Published in Behavioral Ecology and Sociobiology 66, issue 1, 85-96, 2012
which should be used for any reference to this work

The anti-predator behaviour of wild white-handed gibbons (*Hylobates lar*)

Esther Clarke · Ulrich H. Reichard · Klaus Zuberbühler

Abstract Predation on gibbons is rarely observed in the wild. However, the gibbons' moderate body size and relatively small social groups suggest high vulnerability to predation. To assess the role of predation and to study their anti-predator behaviour, we presented visual predator models to nine groups of wild white-handed gibbons at Khao Yai National Park, Thailand. We measured subjects' immediate and delayed responses to four potential predators: tiger, clouded leopard, crested serpent eagle and reticulated python. Subjects reliably approached all four predators. In response to tigers and leopards, they additionally produced predator-specific songs and defecated copiously. In terms of delayed responses, distance between mated adults decreased, but only after exposure to the tiger model. In response to eagles and pythons, gibbons consistently vocalised, but this did not always include predator singing, and we found no long-term effects in overall activity or strata use. However, during 6 of 26 predator encounters, the gibbons produced songs with a structure that was intermediate between a duet song and a predator song more than 20 min after the predator encounter, indicating a long-term effect on their vocal behaviour. This study demonstrates that gibbons discriminate between different potential predators and respond to them with adaptive anti-predator behaviour, which include predator-specific vocal responses. We conclude that gibbons are not immune to predation and that terrestrial predators elicit consistent immediate and delayed anti-predation responses.

Keywords Gibbon · Predation · Alarm calls · Duet songs · Anti-predator behaviour · Ape vocalisations

Introduction

Avoiding predation has been a central theme for the evolution of sociality in animals and hominids (Alexander 1974; Waterman 1997; Goldspink et al. 2002; Alcock 2005; Deecke et al. 2005; Hart and Sussman 2009). Across animal orders, there is evidence of both morphological and behavioural anti-predator adaptations. Morphological adapta-tions include cryptic colouring in Rodentia (Krupa and Geluso 2000), Lepidoptera (Grant 2007), and Squamata (Stuart-Fox et al. 2004), and mimicry in Octopoda (Norman et al. 2001) and Caudata (Kuchta et al. 2008). Behavioural adaptations include warning signals in Passeriformes (Greisser 2009), Sepiida (Langridge et al. 2007) and Rodentia (Slobodchikoff and Placer 2006), and predator mobbing in Rodentia (Owings and Coss 1977), Passeriformes (Krams and Krama 2002) and Primates (Eberle and Kappeler 2008).

In primates, most species living in undisturbed habitats face a range of natural predators that include mammalian carnivores (Boesch 1991; Fay et al. 1995), raptors (Struhsaker and Leakey 1990) and snakes (Heymann 1987; Gursky 2006). Predation can influence the size and composition of groups, reproductive and vocal behaviour, cognitive abilities and habitat use (van Schaik and van Hooff 1983; van Schaik et al. 1983; Hill and Lee 1998; Zuberbühler and Jenny 2002; Janson 2003; van Schaik et al. 2004). For example, preference for high forest canopies

---

Communicated by A. Widdig

E. Clarke · K. Zuberbühler (✉)
School of Psychology, University of St Andrews,
St Andrews KY16 9JP, UK
e-mail: kz3@st-and.ac.uk

E. Clarke
e-mail: esther.a.e.clarke@gmail.com

U. H. Reichard
Department of Anthropology, Southern Illinois University,
Carbondale, IL, USA

is a likely adaptation to increase protection from ground predators (van Schaik et al. 1983), while living in larger groups provides some safety in numbers and improves predator detection as well as chances of escape (Goldspink et al. 2002; Zuberbühler and Jenny 2002; Zuberbühler and Byrne 2006). In addition, group living enables individuals to engage in cooperative defence behaviours that have a dissuasive effect on some predators, such as mobbing and alarm call chorusing (van Schaik and Hörstermann 1994; Zuberbühler et al. 1999).

Gibbons are particularly relevant for understanding the impact of predation on the evolution of primate behaviour because of their basal position within the Hominoidea superfamily and the abundance of extant species. Despite the fact that they have been studied in the wild for decades (Carpenter 1940), surprisingly little is known about the role of predation on gibbon evolution. Similar-sized and even larger monkeys are well within the prey spectrum of most big cats, eagles and snakes (van Schaik et al. 1983; Gursky 2006; Matsuda et al. 2008). However, gibbons may be better protected from predation than other groups of primates with comparable body and group sizes due to their highly specialised rapid locomotion and preference for the high canopy.

Strictly arboreal, these primates live in the forests of South-East Asia. Their social system is mostly monogamous, although extra-pair copulations and polyandrous mating are not uncommon (Palombit 1994; Reichard 1995, 2009; Malone and Okatvinalis 2006; Lappan 2007, 2008; Barelli et al. 2008). Groups are small, between two and six individuals, and typically consist of an adult breeding pair with adult, sub-adult, juvenile and/or infant offspring (Bartlett 2007). Offspring of both sexes remain in their natal groups until adulthood before dispersing (Reichard and Barelli 2008), often into areas adjacent to their parents' home range (Brockelman et al. 1998; Lappan 2007; Reichard 2009; Savini et al. 2009). As a consequence, neighbouring groups may often contain closely related individuals (Lappan 2007), which would give callers an incentive to produce loud alarm calls upon spotting a potential predator that can be heard over long distances.

At Khao Yai National Park, Thailand, gibbons (*Hylobates lar*) interact with ten potential predator species: the clouded leopard (*Neofelis nebulosa*), marbled cat (*Pardofelis mar-morata*), Asian golden cat (*Felis temminckii*), leopard cat (*Prionailurus bengalensis*), Asiatic tiger (*Panthera tigris*), reticulated python (*Python reticulatus*), changeable hawk eagle (*Spizaetus cirrhatus*), mountain hawk eagle (*Spizaetus nipalensis*), black eagle (*Ictinaetus malayensis*) and crested serpent eagle (*Spilornis cheela*) (Uhde and Sommer 2002). Despite these risks, Uhde and Sommer (2002) estimated that predation rates at Khao Yai were very low, with little direct or indirect evidence of predation. Yet, female gibbons with infants choose sleeping sites that are significantly higher than other group members (Reichard 1998), suggesting that predation does affect gibbon behaviour, especially when infants are present.

