great calls at more or less regular intervals. The other group members immediately became silent each time the female sang a great call. This unusual type of call bout was tape-recorded in a family group of three individuals at the Berlin Zoo (Germany), and then played back to the same group the following morning. The whole group immediately responded by inserting bursts of *wa* notes in synchrony with those on the tape. Each burst on the tape immediately triggered an identical one from the group, until the recorded song ended.

Description of Male Song Bouts

Male phrases consist of simple hoots (*wa*) and various more complex hoots. Of the latter type, longer hoots with one or two frequency inflections (*wa-oo*, *wa-oo-wa*) are particularly prominent for this species (Fig. 2f–i). Some males regularly produce biphasic hoots (i.e., a *wa* note followed by an inhalation note, but softer than the very prominent inhalation notes of *H. agilis* and *H. pileatus*). Only a few males were heard to include short trills in their phrases.

Male phrases are extremely variable [Geissmann et al., in press]. Even simple hoots in male phrases are rarely simple repetitions of identical notes, but often show a broad variability in frequency range and speed of frequency change. Whereas males in many gibbon species produce well patterned phrases (e.g., *H. klossii* and all species of the genus *Nomascus* [Geissmann et al., in press]), the male silvery gibbons were often heard singing with highly variable phrase patterns, and sometimes they sang for minutes with no distinct pauses (which would have helped us recognize the beginning of a new phrase).

Like males of other gibbon species [Geissmann, 1993, 1995], silvery gibbon males gradually build up their phrases, beginning with single, simple notes, uttered at long intervals. As less simple notes are introduced, these notes are combined to form increasingly complex phrases, and reach a fully developed form only after several minutes of singing. Male solo song bouts of silvery gibbons usually start with short, soft hoots, which resemble the ''disturbance hoots'' that are occasionally uttered when the observer is detected. Although disturbance hoots do not necessarily develop into a male song, at least one male song during our study was produced after we met up with a group and after several minutes of disturbance hooting by the group's male.

The excerpts of male solo songs shown in Fig. 2f–i show distinct differences among the males. Because each male was heard only few times, however, it is difficult to determine whether these differences represent individual-specific song characteristics, intra-individual variability, or context-specific differences (i.e., different types of male song). It was our impression that the male songs of silvery gibbons were quieter (and probably carried less far) than the female songs.

Timing of Male and Female Song Bouts

During 11 consecutive days in September–October 1998, we heard a total of 122 song bouts and scream bouts in at least 12 groups. Most groups could be identified by individual-specific song characteristics. Most of the song bouts (n=107) were female solo songs, but we also heard at least 10 male solo song bouts. Only five songs were too short or too far away to be reliably sexed. No duet songs were heard. No male phrases were heard as a response (coda) to female great call phrases, between female great calls, or during other female short phrases (see above). The difference in the abundance of male and female song bouts is statistically significant (Chi-square test, df=1, $P<0.0001$).

Individual females sang on most days, and mostly once. Occasionally they sang twice a day, and rarely three times or not at all. The average number of songs per day of the adult female in the two closely monitored groups (AS9 and AS2) was 1.2 (SD=0.83; n=9) and 1.2 (SD=0.63; n=10), respectively.

All female songs in the Dieng mountains started after 0500 hr, and female singing activity peaked around 0600 hr (Fig. 3). Compared to females at Ujung Kulon, the females in the Dieng mountains appear to sing slightly earlier (peak singing activity at ~0600 hr vs. ~0630 hr), and calling is spread out more equally over the morning. The starting times of all gibbon songs in Ujung Kulon differ between studies: those reported by Gurmaya et al. [1995] had mean starting times that peaked as late as ~0900 hr.

Most male songs (60%) in the Dieng mountains started between 0355–0440 hr, when it was still dark. We heard at least 10 male songs during 11 consecutive days of predawn-to-dusk observations. Considering that female songs of at least 12 individual gibbon groups could be heard from our listening post, the average number of male songs/day/group can be estimated as 0.08. It should be noted that this is a very conservative estimate. It includes one all-male chorus for which only a minimum number of participants is available. In addition, male songs appeared to be quieter than female songs, and could more easily go undetected than female songs.

