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Song Activity of the Pileated Gibbon, *Hylobates pileatus*, in Cambodia

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Abstract: The song structure of pileated gibbons (*Hylobates pileatus*) was studied in eight locations in southwestern Cambodia. Male and female vocalizations were recorded daily between 07:00 and 13:00 for five consecutive days at each. The results showed that peak calling activity occurs around 10:00, with slight variation between different locations. A female's song is typically made up of approximately seven to eight phrases of great calls (average = 7.63 ± 2.36), each lasting an average of 13.25 ± 6.09 seconds. Matching male call phrases are relatively stable at 11.55 ± 3.82 seconds and are positively correlated with the duration of matching female songs, whereas solo male call phrases are shorter, 10.66 ± 9.16 with no correlation to female songs. The number of great call phrases, the sequences, and duration in female songs varied significantly between individuals from different localities. This suggests that gibbon develop local dialects and that songs constitutes an important parameter in pair formation and social structures.

Key words: Gibbon, *Hylobates pileatus*, song activity, Cambodia

Introduction

Gibbons (Hylobatidae) occur in most of eastern Asia, from northwest India in the west, to China in the east and Java (Indonesia) in the south. They generally exhibit monogamous social structures with well-defined territories (Mackinnon and Mackinnon 1977; Chivers 1984; Leighton 1987; Brockelman *et al.* 1998) and distinguish themselves from other primates by producing long and loud song bouts (Haimoff 1984; Brockelman *et al.* 1998; Geissmann 1999, 2002). Gibbon duets are well-timed and complex vocal interactions that influence pair-bonding behavior (Chivers 1976; Brockelman and Srikosamatar 1984; Raemakers *et al.* 1984; Palombit 1994; Geissmann 1995, 1999, 2000, 2002). Most of the duets and individual calls are distinctly different from each other; so much so that a trained listener can easily distinguish between, for example, two different vocalizing couples (Geissmann pers. comm.). Some species, for example siamang (*Hylobates syndactylus*), exhibit particularly complex vocal structures, and it is consequently considerably more difficult to distinguish between two different songs without help from an audiogram (Geissmann 1999, 2000).

Maples *et al.* (1989) and Geissmann (1999, 2000) provided evidence that the duet of siamangs (*H. syndactylus*) plays an important role in pair bonding. Such duets are the

result of learned behavior, primarily through intensive adaptive vocal interaction between a male and a female (Maples *et al.* 1989; Geissmann 1999, 2000). This suggests that gibbons have a larger song repertoire than normally recorded in the field and that song activity can be adapted to a new partner. Although it is well known that two or more groups of gibbons can be distinguished from their songs alone, it is possible that even individuals differ in their song composition on different days. It has been suggested that it is possible to build a phylogenetic relationship on the basis of acoustic repertoire (Geissman 2002; Konrad 2004). Takacs *et al.* (2005) revealed that a phylogenetic relationship based on acoustic repertoire alone does not necessarily match that of a phylogenetic relationship using DNA sequences. Nevertheless, differences in female great calls can be easily detected in an audiogram, and differences—if any—in song composition, duration, time, and structure should be possible to record directly in the field.

The pileated gibbon, *Hylobates pileatus*, is found in Thailand, Cambodia, and Laos west of the Mekong River (Lekagul and McNeely 1988; Corbet and Hill 1992; Traeholt *et al.* 2005). It is abundant in both logged and virgin forests of western Cambodia, and duets usually in the mornings (Traeholt *et al.* 2005). This study was undertaken in conjunction with Fauna and Flora International's Cambodia Primate

Programme and examines the differences in the song structure of pileated gibbons in a number of sites in Cambodia.

Methods

Gibbon songs were recorded from eight locations (Table 1) for five consecutive days at each. All locations were in heavily logged, evergreen forest, although Plot 1 in Chipat was significantly more degraded than the others.

We recorded gibbon duets between 07:00 and 13:00 from three different listening posts forming an equilateral triangle of 1 km on each side. For each duet we recorded time started and ended, duration, date, temperature, weather condition, and location (using a global positioning system) of both males and females. When a female was silent for 15 minutes we considered her great call as terminated (i.e., when the female started another great call in the 16th minute following termination of the previous call we considered it a new song). A male call that was part of a duet was a matching call. Male calls that were not part of a duet we refer to as non-matching calls. We defined a song as consisting of a number of call phrases (i.e., a female's great call is repeated several times in the space of a complete song). Among the gibbons in Chipat and Botum Sakor we recorded the number of phrases by one-zero sampling with 1-minute intervals. An example is given in Table 2. The duration of each female and male call phrases was

measured in seconds. We used the t-test (two-sample, unequal variance: *p* value of 0.05 to accept a null hypothesis) to test for any statistical differences in song duration, number of call phrases, and duration.