Gibbons are well-known for their highly complex vocal behaviour. Mated pairs give loud and coordinated songs (termed 'duets') that transmit over considerable distances, much beyond the callers' home range, suggesting that these signals have evolved to communicate with other conspecifics that are not part of the immediate social group (Raemaekers and Raemaekers 1985; Geissmann 1999; Geissmann and Orgeldinger 2000). Gibbon songs also perform an important function during predator encounters (Uhde and Sommer 2002; Ellefson 1974). A recent study has demonstrated that predator songs given by white-handed gibbons are different from regular duet songs in a number of consistent ways, especially with regards to the structural arrangement of the different song units (Clarke et al. 2006). Anecdotal observations further suggested that after predator encounters, gibbons increase group cohesion, sometimes engage in mobbing and decrease foraging behaviour (Uhde and Sommer 2002).

These observations, along with gibbon female and infant sleeping behaviours, and the fact that unhabituated gibbon groups show distinct anti-predator behaviour to human observers, whereas predator-naive island species do not (Rödl et al. 2007), suggest that predation has been an important selective force on this population favouring behavioural and morphological adaptations (Dawkins and Krebs 1979).

In order to systematically investigate the anti-predatory behaviour of white-handed gibbons in a predator-rich habitat, we conducted a series of experiments that simulated real predator encounters by presenting life-sized predator models in their natural forest habitat. We were interested in the immediate and long-term effects of a predator encounter, since both are indicative of specific adaptations to predation. Empirical studies with free-ranging monkeys have revealed that most species that have been tested possess a number of predator-specific defence responses (Ouattara et al. 2009). For example, savannah-living vervet monkeys (*Cercopithecus aethiops*) run into cover or descend a tree when an eagle flies overhead, or they climb into a tree if a leopard is in the vicinity (Struhsaker 1967; Cheney and Seyfarth 1992). Likewise, Diana monkeys (*Cercopithecus diana*) responded cryptically to the arrival of predatory chimpanzees or generated conspicuous vocal and locomotor behaviour in response to hiding leopards (Zuberbühler 2000). The proboscis monkey (*Nasalis larvatus*) also interacts with clouded leopards (*Neofelis diardi*) and shows some longer term behavioural modifications, such as choosing resting sites bordered by rivers, presumably designed to avoid these and other ground predator encounters (Matsuda et al. 2008).

At Khao Yai National Park, aerial, terrestrial and arboreal predators hunt primates. We predicted that encounters with predators should increase aggregation, that is, decrease distance between mated pairs, increase vigilance and scanning behaviour, and decrease routine activities, such as foraging or social behaviour. Depending on the predator type, gibbons could be expected to use different parts of the vertical strata (e.g. low canopy following exposure to an eagle model). Also, since gibbons alter their singing behaviour depending on context (Clarke et al. 2006), we predicted that the vocal behaviour before, during and after predator exposure would differ.

Methods

Study site and subjects

Khao Yai National Park is situated approximately 130 km NE of Bangkok, Thailand (101' 229E, 14' 269N). Data were collected at the Central Mo Singto study site (elevation 730–860 m) where habituation of groups started during the 1980s. We chose nine groups from which nearly complete social histories were available and all individuals were known for observations (Reichard 2009; Savini et al. 2009). Study groups consisted of between two and six individuals, typically an adult pair and their offspring. In seven out of the nine study groups, offspring were infants or juveniles, the presence of which may reasonably be expected to influence the group's response to potential predators. During the study period, two groups contained two adult males that were not the adult offspring of the mated pair. In these groups, the pair was defined as the adult male and female that regularly engaged in duet singing with each other. In both these groups, the other male could further be distinguished by his increased distance from the rest of the group during normal travel and foraging.

Males and females disperse from their natal group after reaching sexual maturity from about 7–12 years of age (Reichard and Barelli 2008). White-handed gibbons are sexually monomorphic and of light or dark pelage colour, which is unrelated to sex or age. The study site borders on the distribution area of the pileated gibbon (*Hylobates pileatus*) and a hybrid zone exists between the two species.

Immediate and long-term behavioural effects of predator encounters

The types of behavioural responses measured to assess immediate effects of predator encounters are detailed in Table 1. Predator-specific long-term behavioural effects are a good indicator that individuals have some knowledge about their predators' behaviour and possess means to respond to them. Some predators may remain in an area for several days, and increased vigilance and other anti-predatory behaviours may be warranted for extended periods. Vertical strata use and distance between pairs may also be affected. We therefore collected a series of basic behavioural data, some of which are part of their anti-predatory behaviours (Table 1). We also scored the

Table 1 Behavioural variables used to measure effects of model predators and average changes in activities before and after predator model encounters

Activity (definition)	Mean activity change over 12 samples before and after each visual predator model (sample size)[a]			
	Tiger (*N*=7)	Leopard (*N*=3)	Python (*N*=4)	Control (*N*=7)
Grooming (cleaning fur using hands/mouth)	−0.09	0.04	0.05	0.02
Moving (travel within a tree)	−0.01	0.03	0.14	−0.07
Fixing (staring at the model for ≥5 s)	0.01	0.0	−0.03	0.00
Vocalising (engaging in vocal production)	0.06	0.05	0.03	0.08
Resting (reclining/sitting/doing nothing with eyes closed)	0.01	0.0	0.00	0.02
Copulating (engaging in vocal production)	0.00	0.0	0.00	0.01
Feeding (placing items in the mouth and chewing)	−0.09	−0.30	−0.02	−0.05
Scanning (attending to the environment; head rotating by at least 45°. (Koenig 1998))	−0.01	0.0	0.00	0.00
Sitting/hanging (sit or hang on a substrate (Uhde and Sommer 2002))	0.07	0.33	0.01	−0.03
Defecating (exuding faeces and/or urine)	−0.03	0.0	0.00	0.00
Playing (chase behaviour, tickle and play bite; 'play face')	0.03	0.0	−0.04	0.00
Travelling (movement between trees)	−0.01	−0.10	0.06	0.03
Other (any other behaviour not described above)	−0.01	−0.03	0.00	0.00