Apart from one solitary song bout, which began at 0512 hr, all male song bouts uttered before dawn were produced in a chorus fashion, with the songs of at least three individuals overlapping. These predawn male choruses were recorded four times during the whole study: twice during 19 consecutive days in September–October, and twice during 15 days in July–August. This corresponds to a chorus occurrence of about once every 8.5 days. It was difficult to estimate the

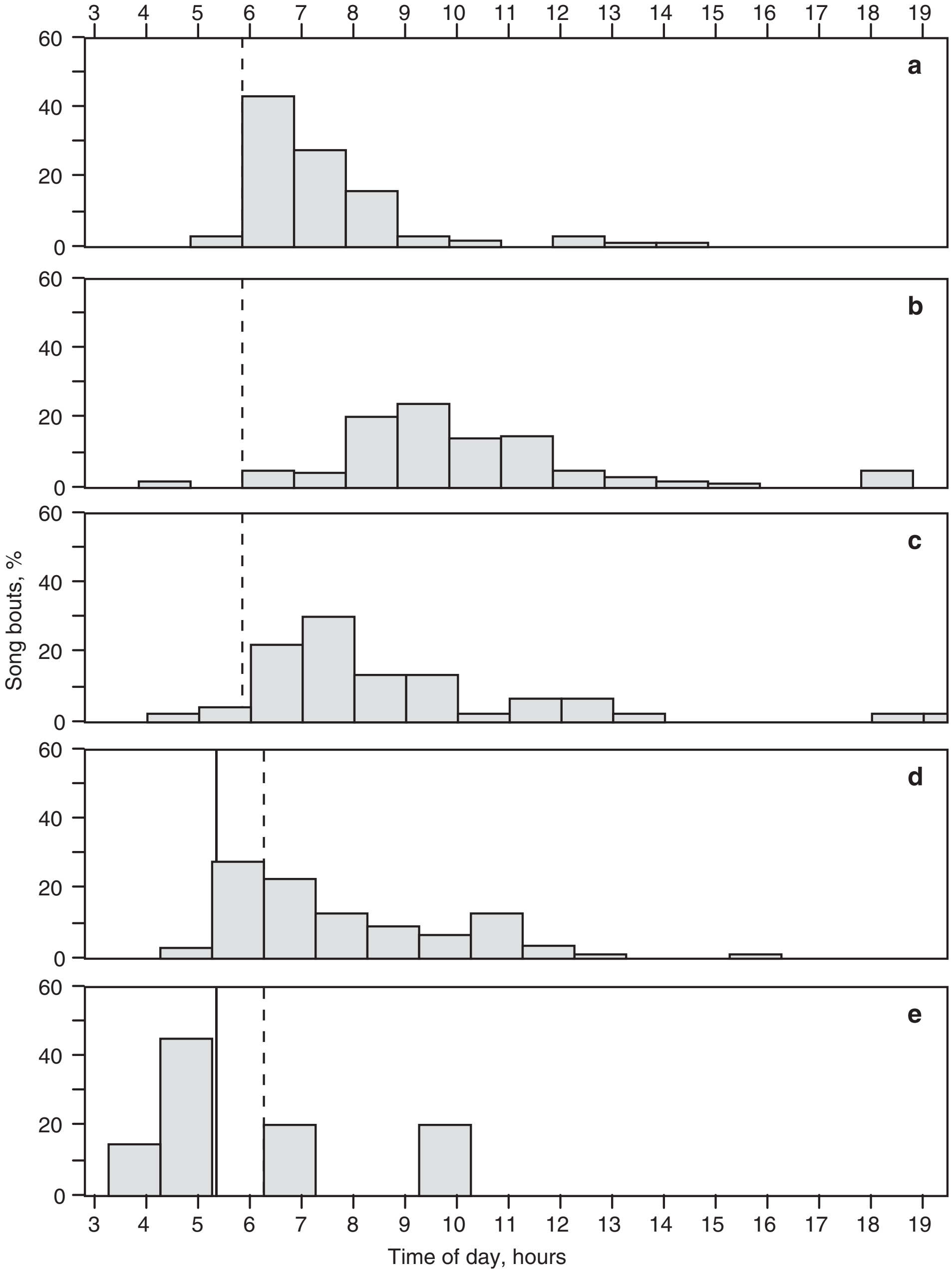

Fig. 3. Frequency distribution of the starting time of gibbon song bouts on Java: (**a**) females in Ujung Kulon (n=392 song bouts [Kappeler, 1984c]); (**b**) gibbons of unspecified sex in Ujung Kulon (n=114 [Gurmaya et al., 1995]); (**c**) gibbons of unspecified sex in Ujung Kulon (n=49 [Rinaldi, 1999]); (**d**) females in Linggo Asri, Dieng (n=107, this study); (**e**) males in Linggo Asri, Dieng (n=20, this study). Dotted line: dawn (not available for Ujung Kulon); dashed line: sunrise. Sunrise in Linggo was determined by the time the sun was first seen at the study site, and hence the time of sunrise may differ between mountainous areas and flat plains even if they are situated at the same longitude. Kappeler provided the time of sunrise [1981, 1984c] for his study site, and determined it in the same way as in the present study (Kappeler, personal communication to T.G.). Gurmaya et al. [1995] and Rinaldi [1999] did not specify the time of sunrise, but we infer it to be similar to that reported by Kappeler.

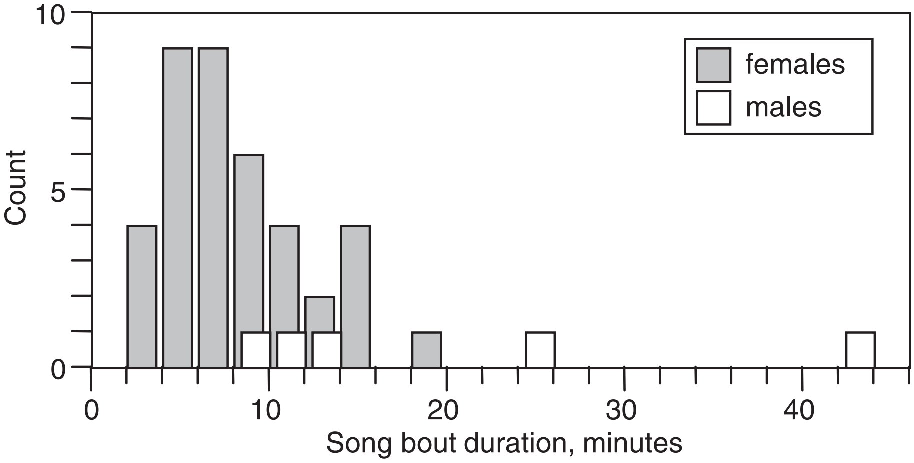

Fig. 4. Frequency distribution of song bout durations during 11 consecutive days at Linggo Asri (females: median=7 min, range=3–18 min, n=39 song bouts; males: median=11 min, range=8–42 min, n=5 song bouts).

number of males involved in a chorus because of the distance between the chorusing gibbons and the observers. The median minimum number of males involved during a single chorus bout was ≥3.5 (n=4 choruses, with a range of ≥3 to ≥5 males).

