The Syntax and Meaning of Wild Gibbon Songs

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Spoken language is a result of the human capacity to assemble simple vocal units into more complex utterances, the basic carriers of semantic information. Not much is known about the evolutionary origins of this behaviour. The vocal abilities of non-human primates are relatively unimpressive in comparison, with gibbon songs being a rare exception. These apes assemble a repertoire of call notes into elaborate songs, which function to repel conspecific intruders, advertise pair bonds, and attract mates. We conducted a series of field experiments with white-handed gibbons at Khao Yai National Park, Thailand, which showed that this ape species uses songs also to protect themselves against predation. We compared the acoustic structure of predatory-induced songs with regular songs that were given as part of their daily routine. Predator-induced songs were identical to normal songs in the call note repertoire, but we found consistent differences in how the notes were assembled into songs. The responses of out-of-sight receivers demonstrated that these syntactic differences were meaningful to conspecifics. Our study provides the first evidence of referential signalling in a free-ranging ape species, based on a communication system that utilises combinatorial rules.

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INTRODUCTION

Primates typically produce acoustic signals when detecting a predator, such as a raptor, large cat, or snake. These vocalisations are termed alarm calls, which function to warn other group members and sometimes also to communicate directly to the predator, for example to attract its attention or advertise perception [1]. For some primates, there is good evidence for reference-like communication. If signalers reliably produce acoustically distinct vocalisations to different classes of predators, then recipients often respond to them as if they have spotted the corresponding predator themselves, presumably because they draw inferences about ongoing external events from the calls [2]. Very little is known about the psychological processes that underlie and drive call production, and hence the term ‘functionally referential’ is sometimes used to describe such cases. In contrast to human speech, such communication systems are not necessarily based on signalers and recipients understanding each other’s intentions [3]. Instead, the default assumption is that primates and other animals do not vocalise to actively inform each other, but information is transmitted as a by-product of signalers responding to evolutionarily important events.

Somewhat strikingly, there is relatively little evidence for referential signalling from our closest living relatives, the apes. This is particularly puzzling in the light of a substantial literature on referential signalling in various monkey species, such as vervet monkeys, Diana monkeys, Campbell’s monkeys, putty-nosed monkeys, or white-faced capuchin monkeys [4–8]. Recently, it has been suggested that captive chimpanzees produce functionally referential calls in response to different types of foods, but it is not yet clear what features of the food the calls denote [9–10].

Gibbons (Hylobatidae), the South-East Asian forests’ smaller apes, are known for a most remarkable behaviour, their loud and conspicuous songs that transmit over long distances, often up to one kilometre or more through dense forest vegetation [11]. Although mostly monogamous, gibbons occasionally engage in extra-pair copulations and take-overs of residents by males or females have been documented [12–13]. In most gibbon species, the mated pair normally sings in the morning in a coordinated fashion, the so-called duet song, most likely to communicate to neighbouring individuals [14–19]. Gibbons sometimes also produce songs in response to predators, but no systematic study has ever been conducted to investigate this phenomenon [20–21]. Their body mass is small compared to other members of the Hominoidea, more comparable to that of a large monkey (5 to 11 kg). This is likely to make them vulnerable to predation from large cats, snakes and birds of prey and, perhaps because of this, gibbons almost exclusively reside in the upper forest canopy [22–25]. We were interested to what extent white-handed gibbons of Khao Yai National Park, Thailand, produced songs in response to potential predators and whether these songs differed from songs given as part of the daily morning routine, the duets.

METHODS

Study site and subjects

Khao Yai National Park is situated approximately 130 km NE of Bangkok, Thailand (101°22’E, 14°26’N). Data were collected at the Central Mo Singto study site, situated at an elevation of 730–860 m [26]. Habitation of groups started during the 1980ies. At the time of the study, 13 groups were available for observations with all group members individually known and social histories documented for most of them (Table 1).

Study groups consisted of between 2 to 6 individuals, mostly an adult pair and their offspring, sometimes with more than one adult

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male [27–29]. Males and females disperse from their natal group at or some years after reaching sexual maturity, starting at about 7–8 years of age. White-handed gibbons are sexually monomorphic, and of either light or dark pelage colour, although this is unrelated to sex or age. The Central Mo Singto study site borders the distribution area of the pileated gibbon (Hylobates pileatus), and a hybrid zone exists between the two species.