[a] Rates were calculated as the difference in the average number of samples in which the behaviour was present both before and after an exposure

following vocal behaviours: *Song duration* (length of song in seconds excluding any introductory ‘hoo notes’—the ‘hoo’ is a low frequency call of short duration, used in many contexts including as a prelude to singing); *latency to first ‘great call’* (time in seconds from the start of singing to the start of the first female-specific great call—the great call is a characteristic call of all female gibbons and allows easy identification of species); *latency to the first male reply* (time in seconds between the end of the female great call and the start of the male reply or coda sequence); and *presence of sharp wow notes*. All vocalisations were recorded using Sony DAT recorders, (TCD-D8 or TCD-D7), and Sennheiser directional microphones (MKH815T or ME66) with wind-shields. Recordings were transformed onto a PC for analysis using Cool Edit 2000. Recordings were sampled at 44,100 and 48,000 Hz and a 16-bit resolution. For a full description of the white-handed gibbon's vocal repertoire, see Raemaekers et al. (1984) and Clarke et al. (2006).

Data collection

Data were collected from April 2004 to August 2005. Behavioural observations of immediate effects took place during the 20-min period in which the gibbons were exposed to each model and were recorded using one–zero sampling when performed by any individual in the group. This method was used because we were mainly interested in the presence or absence of behaviours performed in response to the models. However, if a behaviour occurred repeatedly, such as defecations and branch drops, we provided exact counts and pooled the numbers across individuals. In a number of cases, it was noted that gibbons began concerted group movement within a few minutes after they stopped singing. Because of this, we tested the hypothesis that movement after predator encounters was greater than movement after encounters with the controls. Therefore, we measured all movement that occurred within approximately 1 min after singing had stopped (mean time to measurement=29.9 min, ±5.0). Changes in location in relation to the stimulus were estimated in metres using scale maps of the groups' home ranges. Distances were estimated as soon as the model was removed if gibbons did not vocalise or if they had ceased vocalising before presentation had ended (mean=24.1 min, ±2.8). Both measures gave approximately similar times to measurement, but where songs were much longer than 30 min, a bias may have been introduced.

Long-term effects were assessed using focal animal sampling every 5 min 1 h before and after the presentation and detection of a predator model. Focal animals were the adult male or female of a mated pair. Focal animal scan samples of height in the canopy and distance to mate were taken every 10 min. Each of the adult pair was sampled separately before and after stimulus presentation. The order of sampling was random. Individuals were recognisable to the experimenter using obvious features such as pelage colour, genitalia and body size.

Visual predator models

Models consisted of an Asiatic tiger, clouded leopard, crested serpent eagle and reticulated python. These were chosen as they were either the most abundant, and/or most formidable of the ten potential predators at Khao Yai (Rabinowitz et al. 1987; Sunquist and Sunquist 2002; Matsuda et al. 2008). Gibbon groups were located in the morning by means of their song or, if known, by going to their sleeping site. Once located, the group was followed at least for 2 h before a model predator presentation was initiated. Presentations occurred throughout the day with the majority in the morning between the hours of 8A.M. and 12P.M. Time of presentation could not be consistent since models were shown opportunistically as soon as the initial 2-h sampling period was over. If the group began to sing a duet after the 2-h period, we made sure a minimum of 10 min elapsed before model presentation was attempted to ensure independence of song bouts. If the group encountered a real predator or responded to the alarm calls of another animal with a predator song, presentation was abandoned for that day. The tiger model presentation consisted of a fake tiger print fur draped over a field assistant who then walked slowly hunched over beneath the group (Fig. 1a). The control model was a brightly coloured fabric, presented in exactly the same way (Fig. 1e), to control for presentations of a conspicuous stimulus on the forest floor. The tiger model was shown to nine groups and the control stimulus was shown to eight groups. The order of presentation was alternated so that five groups out of nine saw the tiger model first and four groups out of eight saw the control model first.

The clouded leopard model consisted of a fake fur wrapped around a large rucksack and positioned on a fallen log or boulder (Fig. 1b). The crested serpent eagle model was fabricated from chicken wire and feathers and was positioned in the trees at heights of between 4 and 6 m using a slingshot and weight (Fig. 1c). The reticulated python was fabricated from draught excluders and was positioned at approximately 1 m from the ground (Fig. 1d). More specific details on model descriptions and presentation can be found in Clarke et al. (2006). Each model was removed about 20 min after the group had discovered it. Preliminary observations suggested that gibbons encountered a predator or indirect evidence of a predator every 3–4 days, so we presented models to each group no more than once a week (half the baseline rate) in order to minimise stress to them and surrounding animals. Models were presented usually only once and maximally twice to each group (n=3

a) tiger b) leopard

c) eagle d) snake

e) control

Fig. 1 The visual models used to simulate a predator encounter: **a** tiger, **b** clouded leopard, **c** crested serpent eagle, **d** reticulated python and **e** control fabric

groups saw either the clouded leopard or tiger twice due to equipment failure) to minimise habituation to the stimulus and, where possible, only data from the first exposure were used; exceptions included the use of call statistics. In addition, groups with newly born infants were deliberately avoided for the first month after birth. Therefore, although initially a group was selected for presentation from available groups at random, subsequent selections were based on the time interval since their last presentation, the age of their youngest member, and also in coordination with other researchers who were following them at that time.