In three instances, females started to sing right after the male chorus had stopped, whereas once the last male (of an initial five males) stopped calling within 1 min after the first female started her song. No male choruses and only four male solo song bouts in 11 days were heard after dawn. Male choruses and female solo song bouts appear to be temporally segregated events.

Even outside of their chorus, males appear to avoid singing together with their mates. In both the wild and captivity, males were observed to abort an ongoing song bout as soon as a female song bout started. For instance, at the Munich Zoo (Germany), a pair of *H. moloch* was repeatedly heard to produce solo songs only (male and female solos) during repeated visits, but once a song was recorded that appeared to be a male solo interrupted by female great calls. The male stopped singing as soon as the female great call started, and waited for several minutes before he continued his song bout. The same male was also observed to abort his song bout when a neighboring female of a different species (*Nomascus leucogenys siki*) began a great call. At Howletts Zoo, on the other hand, one group of silvery gibbons with an infant offspring was observed to produce two introductory sequences that included both male and female vocalizations. Both song bouts were aborted after a few minutes, before any great call sequences were produced. Björn Merker (personal communication to T.G.) witnessed a male solo song bout at Gunung Halimun (Java) that lasted nearly 15 min, and was also aborted as soon as a female great call was heard in the distance. This song was sonagraphically analyzed by Geissmann et al. [in press].

Song Duration

The median durations of female song bouts and scream bouts were about 7 min (n=39, range=3–18 min) (Fig. 4). Pure female solo song bouts with one participant had a median duration of 6 min (n=17, range=3–18 min), and female song bouts with two participants of the same group (presumably including an offspring of the main singer) had a longer duration (median=9 min, n=13, range=6–15 min). The difference is significant (Mann-Whitney *U*-test, $P=0.004$).