Vocal behaviour

(a) Single notes: The basic vocal behaviour of white-handed gibbons has been described already [18] and, whenever possible, we used the same terminology (fig. 1). Individual vocal units are termed ‘notes’, of which seven different types can be distinguished: (1) ‘wa’, (2) ‘hoo’, (3) ‘leaning wa’, (4) ‘oo’, (5) ‘sharp wow’, (6) ‘wooo’, and (7) ‘other’. The ‘hoo’ was originally considered part of the ‘wa’ group, but we found that this class was consistently lower-pitched than ‘wa’ (mean frequency = 73.8 Hz ± 36.9, n = 115), of lower amplitude, and usually covering a frequency range of less than 100 Hz. These three parameters were perceptually salient and they allowed us to reliably discriminate between ‘wa’ and ‘hoo’ notes.

(b) Note combinations: Individual notes are rarely produced in isolation but are normally assembled into more complex structures, so-called ‘figures’ or ‘phrases’, to form a ‘song’. Figure 2 depicts two prominent examples of phrases, the relatively rigid ‘female great call’ and the ‘male reply’. If two group members produce songs in a coordinated way, this is termed a ‘duet’.

Data collection and equipment

The study was undertaken between April 2004 and August 2005. All calls were recorded using Sony DAT recorders (TCD-D8 and TCD-D7), and Sennheiser directional microphones (MKH815T and ME66) with windshields. Ad libitum recordings throughout the day resulted in a library of natural duet songs (n = 14) from different groups, which we then compared with predator-induced songs. Natural predator encounters are very difficult to observe in dense rainforest habitats and systematic studies are almost impossible to conduct. Hence, we elicited songs by experimentally presenting realistic life-size predator models to the different study groups.

Our model predators were custom-made, to match photographs of the real predators, and positioned in their natural resting or hiding position [30] (see fig. 3). We tested the gibbons’ responses to the following predator types: clouded leopard (Neofelis nebulae), tiger (Panthera tigris), reticulated python (Python reticulatus), and crested serpent eagle (Spilornis cheela). For the tiger and clouded leopard models, we used two different exemplars. Clouded leopard models consisted of fake-fur wrapped around an object, such as a large rucksack, positioned approximately 1 m from the ground on a log or stone. Tiger models consisted of a person covered by fake-fur. The reticulated python model was made from several draught excluders of approximately 10 cm in diameter, sewn together and painted, to make a tube of about 4 metres in length. The python was placed, usually coiled, at about 1–2 metres above the forest floor in a small tree, tree stump, or log. The crested serpent eagle model, finally, was made from chicken wire and papier-mâché, painted and feathered with feather dusters bought locally. It was hoisted 4–10 m into the trees with a rope, and positioned usually between two parallel branches as though perched on the lower branch. For this, we shot a weight attached to a fishing line over an appropriate branch with a catapult, allowing us to pull the rope over the branch for hosting and positioning the eagle model into the canopy.

Our overall aim was to keep stress for the study animals as low as possible. Some of our observations suggested that natural predation events could occur at a maximum rate of about one per 3–4 days. We decided to present predator models at intervals of no more than one per week per group, considerably below the maximum observed rate. Each group was exposed only once, maximally twice, with a particular model type. Predator models were presented in open forest habitat, so that individuals always had open escape routes.

Experimental protocol

Groups were located usually by their morning duets, or by identifying their sleeping site the night before. Once found, the observer (EC) followed them for at least 2 hours before an experimental trial was initiated. This period permitted the individuals to habituate to the observer’s presence and it provided baseline vocal and non-vocal data before model presentation. If no real predator was encountered during this 2-hour period, a predator model was positioned so that the subjects could not observe the procedure. The model was then displayed for a period of about 20 minutes total, starting from when the gibbons had detected it, and then removed. The observer usually remained with the group for at least two more hours, or until the group reached their final sleeping site for the day. Throughout model presentation, the focal individuals’ behaviour was monitored continuously and recordings were made of their calls. The vocal responses of neighbouring groups were also recorded whenever they occurred.