Results

The pileated gibbon exhibits clear diurnal calling activity (Fig. 1). Peak calling occurred at 10:00 (sample size = 101 recorded songs; Fig. 1). There was, however, a slight difference in calling activity among the Chipat gibbons, who called equally frequently between 10:00 and 11:00 (Fig. 1).

Although all the females' great calls were typical of the species, the number of call phrases in each song, their sequences, and duration varied considerably (Table 3). This was apparent not only between different individuals, but also in the day-to-day activity for the same individual. The sequences of call phrases of the song of female BS1, for example, differed considerably (Table 3). She could produce eight great calls over 11 minutes in one song (sequence 7 in Table 3), and two single phrases over 11 minutes in another (sequence 5 in Table 3).

A female pileated gibbon's song is made up of approximately 7–8 phrases of great calls (Table 4; average = 7.63 ± 2.36). Each phrase lasts for an average of 13.25 ± 6.09 seconds (Fig. 2a). The length of matching male call phrases is relatively stable at 11.55 ± 3.82 seconds (Fig. 2a; high = 24

Table 1. The eight survey locations in Cambodia.

Location	Coordinates	Habitat
Samling 1	103°52' 16.13" E, 11°16' 19.75" N	Secondary tall evergreen forest
Samling 2	103°49' 19.84" E, 11°17' 13.81" N	Secondary tall evergreen forest
Chipat 1	103°28' 27.31" E, 11°29' 44.23" N	Secondary evergreen, low and open canopy
Chipat 2	103°29' 37.63" E, 11°29' 31.81" N	Secondary tall evergreen forest
Kirirom	104°02' 26.80" E, 11°18' 52.03" N	Secondary tall evergreen and sporadic grassland
Phnom Prom	103°58' 10.98" E, 11°23' 25.66" N	Secondary evergreen forest
Botum Sakor 1	103°20' 38.81" E, 11°14' 28.89" N	Secondary tall evergreen forest
Botum Sakor 2	103°22' 14.77" E, 11°10' 11.91" N	Secondary tall evergreen forest

Table 2. An illustration of the one-zero sampling of three different pileated gibbon songs from western Cambodia. To save space the table is incomplete (i.e., it only contains a number of zeros after the last recorded phrase of each respective gibbon song). In reality, each song was considered terminated after 15 minutes (15×0) of silence by the female.

Gibbon																	No of phrases	Duration (min.)
1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	7	7
2	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	6	11
3	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	7	10
Minute	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16		

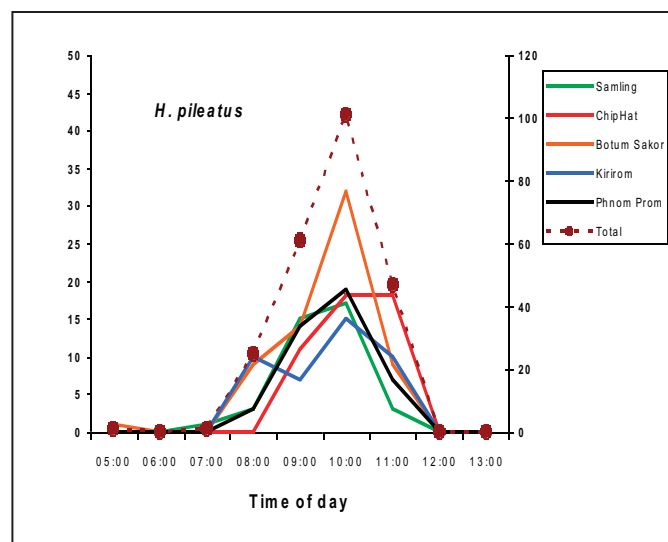


Figure 1. The diurnal calling activity of pileated gibbons from eight different localities in western Cambodia. We did not record any song activity after 12:00.