Male solo song bouts produced outside of male dawn choruses had a median duration of 11 min (n=4, range 8–25 min). These male songs bouts were not significantly longer than the female solo song bouts (Mann-Whitney *U*-test, $P=0.056$), which may reflect the small sample size.

The exact individual song bout durations during predawn choruses could not be determined because of the large distance between the observers and the singing males. At least one male was heard singing continuously for 42 min during one chorus, but this is a minimum estimate because the chorus had started before the singing was detected. If this song is included in the comparison, the median duration of male song bouts is 12 min, and male songs are significantly longer than female songs (Mann-Whitney *U*-test, $P=0.016$).

Two completely monitored predawn male choruses had durations of 1 hr 43 min and 1 hr 47 min, respectively, and two choruses that were already under way when detected by us had a minimum duration of 42 min and 45 min, respectively. All lasted much longer than the longest female solo song bout (18 min).

Density Estimation by Use of Song Bouts

The proportion of days in which females called was 8 out of 9 days for group AS-9, and 9 out of 10 days for group AS-2. The fixed point count of identifiable groups in the smaller area revealed that the average number of females that called on a given day was 3.5 (SD=1.3; n=10). A corresponding density of 1.9–3.7 groups/km^2 was obtained. For the larger area, the average number of females that called on a given day was 6.7 (SD=2.7; n=10), and the density estimate was 1.5–2.4 groups/km^2. The average group size near Linggo (i.e., at an altitude of 400–650 m) was 3.5 (SD=1.2, n=15 groups, range=2–6). This corresponds to a density of 6.7–13.1 and 5.3–8.5 individuals/km^2 for the smaller and larger areas, respectively.

DISCUSSION

Frequency of Male and Female Singing

In virtually all gibbon species, mated males spend at least as much time singing as mated females [Geissmann et al., in press]. In the silvery gibbon, however, Kappeler [1981, 1984c] heard only a single male song during 130 full days of listening in Ujung Kulon. This song was produced by an unmated "floating" male. Another single male song was heard outside of the study area [Kappeler, 1984c]. Because no song was heard by any of the resident males in his main study area (Ujung Kulon), Kappeler [1981, 1984c] concluded that territorial male silvery gibbons apparently do not sing. Kappeler did not indicate how many songs he heard during his whole study, but did note that he heard 392 female song bouts in his study area during 89 days scattered over the whole year [Kappeler, 1984c]. Because he heard only one male song bout within his study area, one can estimate that less than 0.3% of all song bouts he heard were male songs. In contrast, we heard at least 10 male song bouts during 11 consecutive days of predawn-to-dusk observations, and several more during 23 additional predawn surveys. Hence, male song bouts in the Dieng mountains constitute at least 8.5% of the total number of song bouts produced, and 50% of the male songs heard during predawn-to-dusk observations were produced in all-male predawn choruses.

Regular male singing, male chorusing, and regular predawn singing have not previously been reported for silvery gibbons. Whether this is because there was a lack of focused research at the appropriate time, or because predawn calling is restricted to certain populations only is unclear. In our study area, male predawn choruses occurred only about once per week (once every 8.5 days). It is possible that in previous studies, many male solo song bouts and all choruses were missed because they occurred before dawn, or because the observers were unfamiliar with male calling. Two brief visits to Gunung Halimum in West Java, totaling 11 days (one by V.N. of 4 days, and one by Björn Merker of 7 days; personal communication to T.G.), both revealed that male calling does occur in this population. Because all previous data on the singing behavior of silvery gibbons was collected in the westernmost population of the species (Ujung Kulon), it is also possible that male calling and predawn chorusing are more common in the more eastern part of the gibbons distribution range.

Density Estimation by Use of Song Bouts

Gibbon songs proved to be an appropriate means of estimating gibbon density in the Dieng mountains. Data from the fixed point count suggest that densities in the surrounding area of Linggo are on the order of 1.9–3.7 groups/km^2, based on a small area (≤ 1.2 km^2) with individually recognizable groups, and 1.5–2.4 groups/km^2, based on a larger area (≤ 5.1 km^2), including nonidentified groups. The lower estimate for the larger area may reflect nonhomogeneous densities or greater inaccuracy in estimating the number of groups and distance for more remote groups. The median densities reported from lowland sites on Java is 2.6 groups/km^2 ($n=11$, range=0.5–6.3), with average group sizes of three to five individuals (summarized in Nijman [2004]). Our density estimate is higher than that previously reported by Nijman and van Balen [1998]. Taking into account the higher densities of gibbons in the Dieng mountains, and the fact that Nijman and 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] may be an underestimate.