Data analyses

As outlined, we were interested in the structural differences of gibbon songs produced (a) as part of their early morning routine and (b) in response to predators. We decided to exclude the responses to the tiger model from the main analyses because of the rarity of real tigers in the study site. Since January 1999, only two sightings have been made in the entire park, despite intensive

| Group | Number of individuals | Composition | Habitation |
|-------|-----------------------|-------------|------------|
| A     | 5                     | 3AM, 1AF, 1JM | ***        |
| B     | 3                     | 1AM, 1AF, 1SAM | ***        |
| C     | 2                     | 1AM, 1AF | ***        |
| D     | 5                     | 2AM, 1AF, 1JM, 1? | *         |
| Ef    | 3                     | 1AM, 1AF, plus 1AF piledate | ***        |
| H     | 4                     | 2AM, 1AF, 1JM, 1? | ***        |
| J     | 5                     | 2AM, 1AF, 1JF, 1? | *         |
| N     | 4                     | 2AM, 1AF, 1JM | ***        |
| R     | 3                     | 1AM, 1AF, 1JF | ***        |
| S     | 4                     | 1AM, 1AF, 1SF, 1JF | ***        |
| T     | 3                     | 1AM, 1AF, 1JF | ***        |
| W     | 5                     | 1AM, 1AF, 1SAM, 1JM, 1? | ***        |
| NOS   | 5                     | 2AM, 1AF, 1J, 1SAM, 1JF | *         |

1 Mixed species group containing one piledate gibbon female (H. pileatus). M = male, F = female, ? = sex unknown. Age classes follow Reichard [26], A = adult (>8 years, fully grown), SA = sub-adult (6–8 years), J = juvenile (2–6 years), I = infant (0–2 years). Habituation status: *** well habituated (4 or more years of regular observations by researchers). * partially habituated (<4 years of regular observations by researchers).

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Figure 1. Gibbon song notes as distinguished by Raemaekers et al. [18]: (1) The ‘wa’ note is a short and steeply rising note, appearing as a more or less straight line on the spectrogram; sometimes appearing slightly concave. It consistently spans over 100 Hz in the frequency domain, which sets it aside from the ‘hoo’ note. (2) The ‘hoo’ is a low frequency quiet note consistently spanning a much narrower frequency range than ‘wa’ notes. (3) The ‘leaning wa’ notes may be more or less straight like the ‘wa’ notes but longer in duration, and therefore lean more to the right; sometimes they have a slight bump in the middle. (4) The ‘oo’ note is of a relatively even pitch and therefore produces a flat note, as seen on the spectrogram, of varying duration. Sometimes it may rise slightly at the start. (5) The ‘sharp wow’ note is a loud and penetrating note. It rises steeply at first then falls steeply to produce a concave curve. It invariably spans more than 700 Hz in the frequency domain. The end of the note may be prolonged horizontally. (6) The ‘wao’ note is highly variable. It always rises steeply at first, but then may hold pitch at an even level or fall in pitch to create a convex curve. It spans a much lower frequency range than the ‘sharp wow’. (7) Notes that did not fit in with the shapes and definitions of the other six notes described above were allocated as ‘other’. These were highly variable, and some may warrant their own unique note category, but for the purposes of this study they are grouped together. This category also describes the above six note shapes when given with major pitch modulations that give them a wobbly or trembling quality. Finally, the ‘ooaa’ is extremely rare and was not found in any of the analysed recordings in this study, and so is not described here.

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Nevertheless, groups responded strongly to this predator model, in one case also triggering a vocal response from a neighbouring group.

Whenever we recorded neighbour responses to the focal groups’ singing behaviour to a predator, we analysed these calls as well, as this provided us with a natural experiment: Since we knew exactly what the focal group responded to, we could determine what information their songs potentially transmitted to recipients in adjacent home-ranges or to group members who were temporarily away from the group. We included the response to the tiger model for this analysis due to the low sample size.

Calls were digitised using Cool Edit 2000 software. Spectrograms were made using Raven 1.2.1 with a Hanning window function, 8.71 Hz filter bandwidth, 0.5 Hz frequency resolution and 15 s grid time resolution. Gibbons’ singing is a crescendo of notes, particularly in response to predators. Vocal behaviour usually starts with a series of very soft ‘hoo’ notes, initially only audible at close range, but rapidly grading into much louder units carrying over long distances. Hence, for each song we defined its start as the first loud non-‘hoo’ note. Then, we determined the following: (a) number of ‘hoo’ notes and (b) duration of ‘hoo’ sequence before song onset. After song onset we determined (c) presence of and (d) latency to first ‘sharp wow’ note, (e) latency to first female great call and (f) latency to male reply, and (g) total duration of singing. We also conducted a sequential analysis to compare the first 10 notes per song in the duet and predatory contexts.