Total number of predator trials was 34 and the total number of control trials was eight. All nine groups were shown all models with the following exceptions when other researchers closely followed groups prohibiting model presentations in a timely manner: control to group T; clouded leopard to group T; eagle to groups N and T. Further details on methods have recently been published in Clarke et al. (2006). After presentation, the groups were then followed for a further 2 h or until they had reached their sleeping site for the day.

Data analyses

Statistical analyses were conducted with SPSS v.12 using non-parametric testing (Kruskal–Wallis, Wilcoxon, Mann–Whitney *U*, chi-square and Fisher's exact statistical tests). All tests were conducted at the 0.05 levels, except if multiple comparisons necessitated a Dunn-Sidak correction, the formula of which is $1-(1-\text{alpha})^{1/k}$, where k is the number of comparisons. In this case, for an alpha level of 0.05, the formula is $1-(1-0.05)^{1/10}$, which gives a corrected alpha of ≤ 0.005 (McDonald 2009). For long-term activity data, we calculated the proportion of times a particular behaviour occurred in the 12 samples taken each hour before and after model exposure.

Sample sizes varied across the different behavioural measures due to occasional difficulties in observing the animals in the canopy. This was particularly true of the proximity measures for the tiger model, which was presented differently than the other models as described above, and therefore was not always in direct sight. If a behaviour occurred but could not be qualified (or quantified in the case of branch drops, defecations, proximity to stimulus and distance moved), the data were disregarded. Long-term reactions were based on data taken before and after model exposure in the same group, and were therefore analysed with matched-sample tests (Wilcoxon's signed rank). Data from immediate reactions were unmatched and so were analysed with unrelated samples tests (Kruskal–Wallis or Mann–Whitney *U* tests). Where data were categorical, chi-square tests were performed when expected frequencies were above five and Fisher's exact tests when they were not.

Results

Immediate responses to visual predator models

Gibbons reliably responded to all predator models, but not controls, by becoming more vigilant (fixed stares and scanning surroundings), dropping branches, defecating and dropping in canopy height. In addition, they sang predator songs to all but the eagle model, which elicited quiet breathy 'hoo' calls only that never escalated into full song. Figure 2a, b provide information on the anti-predator responses observed in the different groups. Non-parametric statistical tests revealed a number of significant effects as a function of stimulus type. During the study period, it was noted that other predator responses sometimes varied as a function of predator type. Therefore, where possible, predator model types were statistically compared, as well. This may be relevant since each predator has an alternate hunting strategy and may warrant different anti-predation behaviours.

Defecations

Gibbons defecated copiously in response to the leopard and snake, but not the other models (Kruskal–Wallis test, H= 17.28, df=4, p=0.002). Post hoc, Dunn-Sidak-corrected Mann–Whitney U tests revealed significantly more defections to the leopard than the control model (U=4.00, p= 0.001, N_{leopard}=8, N_{control}=8) and significantly more defecations to the snake than the control model (U=12.00, p= 0.005, N_{snake}=9, N_{control}=8).

Distance moved

Gibbons typically moved quickly and further away from an encounter with a tiger model than the other models (Kruskal–Wallis test, H=12.28, df=4, p=0.015). Post hoc Mann–Whitney U tests revealed the following effects of model type: Gibbons moved significantly further after seeing the tiger model than the control model (U=0.00, p=0.003, N_{tiger}=7, N_{control}=5).

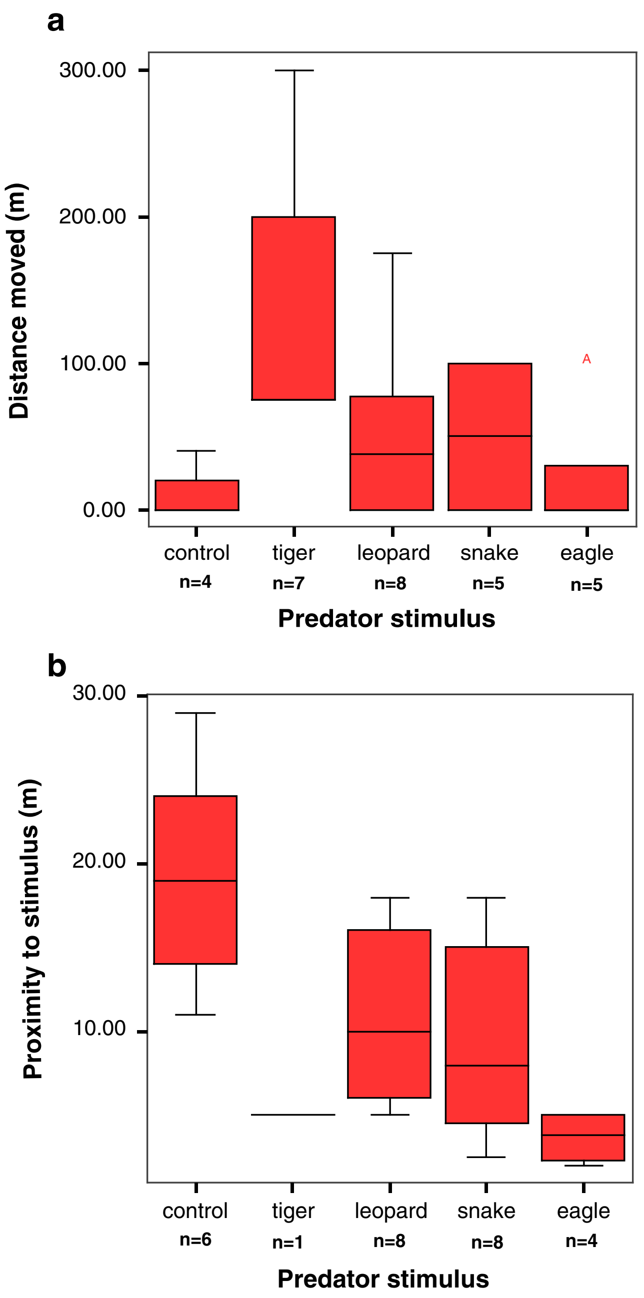

Fig. 2 **a** The median distance groups moved away from the site after predator presentation had ended, and **b** The closest proximity a group member had to a predator model during presentation. *Box plots* represent median lines and interquartile ranges

Predator inspection

Gibbons did not differ in how close they approached the different predator models (Kruskal–Wallis test, H=5.23, *df*=2, *p*=0.07). The tiger and eagle conditions were excluded from this analysis because of small sample sizes (*n*=1, *n*=4, respectively).