Primates are frequently used as indicator species in monitoring programs. Although the use of 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 (e.g., 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 in previous studies of silvery gibbons [Kappeler, 1981, 1984a; Kool, 1992; Nijman & van Balen, 1998; Nijman, 2001, 2004]. Because Kappeler's [1981, 1984c] study suggested that only mated female silvery gibbons sing, it has been assumed that every vocalizing 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. Our findings indicate that at least 8.5% of the gibbon calls heard in central Java were male songs. We have little information concerning male calling in other parts of Java, but Gurmaya et al. [1995] and Rinaldi [1999] reported that gibbon songs are occasionally heard well before dawn in Ujung Kulon (see Fig. 3). These calls may well be produced by males. If in other areas (e.g., Linggo) some 8.5% of the songs heard are in fact male songs, it may imply that previous studies may have considerably overestimated densities. To accurately estimate densities, a (site-specific) correction factor should be taken into account, or, better still, male and female calls should be separated during data collection.

With practice, one can recognize silvery gibbons individually by their song [Kappeler 1984c; Dallmann & Geissmann, 2001a,b]. 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 studying this highly endangered primate than some traditional methods. Furthermore, vocal recognition facilitates longitudinal studies [Baptista & Gaunt, 1997], which otherwise often require intrusive methods.

Song Comparisons in a Phylogenetic Context

Whereas many gibbon species sing duet song bouts only (i.e., in all species of the genera *Bunopithecus*, *Nomascus*, and *Symphalangus*), male solo song bouts occur together with duet song bouts in most species of the genus *Hylobates*. However, in the silvery gibbon, duet song bouts do not occur. Instead, both males and females produce solo song bouts. The absence of duetting and the occurrence of female solo song bouts are characteristics that the silvery gibbon [Kappeler, 1981, 1984c] (this study) shares only with Kloss's gibbon from the Mentawai Islands [Tenaza, 1976; Whitten, 1980, 1982] (see also Geissmann [1993, 2002a] for a discussion regarding the evidence for the absence or presence of duetting in *H. klossii*). The absence of duetting and the occurrence of female solo song bouts appear to represent a synapomorphy shared by *H. moloch* and *H. klossii* [Geissmann 1993, 2002a].

In addition, males and females tend to sing at different times of the day. Most male song bouts occur before dawn, while most female song bouts occur after dawn. In some other species of the genus *Hylobates* (such as *H. agilis* and *H. lar*), males also tend to produce their solo songs before or at dawn, but they resume singing again later in the day, when they participate in the duet songs with their mates [Geissmann, 1993, 2002a]. In the silvery gibbon, however, no male choruses were heard after dawn.

Similarly separated periods of male and female solo songs were also observed in Kloss's gibbons [Tenaza, 1976; Whitten, 1980, 1982]. In this species also, males preferentially sing solo song bouts before dawn, and females preferentially sing solo song bouts after dawn. This may represent another derived characteristic shared by *H. moloch* and *H. klossii* [Geissmann, 1993].

However, only the silvery gibbon appears to have gone one step further. As pointed out by Geissmann [2000], gibbon songs probably evolved from male loud calls, which are similar to common calls in most recent Old World primates. In most Old World primates, females are not known to produce loud calls, or they utter only incomplete versions [e.g., Gautier, 1988; Herzog & Hohmann, 1984; Marler & Hobbett, 1975; Mitani, 1985c; Oates & Trocco, 1983; Steenbeek & Assink, 1998; Tenaza, 1989]. Although male singing apparently occurred considerably more frequently in our study than it did in Kappeler's study, the rate of male singing is still very low in comparison with other gibbon species. In most gibbon species, males participate in 0.18–1.90 song bouts per day [Gittins, 1984b], which in many species include both male solo and duet song bouts. Kloss's gibbon males (*H. klossii*) produce about 0.59 solo song bouts/day (calculated from data presented by Whitten [1982, 1984]). The lowest values were recorded in siamang populations. Although mated siamangs are not known to produce solo songs, 0.18–0.31 duet song bouts/day were recorded [Chivers, 1974; Gittins, 1984], which is still more than two to three times higher than our estimated male singing rate for silvery gibbons (about 0.08 song bouts/day). In silvery gibbons, the low rate of male singing combined with a high rate of female singing (about 1.2 song bouts/day) appears to represent a complete reversal of the hypothetical ancestral situation.