The identity of each gibbon’s voice was distinguishable to the experimenter, and the order in which each group member called was also noted at the time of predator presentation to facilitate analyses. Statistical analyses were conducted using SPSS software, mainly non-parametric procedures such as Mann-Whitney U-tests and Fisher’s exact tests.

RESULTS

Predator-induced songs

Gibbons reliably sang in response to the terrestrial, but not the raptor, predator models: clouded leopard (8/8 trials), tiger (9/9 trials), reticulated python (3/9 trials), crested serpent eagle (0/7), suggesting that singing is a firm part of these primates’ natural defence to ground predators.

Song composition: early differences

Although there were no obvious acoustic differences between the songs given in duet contexts and those given in response to predators, more detailed analyses revealed a number of subtle differences. As soon as an individual began to sing (by producing loud non-‘hoo’ notes) we compared the first 10 notes for each song between the two contexts, which is roughly equivalent to about 15 s of singing (mean duration = 12.46 ± 9.13 s, n = 38). We were particularly interested in this initial song segment because, if gibbons conveyed any information about external events, they should do so as early as possible to benefit conspecific recipients, particularly during predator encounters. Two main differences emerged. First, ‘leaning wa’ notes were significantly less likely to occur in the predatory than the duet context (Fisher’s exact test, p < 0.001). Second, there were significantly more ‘hoo’ notes nested within the other call units in the predatory than in the duet context (N_{duet} = 18; N_{predatory} = 20; U = 111.5; p < 0.05; Mann-Whitney U-test, two-tailed). Figure 4 illustrates the patterns.

Song composition: overall differences

Apart from the first 10 notes only, we found additional overall differences in song composition depending on context: ‘sharp wow’ notes were significantly more common in predatory than in duet songs (Fisher’s Exact test, p = 0.001), appearing on average 236.4 ± 346.8 s into a predatory song (n = 11). We also found ‘sharp wows’ in some duet songs (n = 6/14, mean latency = 71.3 ± 47.2 s), but interestingly, they were all given by groups that had not been fully habituated to human presence (groups D, J, and NOS; table 1). It is likely, therefore, that the ‘sharp wows’ are notes given in response to any disturbance, which can be incorporated into regular duets and predator-induced songs.

Overall, songs given in the predatory context were significantly longer than songs in the duet context (mean duration = 2005.0 ± 1560.0 s, n = 11, versus 625.9 ± 450.7 s, n = 14, U = 28.0, p < 0.01; Mann-Whitney U-test, two-tailed). Predator-induced songs were always introduced by a long series of soft ‘hoo’ notes. The number...
of these notes differed significantly between the predatory and the duet contexts (predatory: 100.9±110.9, n = 11; duet: 9.2±8.3, n = 14; U = 4.0, p<0.001 Mann-Whitney U-test; two-tailed). Correspondingly, the total duration of the ‘hoo’ note series in the predatory context was significantly longer than in the duet context (predatory: 156.7±290.6 s, n = 11; duet: 9.8±13.1 s, n = 14, U = 17, p = 0.001; Mann-Whitney U-test, two-tailed).

Female great calls
The female great call, finally, is a stereotyped sequence of notes described as a phrase, lasting on average 17.43±1.32 s (n = 13). Females reliably produced great calls in both contexts, but during duets they were delivered significantly earlier compared to when responding to predators (duets: 80.0±35.2 s, n = 14; predatory: 682.4±669.8 s, n = 9; U = 2.0, p<0.001, Mann-Whitney U-test, two-tailed) with no overlap: Great calls during the first two minutes were reliably linked with the duet context, whereas great calls given after this time period were always associated with the presence of a predator (Fisher’s exact test, p<0.001). Males usually replied to female great calls with a specific phrase, but these replies came significantly earlier in the predatory than in the duet context (predatory = −1.3±1.7 s, n = 9; duets: 1.0±3.4 s, n = 14; U = 23.0, p = 0.012, Mann-Whitney U-test, two-tailed). Figure 5 summarises the main differences.