Branch dropping

Gibbons consistently dropped greater numbers of branches during an encounter with a clouded leopard than during encounters with any of the other models (Kruskal–Wallis test, *H*=11.98, *df*=4, *p*=0.018). Further tests showed they dropped more branches in response to the leopard model than the control model (Mann–Whitney *U* test, *U*=16.00, *p*=0.027, $N_{\mathrm{leopard}}=8$, $N_{\mathrm{control}}=8$), although this was no longer significant after the Dunn-Sidak correction was applied.

Vocal behaviour

Gibbons always sang in response to tiger and leopard models (100%), sometimes sang to the snake model (44%) and never sang to the eagle model (0%). In contrast, the eagle model elicited only hoos (86%) or silence (14%), and the snake model sometimes elicited hoos (44%). A Fisher's exact test (5×3 contingency table) showed that this distribution was significantly different from chance ($p<0.001$, $N_{\mathrm{singing}}=22$, $N_{\mathrm{hoos}}=12$, $N_{\mathrm{silence}}=7$).

Drop in canopy height

Gibbons often dropped in canopy height when a leopard (83%), tiger (75%) or eagle (60%) was displayed but never did this to a control model (0%) (Fisher's exact test, *p*=0.001, $N_{\mathrm{control}}=7$, $N_{\mathrm{tiger}}=8$, $N_{\mathrm{leopard}}=6$, $N_{\mathrm{snake}}=8$, $N_{\mathrm{eagle}}=5$).

Vigilance

Gibbons always became vigilant when the tiger, leopard, snake or eagle models were shown, but never exhibited vigilant behaviours in response to the control models (Fisher's exact test, $p<0.001$, $N_{\mathrm{control}}=8$, $N_{\mathrm{tiger}}=9$, $N_{\mathrm{leopard}}=8$, $N_{\mathrm{snake}}=9$, $N_{\mathrm{eagle}}=5$).

Long-term effects

Daily activity and vertical strata use

Exposure to predator and control models did not affect the gibbons' daily activities in the long-term (Wilcoxon's tests, $p>0.05$; values range from 0.109 to 1.000). Table 1 summarises the results; these data represent the difference in the average number of samples in which the behaviour occurred out of 12 possible samples both before and after model exposure. For example, if a gibbon was observed sitting and hanging on 7 out of 12 samples before seeing a predator, and then for 7 out of 12 samples after seeing the predator, the change would be zero. Gibbon vertical strata use also was unaffected by model exposure (Wilcoxon's tests, $p>0.05$; values range from 0.070 to 0.905; see Table 1).

Distance between pairs

Distance between mated pairs decreased significantly after seeing the tiger model, but not after any of the other models (Wilcoxon's test, *Tiger* *p*=0.004, *Z*=−2.907, *n*=25; *Control* *p*=0.837, *Z*=−0.205, *n*=29; *Leopard* *p*=0.779, *Z*=−0.280, *n*=8; *Snake* *p*=0.173, *Z*=−1.363, *n*=7; see Table 2).

Post-predator vocalisations

On 6 out of 26 occasions after seeing and responding vocally to a predator model (tiger *N*=9; leopard *N*=8; snake *N*=9), the gibbons sang for a second time on the same day. These ‘post-predator’ songs came after four groups saw the tiger model and two groups saw the snake model and were different to both duet songs and predator songs (see Clarke et al. 2006). Firstly, these post-predator songs were significantly more likely to contain sharp wow elements than normal duets (Fisher's exact test, *p*=0.042, *n*=20). Secondly, post-predator songs' great calls were delivered significantly earlier than in a typical predator song (Mann–Whitney *U* test, *U*= 11.00, *p*=0.005, $N_{\mathrm{post\text{-}predator\ song}}=6$, $N_{\mathrm{predator\ song}}=17$), and also significantly later than a normal duet (Mann–Whitney *U* test, *U*=18.00, *p*=0.048, $N_{\mathrm{post\text{-}predator\ song}}=6$, $N_{\mathrm{duet}}=14$). Thirdly, post-predator songs' sharp wows were delivered significantly later than those found (rarely) in normal duets (Mann–Whitney *U* test, *U*=5.00, *p*=0.037, $N_{\mathrm{post\text{-}predator\ song}}=6$, $N_{\mathrm{duet}}=6$), a distinction also shared with predator songs. A summary of the comparisons is shown in Table 3. Clarke et al. (2006) have shown that conclusively that predator songs differ in a number of respects to the more typical duet song, and include elements typical of primate alarm calls such as high-pitched screams, known in the gibbon literature as

Table 2 Average gibbon height and distance (metre) between male and female before and after predator stimuli

	Control	Tiger	Leopard	Snake
Female height				
Before stimulus	21.9	28.1	20.7	18.9
After stimulus	20.9	27.6	19.1	19.7
Male height				
Before stimulus	22.1	25.1	19.7	17.8
After stimulus	20.4	24.0	19.6	18.8
Distance between male and female				
Before stimulus	9.3	14.8	6.9	1.7
After stimulus	8.1	9.0	8.3	3.7

Table 3 Comparisons of song composition depending on external context, partially adapted from Clarke et al. (2006)

Acoustic parameter	Song type		
	Duet (*N*=14)	Predator (*N*=26)	Post-predator (*N*=6)
Percent songs with 'sharp wow'	42.9	100	100
Latency to first 'sharp wow' (s)	71.5	193.0	250.7
Latency to first great call (s)	80.1	802.2	167.9
Latency to male reply (s)	1.1	−0.05	−0.91
Song duration (s)	625.9	1794.8	933.6

'sharp wows' (see above). These calls typically appear several minutes into the bout however, and the earlier part of the song is indistinguishable in many ways from the duet song. Close analyses of initial call units revealed that it is the combination of units rather than their identity that is crucial in characterising the onset of these two types of song bout. Aside from these temporal and combinatorial differences, there are probably more fine-grain structural distinctions that remain to be found. The post-predator songs, therefore, also offer an interesting avenue for future research.