Why do silvery gibbons (and Kloss's gibbons) not produce duet song bouts? The ultimate selective forces that may have contributed to the loss of duet structures that are so typical of all other gibbon species remain unknown. As documented in this paper, male silvery gibbons appear to avoid singing during female song bouts and tend to abort their ongoing solo song bouts when they hear a female great call–even when they hear the great call of a different gibbon species. Female silvery gibbons, on the other hand, do not appear to be reluctant to interrupt an ongoing male song. They may even produce regular duet songs with males of other, duetting gibbon species, as reported by Geissmann [2002a]. This suggests that the behavior of the males, but not of the females, provides the proximate cause for the absence of duetting in silvery gibbons. In future studies, our hypothesis should be tested with playback experiments. According to our hypothesis, male silvery gibbons should be more likely to abort an ongoing song when presented with a song of the other sex.

ACKNOWLEDGMENTS

We thank the Indonesian Institute of Sciences (LIPI) and the Directorate General for Forest Protection and Conservation (PHKA) for granting us permission to conduct research on Java. This study was supported in part by a grant from Stichting het Kronendak (to V.N.). We also thank the officials and staff members of the numerous zoos for their permission to study the animals in their care and for useful information about the animals' history. Additional tape-recordings of silvery gibbons used in the present study were kindly made available by Dr. Markus Kappeler and Dr. Björn Merker, who also shared unpublished observations on silvery gibbons at Gunung Halimun. We are particularly grateful to Robert Dallmann and Sylke Eyring for digitizing parts of our tape-recordings. Professor Dr. Elke Zimmermann, Professor Dr. Steph B.J. Menken, Dr. Robert Dallmann, and two anonymous reviewers commented on an earlier version of this manuscript.

REFERENCES

Andayani N, Supriatna J, Morales JC, Melnick DJ. 1998. The phylogenetic studies of Javan gibbons (*Hylobates moloch*) using mtDNA analysis. In: Proceedings of the 3rd International Great Apes of the World Conference, Kuching, Sarawak, Malaysia, July 3–6, 1998. Los Angeles, CA: Orangutan Foundation International. Abstract no. 042.

Asquith NM, Martarinza, Sinaga RM. 1995. The Javan gibbon (*Hylobates moloch*): status and conservation recommendations. Trop Biodivers 3:1–14.

Baptista LF, Gaunt SLL. 1997. Bioacoustics as a tool in conservation studies. In: Clemmons JR, Buchholz R, editors. Behavioral approaches to conservation in the wild. Cambridge: Cambridge University Press. p 212–242.

Brockelman WY, Ali R. 1987. Methods of surveying and sampling forest primate populations. In: Marsh CW, Mittermeier RA, editors. Primate conservation in the tropical rain forest. New York: Alan R. Liss, Inc. p 23–62.

Brockelman WY, Srikosamatara S. 1993. Estimation of density of gibbon groups by use of loud songs. Am J Primatol 29: 93–108.

Charif RA, Mitchell S, Clark CW. 1995. Canary 1.2 user's manual. Ithaca, NY: Cornell Laboratory of Ornithology.

Chivers DJ. 1974. The siamang in Malaya—a field study of a primate in tropical rain forest (Contrib Primatol vol. 4). Basel/New York: Karger. 335p.

Cowlishaw G. 1992. Song function in gibbons. Behaviour 121:131–153.

Dallmann R, Geissmann T. 2001a. Different levels of variability in the female song of wild silvery gibbons (*Hylobates moloch*). Behaviour 138:629–648.

Dallmann R, Geissmann T. 2001b. Individuality in the female songs of wild silvery gibbons (*Hylobates moloch*) on Java, Indonesia. Contrib Zool 70:41–50.

Eudey AA. 1987a. Priorities in Asian primate conservation. Primate Conserv 8:172–174.

Eudey AA. 1987b. Action plan for Asian primate conservation: 1987–91. Gland: IUCN/SSC Primate Specialist Group.

Eudey AA. 1996/1997. Asian primate conservation—the species and the IUCN/SSC primate specialist network. Primate Conserv 17:101–110.

Gautier J-P. 1988. Interspecific affinities among guenons as deduced from vocalizations. In: Gautier-Hion A, Bourlière F, Gautier J-P, Kingdon J, editors. A primate radiation. Evolutionary biology of the African guenons. Cambridge/New York: Cambridge University Press. p 194–226.