Conspecific responses to gibbon songs
Sometimes, some individuals spend time away from the rest of the group. This happened on three occasions during clouded leopard model presentations (group H: adult male; group J: second adult male; group N: second adult male). In all cases, the absent individual responded with his own songs after hearing the groups’ songs to the predator models, before reappearing to join the group again. We never observed this behaviour when the adult pair gave duet songs, despite the fact that in some groups the second males...
Figure 4. Sequential analyses of the first 10 song notes in both predatory and duet song contexts (see figure 1 for description of song notes)
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Figure 5. Differences in the composition of songs given as part of normal duets or in response to predators: The top two graphs portray the number of notes present in the sequential analyses of just the first ten song notes, where n-values represent the number of individuals (only adult males and females are included).

The lower six graphs show overall compositional differences in song types according to the parameters measured. N-values represent the number of song bouts in each context.

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were often absent as well, suggesting that these individuals distinguished predator-induced from normal songs. During four other predator trials, a neighbouring group began to sing after the commencement of the study group’s singing, allowing us to analyse the structure of these calls with regards to two indicators of predator-induced songs: the presence of ‘sharp wows’ and the delay of the female great call beyond 2 min. Our analyses showed that all seven response songs contained ‘sharp wow’ notes (neighbouring groups: n = 4, absent group members: n = 3). In addition, in two of the four neighbouring groups, the first female great call was delayed beyond the critical 2 min threshold, further demonstrating that these groups perceived and responded to the songs of their neighbours with the correct and matching predator songs.

We were also able to analyse a number of songs that were given in response to the regular duets by a neighbouring group (n = 4). As predicted, in all cases the first female great call was delivered during the first 2 min, indicating a normal duet context, and we never recorded any ‘sharp wow’ notes. Table 2 summarises the main results.

**DISCUSSION**

We were interested in gibbon songs because, apart from human speech, these vocalisations provide a remarkable case of acoustic sophistication and versatility in primate communication. Individuals combine a finite number of call units into structurally more complex sequences in rule-governed ways, hereby conveying a high degree of structural and functional organisation. In particular, we observed a predator-specific delay in the production of the first great call, as well as the inclusion of ‘sharp wow’ notes in all cases in which neighbours responded to the predator-induced song. We never observed these patterns in the response songs of neighbours to normal duets. In all observed cases, absent males began to sing while returning to the rest of the group. Again, we never observed such behaviour during normal duets. The returning males’ songs always included ‘sharp wow’ notes, a convincing sign that they understood the meaning of the song produced by their group.

Why do gibbons produce these loud and conspicuous songs in response to ground predators? One function of alarm calling is to alert kin to the presence of a predator [33]. The gibbons at Khao Yai frequently change group compositions, and as a result close relatives often live in neighbouring groups [13]. For example, members of groups A and B are closely related because the adult male from B is a brother of the adult males and juvenile male from group A. For example, members of groups A and B are closely related because the adult male from B is a brother of the adult males and juvenile male from group A.

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**Table 2. Recipients’ responses to predator-induced and duet songs**

| Context          | Focal group | Recipient  | 'Sharp wows' | Latency to 1st great call* |
|------------------|-------------|------------|--------------|---------------------------|
| Clouded leopard  | B           | Group A    | Present      | 883.9                     |
| Clouded leopard  | N           | Group H    | Present      | 35.7                      |
| Tiger            | W           | Group N    | Present      | 479.8                     |
| Snake            | N           | Group H    | Present      | 105.3                     |
| Clouded leopard  | H           | AM, Felix  | Present      | —                         |
| Clouded leopard  | J           | AM2, Frodo | Present      | —                         |
| Clouded leopard  | N           | AM2, Nithat| Present      | —                         |
| Duet             | D           | Group ?    | Absent       | 48.9                      |
| Duet             | T           | Group ?    | Absent       | 65.4                      |
| Duet             | W           | Group S    | (Absent)     | 30.0                      |
| Duet             | T           | Group E    | Absent       | 41.1                      |

*Great calls in predator-induced songs are usually delayed by 120 s or more. (I) Incomplete recording

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group A, perhaps explaining group A’s strong response to group B’s song to the clouded leopard model. Kin selection, in other words, could explain long-distance alarm calling in this and other species of gibbons [34]. In the case of large cats, empirical work has shown that primate alarm calls have a direct deterring effect on hunting behaviour [35], perhaps further explaining why it is adaptive to produce loud songs when hearing a neighbouring group singing to a predator. The quiet ‘ho’ note series, which reliably precedes a predatory song, could function to alert immediate group members to the location of the predator, and perhaps even to signal detection to a nearby predator. Another interesting finding was that the gibbons did not produce songs to raptor models, although other types of alarm calls are produced to real raptors and models, a topic of ongoing research.