Table 3. An example of one-zero sampling of gibbon songs from Chipat (CHP) and Botum Sakor (BS). CHP3 = gibbon #3 from Chipat, BS1 = gibbon #1 from Botum Sakor. *) The duration of this song exceeded the number of columns available in this table. Hence the number of phrases (7) does not match the counted number in Table 4.

	Gibbon																			No. of Phrases	Duration (min.)
1	CHP1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	7	7
2	CHP3	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	6	11
3	BS1	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	5	9
4	BS1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	6	10
5	BS1*)	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	7*)	32*)
6	BS1	1	0	1	1	1	1	0	1	0	0	1	0	0	1	0	0	1	0	10	19
7	BS1	1	1	1	0	1	0	1	1	1	0	1	0	1	0	0	1	0	0	10	16
8	BS4	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	4	9
	Minute	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	

Table 4. The number of call phrases and total song duration of three female *H. pileatus* songs in Chipat and five individuals in Botum Sakor, Cambodia. Numbers in parentheses refer to the number of recorded songs assigned to the respective individual. For example, BS1 (5) denotes that we recorded five songs from Botum Sakor Gibbon Number 1.

Location	Gibbon	No. of phrases	Average	Average/min	Song duration (min)	Average song duration (min)
Chipat	CHP1 (1)	7		1.00	7.00	7.00
	CHP2 (1)	10		0.77	13.00	13.00
	CHP3 (1)	6		0.46	13.00	13.00
	Average/song	7.67 ±1.70			Average (N = 3)	11.00 ±2.83
Botum Sakor	BS1 (5)	38	7.6	0.44	86.00	17.20
	BS2 (1)	8		0.73	11.00	11.00
	BS3 (2)	19	9.5	0.83	23.00	11.50
	BS4 (4)	26	6.5	0.52	50.00	12.50
	BS5 (1)	8		0.89	9.00	9.00
	Average/song	7.62 ±2.50			Average (N = 13)	13.77 ±6.55

seconds, low = 7 seconds), whereas male call phrases that are not part of a duet song are relatively shorter, 10.66 ± 9.16 seconds but with much higher fluctuation (Fig. 2a; high = 73 seconds, low = 2 seconds). There are no significant differences in the phrase duration of matched and unmatched male calls, although two phrases of unmatched calls lasted for 45 and 73 seconds, respectively. These appear to be uncharacteristic song activity, and omitting these two calls from the statistical analysis results in a significant difference in the phrase length of matched and unmatched male calls ($p < 0.005$, t-test). Furthermore, the lengths of matched phrases were positively correlated with those of female call phrases (Fig. 4; $k = 0.1568$), whereas the length of unmatched call phrases were negatively correlated with the length of female call phrases ($k = -0.0303$). The sequences of call phrases in a complete female song differed between individuals irrespective of their location (Table 4). Differences were also recorded within inter-day call activity of the same female (Fig. 2b), however, there were no significant differences in average number of phrases per song and the total song duration between groups from different localities (Table 4, Fig 2c). Botum Sakor gibbons, however, used significantly longer call phrases in their songs than their conspecifics in Chipat ($p < 0.001$, t-test) (Fig. 3). Within the Botum Sakor population there is also a significant difference between the longest and shortest female phrase duration ($p < 0.005$, t-test).

Discussion

Communication within and between couples of pileated gibbons consist of complex structures of call phrases of different duration, frequency, and number. There is no doubt that frequent calling plays an important role in the social structure of gibbons but it is not yet clear to what extent such songs play a role in pair formation. It has been suggested that songs play a crucial role in pair formation of siamangs, *Symphalangus syndactylus*, and that couples often adjust their calling to each other (Maples *et al.* 1989; Geissman 1999, 2000, 2002). This could suggest that there is a continuous evolution of song patterns among Hylobatidae, and that gibbon groups that become isolated for a period of time will develop distinctly different song patterns. Although differences in individual female great calls can easily be detected in an audiogram and even be noted by an experienced listener in the field, it is less clear if there are any structural differences in songs of gibbon groups from one locality compared with another.