Geissmann T. 1993. Evolution of communication in gibbons (Hylobatidae). Ph.D. dissertation, Zürich University, Zürich, Switzerland.

Geissmann T. 1995. Gibbon systematics and species identification. Int Zoo News 42: 467–501.

Geissmann T. 1999. Duet songs of the siamang, *Hylobates syndactylus*: II. Testing the pair-bonding hypothesis during a partner exchange. Behaviour 136:1005–1039.

Geissmann T. 2000. Gibbon songs and human music in an evolutionary perspective. In: Wallin NL, Merker B, Brown S, editors. The origins of music. Cambridge, MA: MIT Press. p 103–123.

Geissmann T, Orgeldinger M. 2000. The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus*. Anim Behav 60:805–809.

Geissmann T. 2002a. Duet-splitting and the evolution of gibbon songs. Biol Rev 77: 57–76.

Geissmann T. 2002b. Taxonomy and evolution of gibbons. In: Soligo C, Anzenberger G, Martin RD, editors. Anthropology and primatology into the third millennium: the Centenary Congress of the Zürich Anthropological Institute (Evol Anthropol Vol. 11, Suppl 1). New York: Wiley-Liss. p 28–31.

Geissmann T. 2003. Vergleichende primatologie. Heidelberg/New York: Springer Verlag.

Geissmann T, Bohlen-Eyring S, Heuck A. The male song of the Javan silvery gibbon (*Hylobates moloch*). Contrib Zool (in press).

Gittins SP. 1984a. The vocal repertoire and song of the agile gibbon. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes. Evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 354–375.

Gittins SP. 1984b. Territorial advertisement and defence in gibbons. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes. Evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 420–424.

Gurmaya KJ, Adiputra IMW, Saryatiman AB, Danardono SM, Sibuea TT. 1995. Primate survey, population and ecology: Gunung Honje range Ujung Kulon National Park. Ujung Kulon National Park Project Phase II, 1993–1995. Jakarta, Indonesia: Department Kehutanan and New Zealand Ministry of Foreign Affairs and Trade.

Haimoff EH. 1984. Acoustic and organizational features of gibbon songs. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes. Evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 333–353.

Haimoff EH. 1985. The organization of song in Müller's gibbon (*Hylobates muelleri*). Int J Primatol 6:173–192.

Haimoff EH, Yang X-J, He S-J, Chen N. 1986. Census and survey of wild black-crested gibbons (*Hylobates concolor concolor*) in Yunnan Province, People's Republic of China. Folia Primatol 46:205–214.

Herzog MO, Hohmann GM. 1984. Male loud calls in *Macaca silenus* and *Presbytis johnii*. A comparison. Folia Primatol 43:189–197.

IUCN. 2003. 2003 IUCN red list of threatened species. <www.redlist.org>. Downloaded on 16 September 2004. IUCN (International Union for Conservation of Nature and Natural Resources), Gland, Switzerland.

Kappeler M. 1981. The Javan silvery gibbon (*Hylobates lar moloch*). Ph.D. dissertation, Universität Basel, Basel, Switzerland.

Kappeler M. 1984a. The gibbon in Java. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes. Evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 19–31.

Kappeler M. 1984b. Diet and feeding behaviour of the moloch gibbon. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes. Evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 228–241.

Kappeler M. 1984c. Vocal bouts and territorial maintenance in the moloch gibbon. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes. Evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 376–389.

Kool KM. 1992. The status of endangered primates in Gunung Halimun Reserve, Indonesia. Oryx 26:29–33.

Leighton DR. 1987. Gibbons: territoriality and monogamy. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago/London: University of Chicago Press. p 135–145.

MacKinnon J. 1984. The distribution and status of gibbons in Indonesia. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes. Evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 16–18.

MacKinnon K. 1987. Conservation status of primates in Malesia, with special reference to Indonesia. Primate Conserv 8:175–183.

Marler P, Hobbett L. 1975. Individuality in a long-range vocalization of wild chimpanzees. Z Tierpsychol 38:97–109.

Mitani JC. 1984. The behavioral regulation of monogamy in gibbons (*Hylobates muelleri*). Behav Ecol Sociobiol 15:225–229.

Mitani JC. 1985a. Gibbon song duets and intergroup spacing. Behaviour 92:59–96.

Mitani JC. 1985b. Location-specific responses of gibbons (*Hylobates muelleri*) to male songs. Z Tierpsychol 70:219–224.