Sexual selection has been proposed as the main evolutionary mechanism for the evolution of gibbon song: males and females produce sexually dimorphic song bouts and songs are used in mate and home range defence, and in mate attraction [36]. In a recent review on the role of sexual selection on primate vocal behaviour, Snowdon [37] noted that the primate literature was weak on evidence of how individual variation in vocal behaviour impacted on reproductive decisions. In contrast, in many species of songbirds, call complexity is linked with male-male competition and mate attraction [32]. The general finding is that better quality males sing more or better than other males, usually leading to higher reproductive success because this is attractive to females or because it increases the male’s ability to defend a territory. Although there is no comparable evidence for the gibbons, a number of parallels are striking. The gibbons’ monogamous mating system is highly unusual, with some studies even reporting sexual polyandry [12,27–28,38–39]. Vocal behaviour appears to function as a powerful tool to deal with the immense sexual competition under which these primates operate, and it may not be surprising that they have evolved unusually complex vocal skills to deal with these social challenges. Not unlike humans, gibbons assemble a finite number of call units into more complex structures to convey different messages, and our data show that distant individuals are able to distinguish between different song types and infer meaning. This study thus offers first evidence of a functionally referential communication system in a free-ranging ape species, which is based on a simple phonological syntax [40].

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Author Contributions

Conceived and designed the experiments: KZ. Performed the experiments: EC. Analyzed the data: EC. Contributed reagents/materials/analysis tools: KZ UR. Wrote the paper: KZ EC. Other: Director of gibbon field site at Khao Yai, provided access to study site, habituated animals, provided permits and invaluable background information on the gibbons: UR.