Our findings revealed that the number of great call phrases per female song was relatively constant throughout the study area (Table 4); however, this does not exclude the possibility that differences in number of call phrases can be found between groups of gibbons much farther apart. For example, pileated gibbons in Thailand may use significantly more phrases than pileated gibbons in southern Laos. The cur-

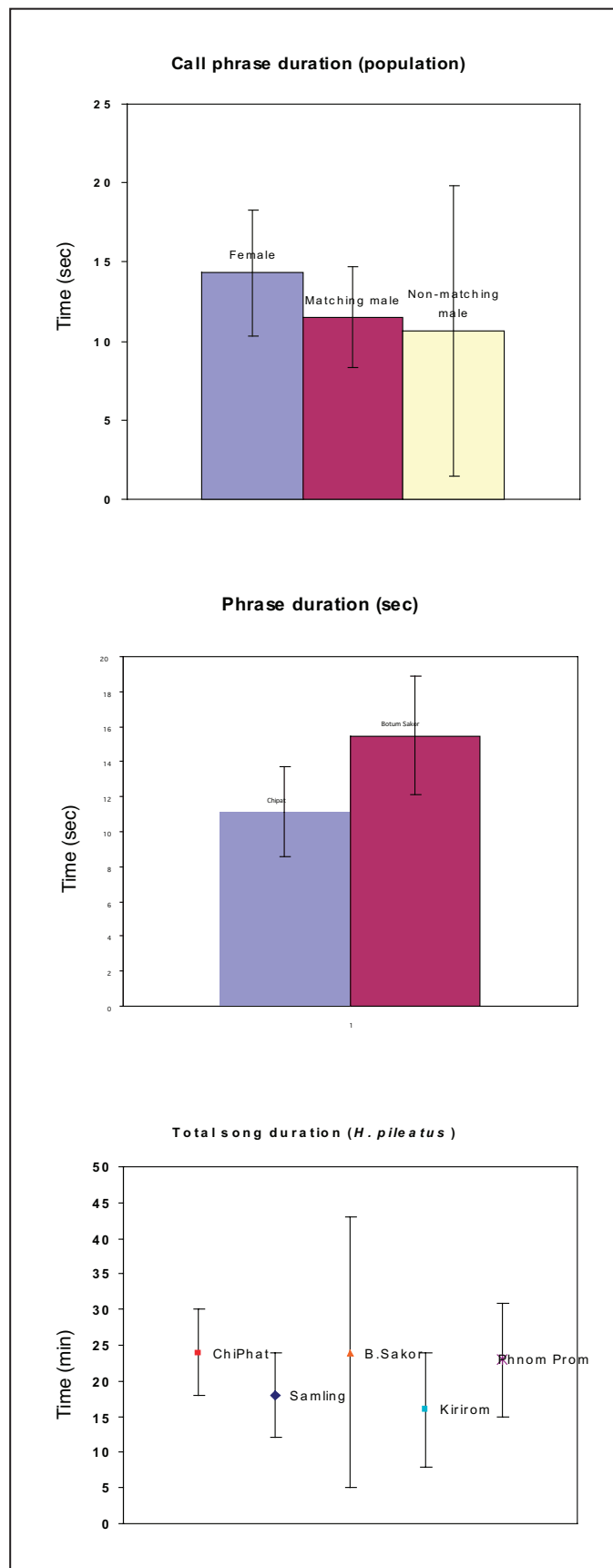


Figure 2a–c. Call phrases and song durations of female and male *Hylobates pileatus* in western Cambodia. The average phrase duration of females, matching male's phrases and un-matching male's phrases are illustrated in Figure 2a, the inter-day call activity of a single female is illustrated in Figure 2b, and the total female song duration from each survey location is illustrated in Figure 2c.

rent data do not allow us to draw any definite conclusions, and consequently, the question remains open as to what extent the number of phrases per song can be used as a parameter to distinguish between different groups or even subgroups of pileated gibbons.

Female pileated gibbons show distinctly different individual song patterns in relation to phrase duration and frequency. Although we found no significant differences in the total song duration of gibbons from different areas (Fig. 2c), we were able to detect significantly longer call phrases among Botum Sakor