Discussion

During this study, we systematically investigated the reactions of white-handed gibbons to four potential predator models with the following results. First, gibbons reliably produced anti-predator responses to all models of predators, but not to a control model. For example, they defecated significantly more often in response to the clouded leopard (seven out of eight trials) or snake (six out of nine trials) than the control (none of the eight trials). Defecation is considered a sign of distress (see Boissy 1995) as well as a potential predator repellent (Tillmann 2009). Groups also moved significantly further away from the site of presentation after seeing the tiger than the control or leopard model, although they did not move further after the leopard compared with the control. They were significantly more likely to drop in canopy height when presented with the leopard or eagle compared to the control model, and finally, they were significantly more likely to increase their vigilance after detecting the tiger, leopard or snake compared to the control model.

In terms of their vocal behaviour, gibbons always gave 'hoo' calls followed by a full predator song when presented with the tiger or leopard model (17/17 trials), but they were significantly less likely to do so when they saw the control or eagle model, which never elicited singing. Instead, gibbons nearly always produced 'hoos' to the eagle model (six of seven trials) but were far less likely to do so to the control model (three of eight trials). The remaining trials (eagle, one of seven; control, five of eight) elicited no vocal response, whatsoever. The snake model received mixed responses (five of nine trials, hoos; four of nine trials, singing), perhaps because of differences in prior knowledge of this predator among different groups (Gursky 2006). The general trend was that gibbons gave different responses to the aerial and the ground predators.

Overall, our results show that gibbons respond very flexibly when coming in contact with potential predators. Whereas tiger and leopard encounters nearly always elicited strong and clear anti-predation behaviour such responses were weaker during encounters with snakes and raptor models. It was impossible to determine whether the presence of young offspring influenced the response magnitude of the groups since there were only two out of nine groups with only sub-adult or no offspring.

Further studies are needed to determine whether the behaviours following exposure to different predator models represent a true predator-specific response. One possibility is that the Asian eagles, being smaller than their African counterparts, are not a real threat to adults and that the infants can be protected relatively easily by more mature individuals that approach a perched eagle (UR personal observation), or exhibit other anti-predation behaviour. Uhde and Sommer (2002) described responses to aerial predators as follows: '[they] invariably caused the gibbons to give brief alarm calls and immatures to drop from the tree crown to crouch towards the trunk'. Differential responses to raptor models in this study may also be due to the gibbons' understanding of the model or an ability to assess threat urgency, which may vary considerably between a raptor swooping through the canopy and our predator models mimicking a perched raptor (Boissy 1995).

The gibbons' longer-term reactions were mixed, showing some evidence of altered behaviour after predator exposure as follows. Firstly, they did not significantly change their activities after seeing a predator model. They did not groom or forage less, nor become more vigilant in the 2 h following a predator sighting as compared to the same period before detection. Vertical strata use did not alter either; seeing a ground predator did not cause the gibbons to utilise higher substrates although there were insufficient data to decide whether seeing an aerial predator had the opposite effect. This lack of behavioural modification is surprising because Uhde and Sommer's (2002) study reported that the gibbons significantly decreased the time they spent at low canopy heights (0–10 m), following an encounter with a real tiger. Also, evidence from other diurnal primates suggests that they adjust their longer-term behaviour in response to predator exposure (Treves 1999; Barros et al. 2004). Our observations therefore could be interpreted in several ways that are not mutually exclusive. Assuming sample sizes were adequate to detect subtle long-term changes in behaviour the following seems possible. Firstly, gibbons may have realised that the predator was fake and that no behavioural modifications were needed. Secondly, gibbons may have a sophisticated understanding of predator behaviour and use of anti-predator measures as pursuit-deterrent signals (though evidence of gibbon groups returning to the site of predator encounter to vocalise belies this interpretation). Thirdly, there could have been a ceiling effect due to the fact that they spend a considerable amount of time at the highest points in the canopy, feeding on ripe fruit (Uhde and Sommer 2002). Fourthly, increasing vigilance in the long-term, beyond the initial reaction to a predator, may be costly since an accompanying reduction in foraging rate impacts an individual's energy budget. In this instance, gibbons may favour a low-cost behavioural modification such as crypsis—meaning attempts to avoid observation. The gibbons' small group size clearly favours crypsis as a more probable anti-predator behaviour than the dilution effect, and encounters with unhabituated groups suggest that gibbons can move silently at great speed, as well as evade all but the most persistent efforts at detection by hiding silently amidst the foliage (EC personal observation). Diurnal sifakas utilise crypsis by positioning themselves at different heights in the trees during vulnerable sleeping periods—lower in the canopy during the day to avoid raptors, and higher at night to avoid terrestrial predators (Wright 1998). There is also evidence that they alter the travelling order of individuals to allow more vulnerable members of the group to remain less visible during their leaping progressions. Perhaps gibbons' stealthy and silent flight behaviours are cryptic adaptations designed to evade the detection of specific predators in Southeast Asian forests. Further research may shed light here since crypsis is largely an understudied response to predation risk (Taylor 1979; Janson and Goldsmith 1995). Clearly, vocal responses to predators are inconsistent with a general cryptic strategy, unless the signals are produced at strategically favourable locations when callers feel secure. Nevertheless, there is evidence that gibbons exhibit relatively flexible behaviours towards predators and, there-fore, crypsis may be an exclusive strategy towards certain predators or certain levels of threat, whereas singing may be used more favourably and more commonly towards others. For example, Kappeler (1981) describes how the Javan silvery gibbon (*Hylobates moloch*) has four distinct reactions to the presence of man, including quiet observation, cryptic withdrawal, swift conspicuous flight or harassment (equiva-lent to predator singing) dependent on how threatened they feel, and how many times they have been exposed to man before. Kappeler found that gibbons initially harassed man in a manner akin to that used for other ground predators, but that after just two or three exposures substituted this response for immediate flight. Presumably, gibbons adapted their behaviour after noting that man does not withdraw, as say a leopard does, but stays to observe the behaviour.