REFERENCES

1. Zuberbühler K (2006) Alarm calls - Evolutionary and cognitive mechanisms. In: Brown K, ed. Encyclopedia of Language and Linguistics. 2 ed. Oxford: Elsevier. pp. 143–153.
2. Arnold K, Zuberbühler K (in press) Reference or inference? Antipredator communication in a forest gibbon. In: Sommer V, Ross C, eds. The monkeys and apes of Gashaka: Primate socio-ecology and conservation in Nigeria’s biodiversity hotspot.
3. Grice HP (1969) Utterers’ meaning and intentions. Philosophical Review 78: 147–177.
4. Seyfarth RM, Cheney DL, Marler P (1980) Vervet monkey alarm calls: Semantic communication in a free-ranging primate. Animal Behaviour 28: 1070–1094.
5. Zuberbühler K, Noe R, Seyfarth RM (1997) Diana monkey long-distance calls: messages for conspecifics and predators. Animal Behaviour 53: 589–604.
6. Zuberbühler K (2001) Predator-specific alarm calls in Campbell’s guenons. Behav Ecol Sociobiol 50: 414–422.
7. Arnold K, Zuberbühler K (2006) Language evolution: semantic combinations in primate calls. Nature 441: 303.
8. Fichtel C, Perry S, Gros-Louis J (2005) Alarm calls of white-faced capuchin monkeys: an acoustic analysis. Animal Behaviour 70: 165–176.
9. Slocombe KE, Zuberbühler K (2005) Functionally referential communication in a chimpanzee: Current Biology 15: 1779–1784.
10. Slocombe KE, Zuberbühler K (2006) Food-associated calls in chimpanzees: Responses to food types or food preferences? Animal Behaviour 72: 989–999.
11. Marshall JT, Marshall ER (1976) Gibbons and their territorial songs. Science 193: 235–237.
12. Reichard U (1995) Extra-Pair Copulations in a Monogamous Gibbon (Hylobates lar). Ethology 100: 99–112.
13. Brockelman WY, Reichard U, Tresescon U, Raemaekers JI (1998) Dispersal, pair formation and social structure in gibbons (Hylobates lar). Behav Ecol Sociobiol 42: 329–339.
14. Geissmann T, Orgelginder M (2000) The relationship between duet songs and pair bonds in siamangs, Hylobates syndactylus. Animal Behaviour 60: 805–809.
15. Geissmann T (1999) Duet songs of the siamang, Hylobates syndactylus: II. Testing the pair-bonding hypothesis during a partner exchange. Behaviour 136: 1005–1039.
16. Haraway MM, Maples EG (1998) Flexibility in the species-typical songs of gibbons. Primates 39: 1–12.
17. Mitani JC (1985) Gibbon Song Duets and Intergroup Spacing. Behaviour 92: 59–96.
18. Raemaekers JI, Raemaekers PM, Hainolf EH (1984) Loud calls of the gibbon (Hylobates lar): repertoire, organization and context. Behaviour 91: 146–169.
19. Todd NPM, Merker B (2004) Siamang gibbons exceed the saccular threshold: Intensity of the song of Hylobates syndactylus. Journal of the Acoustical Society of America 113: 3077–3080.
20. Raemaekers JI, Raemaekers PM (1985) Field playback of loud calls to gibbons (Hylobates lar): Territorial, sex-specific and species-specific responses. Animal Behaviour 33: 401–403.
21. Udoh NL, Sommer V (2002) Antipredatory behavior in gibbons (Hylobates lar), Khao Yai/Thailand. In: Miller LE, ed. Eat or be eaten. Cambridge: CUP. pp. 260–282.
22. van Schaik CP, van Hooff JA (1983) On the ultimate causes of primate social systems. Behaviour 85: 91–117.
23. Leighton DR (1986) Gibbon: territoriality and monogamy. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds. Primate Societies. Chicago: Univ. of Chicago Press. pp. 133.
24. Reichard U (1998) Sleeping sites, sleeping places, and predeparture behavior of gibbons (Hylobates lar). American Journal of Primatology 46: 35–62.
25. Bartlett TQ (2006) The hylobatidae small apes of Asia. In: Campbell CJ, Fuentes A, MacKinnon K, Panger M, Bearder SK, eds. Primates in perspective. Oxford: Oxford University Press. pp. 274–289.
26. Reichard UH (2003) Social monogamy in white-handed gibbons: the male perspective. In: Reichard UH, Boesch C, eds. Monogamy: Mating strategies and partnerships in birds, humans and other mammals. Cambridge: Cambridge University Press. pp. 274–289.
27. Sommer V, Reichard U (2000) Rethinking monogamy: the gibbon case. In: Kappeler PM, ed. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. pp. 159–168.
28. Barlow C, Heinermann M, Boesch C, Reichard UH (in press) Sexual swellings in wild white-handed gibbon females (Hylobates lar) indicate the probability of ovulation. Hormones and Behavior.
29. Savini T, Boesch C, Reichard UH (accepted) Home range characteristics and the influence of seasonality on female reproductive success in white-handed gibbons (Hylobates lar) at Khao Yai National Park, Thailand. American Journal of Physical Anthropology.
30. Sunquist ME, Sunquist F (2002) Wild cats of the world. Chicago: UCP.
31. Wildlife Conservation Society (2001) Status, ecology and conservation of tigers in their critical habitats in Thailand Wildlife Conservation Society.
32. Catchpole CK, Slater PJB (1995) Bird song: biological themes and variations. Cambridge: Cambridge Univ. Press.
33. Maynard-Smith J (1965) The evolution of alarm calls. American Naturalist 99: 59–63.
34. Tenaza RR, Tilson RL (1977) Evolution of long-distance alarm calls in Kloss’s gibbon. Nature 268: 233–235.
35. Zuberbühler K, Jenny D, Behary R (1999) The predator deterrence function of primate alarm calls. Ethology 105: 477–490.
36. Cowlishaw G (1996) Sexual selection and information content in Gibbon song bouts. Ethology 102: 272–284.
37. Snowdon CT (2004) Sexual selection and communication. In: Kappeler P, Schaik CV, eds. Sexual selection in primates. Cambridge: Cambridge Univ. Press. pp. 57–70.
38. Reichard UH, Bocch C (2003) Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals. Cambridge: Cambridge University Press.
39. Palombit RA (1994) Extra-pair copulations in a monogamous ape. Animal Behaviour 47: 721–723.
40. Marler P (1977) The structure of animal communication sounds. In: Bullock TH, ed. Recognition of complex acoustic signals. Berlin: Springer. pp. 17–35.