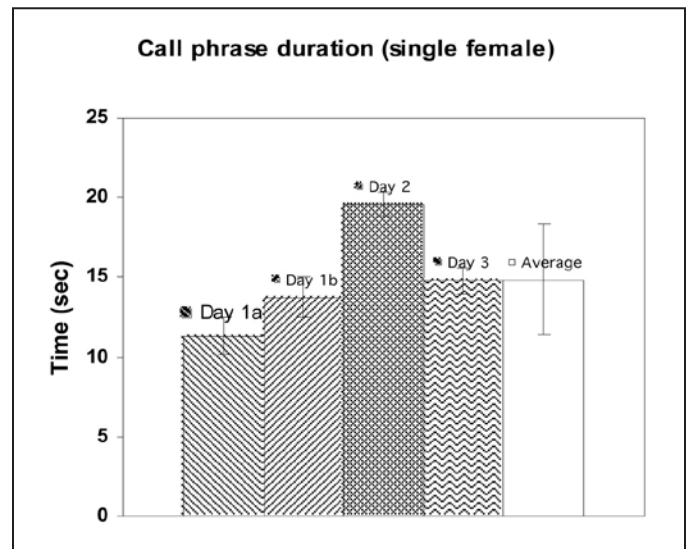


Figure 3. Phrase duration of female great calls in two study sites, Chipat and Botum Sakor. Botum Sakor females' call phrases are significantly longer than the Chipat counter parts ($p < 0.001$, t-test).

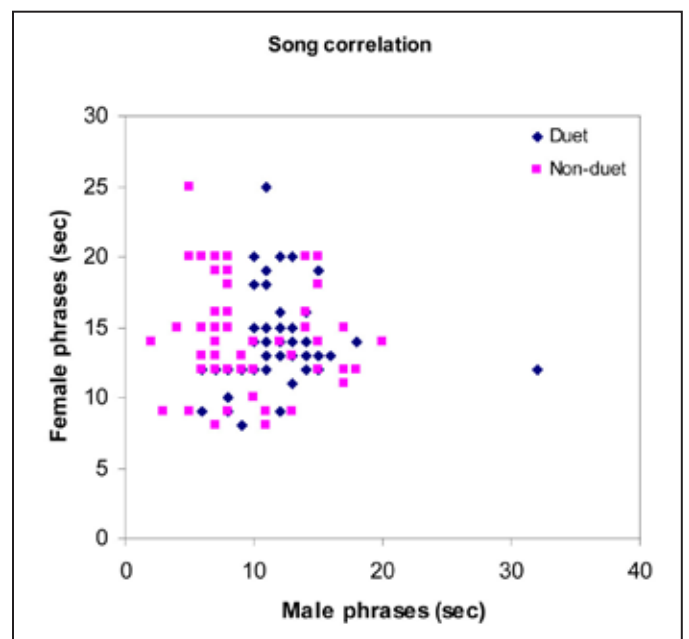


Figure 4. Correlation between male and female call phrases. There is a positive correlation between male phrases that is part of a duet (correlation factor = 0.1568) whereas there is negative correlation between female phrases and "un-matched" male phrases (correlation factor = -0.0303).

groups than Chipat groups ($p < 0.001$, t-test) (Fig. 3). It was not possible, however, to confirm any differences between female call phrase duration in the same area, which was partly due to considerable inter-day individual activity (i.e., the individual inter-day fluctuation diluted the effect of variation between two individuals from two different localities; Fig. 2b). It is not clear what induces the inter-day fluctuation in the duration and sequence of female call phrases. There was, however, a significant difference between gibbon songs in terms of the longest and shortest phrase duration ($p < 0.005$, t-test), suggesting that there may be specific local dialects between subpopulations of pileated gibbons and that such dialects are possibly reflected in the duration of respective call phrases.

There are indications that male calling structure is significantly affected by female great call phrases. Male calls that follow female great call phrases ("matched" call phrases) last significantly longer than "solo" male calls ($p < 0.005$, t-test) and their lengths are positively correlated with the female phrase length ($k = 0.1568$). In contrast, the length of male solo calls are negatively correlated with the length of female call phrases ($k = -0.0303$). Furthermore, male calls that form part of a duet song fluctuate less in terms of duration. This lends support to Geissmann's theory (Geissmann 1984, 1999, 2000, 2002) that duet songs are developed through intensive adaptive vocal interaction between males and females, and that such songs constitute a crucial part of gibbon social structure. From a conservation point of view, this suggests that harvesting of either sex may lead to delayed reproductive performance partly due to prolonged pair formation. This, combined with some gibbon species' slow dispersal rate and reluctance to leave their territory even with significant disturbance (Johns 1985, 1986), indicates that any harvest of established pairs of pileated gibbons as pet animals should remain prohibited until further studies are able to quantify to what extent the speed of new pair formation is dependant on song compatibility and adaptability.

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