Finally, by focusing solely on adults, this study may have missed behavioural modifications made by juveniles who arguably are at a greater risk of predation (Stone 2007).

The only measurable long-term effect seen during our study was that the gibbons significantly decreased distance between mated pairs after seeing the tiger model, but not after any other models. Tigers are rarely seen in the park (WCS 2001) and this could explain why gibbons defecated less and dropped fewer branches compared to the clouded leopard model, but moved further away and showed longer-term changes in behaviour. Alternatively, the partially arboreal clouded leopard may simply elicit a stronger reaction from gibbons. Nevertheless, tigers were relatively abundant in the study area only 15 years ago and some individuals may still be familiar with them. Perhaps then, decreasing distance between pairs is adaptive specifically during tiger encounters. However, it is worth noting that in the tiger trials, the distance between mated pairs before the stimulus (by chance) happened to be higher than that before the other stimuli. It is thus possible that after seeing the tiger model, individuals simply reverted back to a default proximity rather than showing a tiger-specific response.

Finally, gibbons showed a high degree of flexible vocal responses that are good evidence of long-term effects of predator exposure. Six post-predator songs were recorded, which, in structure, were intermediate between a typical predator song and a typical duet song (Clarke et al. 2006). Strikingly, on three of the above six occasions, gibbons returned to the location of predator presentation to sing. It may be beneficial for gibbons to revisit a prior predator location to make sure the predator is no longer there, or to alert the predator to their continued vigilance. The ability to connect an event with a precise location also suggests that gibbons possess a detailed mental representation of their environment similar to the cognitive maps that other primates use to avoid encounters with neighbouring conspecifics (Noser and Byrne 2007) and collect and reuse tools (Boesch and Boesch 1984). Cheney and Wrangham (1987) suggest that predation on primates is generally rare and thus rarely observed directly. This is compounded by the fact that many big cats, a principal threat to primates, hunt at night. However, there are several reports of predation or indirect evidence of predation, especially in the more recent literature (Bianchi and Mendes 2007; Foerster 2008; Matsuda et al. 2008; Morino 2010). One of these involves a siamang gibbon (*Symphalangus syndactylus*) in Indonesia being predated on by the semi-arboreal clouded leopard, one of the gibbons' most formidable potential predators (Morino 2010). In this report however, aside from highlighting the exceptional rarity of such events, the author remarks that the siamangs at the Indonesian field site do not appear to adopt the typical anti-predator behaviours associated with the other gibbons such as *H. lar*. We propose that the white-handed gibbons at Khao Yai experience very low rates of predation because of their effective use of a whole suite of anti-predator behaviours as described above. Pursuit deterrence may also play a role in gibbon predator evasion. Branch dropping from large heights in particular could have a strong deterrence function with the potential to significantly injure animals below. Predator songs may be signals directed at ground predators, as well as conspecifics, and behaviours such as defecation, branch dropping, and predator inspection can serve to visually alert the predator to its detection, and thus thwart any further attempts of approach or attack. Birds are also known to use visual signals to deter predators in open habitats (for example, Jones and Whittingham 2008), suggesting this may be a general adaptive response to ground predators. Asian elephants (*Elephas maximus*) are another mammalian species that experiences relatively low rates of predation, with man being their only genuine threat. These animals traditionally inhabit the same Southeast Asian forests as gibbons and have a sophisticated vocal communication system (de Silva 2010). Interestingly, adult and sub-adult elephants show strong anti-predator behaviours (such as ear flapping, dirt throwing, bunching and vocal harassment) towards jackals and dogs, despite their being at little risk from such small carnivores (de Silva personal communication). It is possible then that these reactions are based on observations of jackals with other carcasses, or that they represent a remnant of an ancient adaptation to the larger more formidable carnivores of the past. This along with evidence from gibbons illustrates that predation can be a persistent and powerful selective force even when it occurs at low rates among animals that have slow life histories with high investment in their offspring.

In summary, in response to predators, gibbons show marked anti-predator behaviour. They emit ‘hoo’ vocalisations, which may or may not escalate into a loud song bout, drop in canopy height, defecate and sometimes drop branches. They also display some evidence of modifying their behaviour in the long-term after seeing a predator, particularly by altering their vocal behaviour, though the expected changes in time spent foraging, vertical strata use and visual scanning behaviour are not seen. From these and previous results (Clarke et al. 2006), it is clear that gibbons are able to recognise and appropriately respond to different potential predators along a sliding scale dependent upon the relative threat that each poses. These results suggest that predation has acted strongly on these animals in the past and still acts strongly today, even in the absence of observed predation events. Gibbons are far from immune to predation, but instead highly attuned to it, the lack of direct evidence of which only serves to illustrate how effective their anti-predator behaviours continue to be.

Acknowledgements We would like to thank the following for their support during data collection: A. Wilkinson, B. Snyder, A. Jeneson, M. Beuerlein, N. Uhde, D. Costa-Schellenberger and the Khao Yai Bird project. We also thank K. Snyder, F. Snyder, P. and S. Snyder, H. and K. Clarke, for support during write-up, and B. Kirk for technical support. S. Homros (Jimmy), C. Mungpoonklang (Adt) and S. Seeboon (Tiang), S. Sornchaipoom (Dtai) assisted with finding and monitoring the gibbon groups. Our gratitude further goes to the National Research Council, the National Park Division, the Wildlife and Plant Conservation Department, and the Ministry of Natural Resources and Environment, and special thanks goes to the superintendent of Khao Yai National Park, Mr. Prawat Vohandee, for the permission to conduct research at Khao Yai. All experiments conducted comply with current Thai laws. This research was sponsored by a BBSRC PhD studentship awarded to Esther Clarke.