Mitani JC. 1985c. Sexual selection and adult male orangutan long calls. Anim Behav 33:272–283.

Mitani JC. 1987. Territoriality and monogamy among agile gibbons (*Hylobates agilis*). Behav Ecol Sociobiol 20:265–269.

Nijman V. 1995. Remarks on the occurrence of gibbons in central Java. Primate Conserv 16:66–67.

Nijman V, van Balen S. 1998. A faunal survey of the Dieng mountains, central Java, Indonesia: distribution and conservation of endemic primate taxa. Oryx 32: 145–156.

Nijman V. 2001. Effect of behavioural changes due to habitat disturbance on density estimation in rain forest vertebrates, as illustrated by gibbons (Hylobatidae). In: Hillegers PJM, de Iongh HH, editors. The balance between biodiversity conservation and sustainable use of tropical rain forests. Wageningen: Tropenbos. p 217–225.

Nijman V. 2004. Conservation of the Javan gibbon *Hylobates moloch*: population estimates, local extinctions, and conservation priorities. Raffles Bull Zool 52:271–280.

Oates JF, Trocco TF. 1983. Taxonomy and phylogeny of black-and-white colobus monkeys. Inferences from an analysis of loud call variation. Folia Primatol 40:83–113.

Raemaekers JJ, Raemaekers PM, Haimoff EH. 1984. Loud calls of the gibbon (*Hylobates lar*): repertoire, organization and context. Behaviour 91:146–189.

Raemaekers JJ, Raemaekers PM. 1985a. Field playback of loud calls to gibbons (*Hylobates lar*): territorial, sex-specific and species-specific responses. Anim Behav 33:481–493.

Raemaekers PM, Raemaekers JJ. 1985b. Long-range vocal interactions between groups of gibbons (*Hylobates lar*). Behaviour 95:26–44.

Regional Physical Planning Project for Transmigration (RePPProT). 1990. The land resources of Indonesia: a national overview from the regional and physical planning program for transmigration. London/Jakarta: Land Resources Department, National Institute Overseas Development Administration and Directorate Bina Program, Directorate Penyiapan Pemukiman, Department Transmigrasi.

Rinaldi D. 1999. Food preferences and habitat utilization of Java gibbon (*Hylobates moloch* Audebert) in Ujung Kulon National Park, West Java, Indonesia. M.Sc. thesis, Georg-August University, Göttingen, Germany.

Seibt U, Wickler W. 1982. Rolle des Duettierens im Leben der Vögel. In: Max-Planck-Gesellschaft Jahrbuch 1982. Göttingen: Verlag Vandenhoeck and Ruprecht. p 351–352.

Steenbeek R, Assink P. 1998. Individual differences in long-distance calls of male wild Thomas langurs (*Presbytis thomasi*). Folia Primatol 69:77–80.

Supriatna J, Tilson R, Gurmaya KJ, Manansang J, Wardojo W, Sriyanto A, Teare A, Castle K, Seal U, editors. 1994. Javan gibbon and Javan langur: population and habitat viability analysis report. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group.

Tembrock G. 1977. Tierstimmenforschung. Die Neue Brehm-Bücherei, Heft 250. Wittenberg Lutherstadt: A. Ziemsen Verlag.

Tenaza RR. 1976. Songs, choruses and countersinging among Kloss' gibbons (*Hylobates klossi*) in Siberut Island, Indonesia. Z Tierpsychol 40:37–52.

Tenaza RR. 1989. Intergroup calls of male pig-tailed langurs (*Simias concolor*). Primates 30:199–206.

Thorpe WH. 1961. Bird-song. The biology of vocal communication and expression in birds. Cambridge monographs in experimental biology. No. 12. Cambridge: Cambridge University Press.

Whitesides GH, Oates JF, Green SM, Kuberdanz RP. 1988. Estimating primate densities from transects in a West African rain forest: a comparison of techniques. J Anim Ecol 57:345–367.

Whitten AJ. 1980. The Kloss gibbon in Siberut rain forest. Ph.D. dissertation, University of Cambridge, Cambridge, UK.

Whitten T. 1982. The ecology of singing in Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. Int J Primatol 3:33–51.

Whitten AJ. 1984. The trilling handicap in Kloss gibbons. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes. Evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 416–419.

Wickler W. 1974. Duette und Paarbindung bei Tieren. Mitt Max Planck Ges 1974:237–252.