Conflict of interest The authors declare that there are no conflicts of interest.

References

Alcock J (2005) Animal behavior: an evolutionary approach. Sinauer Associates Inc, Sunderland, MA

Alexander RD (1974) The evolution of social behaviour. Ann Rev Ecol Syst 5:325–383

Barelli C, Heistermann M, Boesch C, Reichard UH (2008) Mating patterns and sexual swellings in pair-living and multimale groups of wild white-handed gibbons, *Hylobates lar*. Anim Behav 75:991–1001

Barros M, Alencar C, Tomaz C (2004) Differences in aerial and terrestrial visual scanning in captive black tufted-ear marmosets (*Callithrix penicillata*) exposed to a novel environment. Folia Primatol 75:85–92

Bartlett TQ (2007) The Hylobatidae: small apes of Asia. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds). Primates in perspective. New York:Oxford U Pr. pp 274–89

Bianchi RD, Mendes SL (2007) Ocelot (*Leopardus pardalis*) predation on primates in Caratinga Biological Station, Southeast Brazil. Am J Primatol 69:1173–1178

Boesch C (1991) The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117:220–242

Boesch C, Boesch H (1984) Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. Primates 25:160–170

Boissy A (1995) Fear and fearfulness in animals. Q Rev Biol 70:165–191. doi:10.1086/418981

Brockelman WY, Reichard U, Treesucon U, Raemaekers JJ (1998) Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). Behav Ecol Sociobiol 42:329–339

Carpenter CR (1940) A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). Comp Psychol Monogr 16:1–212

Cheney D, Seyfarth R (1992) How monkeys see the world. Behav Brain Sci 15:135–182

Cheney DL, Wrangham RW (1987) Predation. In: Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 227–239

Clarke E, Reichard UH, Zuberbühler KM (2006) The syntax and meaning in wild gibbon songs. PLoS One 1:e73. doi:10.1371/journal.pone.0000073

Dawkins R, Krebs JR (1979) Arms races between and within species. Proc Biol Sci 205(1161):489–511

de Silva S (2010) Acoustic communication in the Asian elephant, *Elephas maximus maximus*. Behaviour 147:825–852

Deecke VB, Ford JKB, Slater PJB (2005) The vocal behaviour of mammal-eating killer whales: communicating with costly calls. Anim Behav 69:395–405

Eberle M, Kappeler PM (2008) Mutualism, reciprocity, or kin selection? Cooperative rescue of a conspecific from a boa in a nocturnal solitary forager the gray mouse lemur. Am J Primatol 70:410–414

Ellefson JO (1974) A natural history of white-handed gibbons in the Malayan Peninsula. In: Rumbaugh DS (ed) Gibbon and siamang, vol 3, pp 2–134

Fay JM, Carroll R, Peterhans JCK, Harris D (1995) Leopard attack on and consumption of gorillas in the Central African Republic. J Hum Evol 29:93–99

Foerster S (2008) Two incidents of venomous snakebite on juvenile blue and Sykes monkeys (*Cercopithecus mitis stuhlmanni* and *C-m. albogularis*). Primates 49:300–303

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

Goldspink CR, Holland RK, Sweet G, Stewart L (2002) A note on group sizes of oribi (*Ourebia ourebi*, Zimmerman, 1783) from two contrasting sites in Zambia with and without predation. Afr J Ecol 40:372–378

Grant JB (2007) Ontogenetic colour change and the evolution of aposematism: a case study in panic moth caterpillars. J Anim Ecol 76:439–447

Greisser M (2009) Mobbing calls signal predator category in a kin group-living bird species. Proc Biol Sci. doi:10.1098/rspb.2009.0551

Gursky S (2006) Function of snake mobbing in spectral tarsiers. Am J Phys Anthropol 129:601–608

Hart D, Sussman RW (2009) Man the hunted: primates, predators, and human evolution. Expanded edition. Westview Press, Boulder, CO

Heymann EW (1987) A field observation of predation on a moustached tamarin (*Saguinus mystax*) by an anaconda. Int J Primatol 8:193–195

Hill RA, Lee PC (1998) Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. J Zool Lond 245:447–456

Janson CH (2003) Puzzles, predation, and primates: using life history to understand selection pressures. In: Kappeler PM, Pereiera M (eds) Primate life histories and socioecology. University of Chicago Press, Chicago, pp 103–131

Janson CH, Goldsmith M (1995) Predicting group size in primates: foraging costs and predation risk. Behav Ecol 6:326–336

Jones KA, Whittingham MJ (2008) Anti-predator signals in the chaffinch *Fringilla coelebs* in response to habitat structure and different predator types. Ethology 114:1033–1043. doi:10.1111/j.1439-0310.2008.01558.x

Kappeler M (1981) Predator Avoidance. http://www.markuskappeler.ch/gib/gibs/chapter5.html. Accessed 3 March 2011

Koenig A (1998) Visual scanning by common marmosets (*Callithrix jacchus*): functional aspects and the special role of adult males. Primates 39:85–90

Krams I, Krama T (2002) Interspecific reciprocity explains mobbing behaviour of the breeding chaffinces, *Fringilla coelebs*. Proc Biol Sci 269:2345–2350

Krupa J, Geluso KN (2000) Matching the color of excavated soil: cryptic coloration in the plains pocket gopher (*Geomys bursarius*). J Mammal 81:86–96

Kuchta SR, Krakauer AH, Sinervo B (2008) Why does the yellow-eyed Ensatina have yellow eyes? Batesian mimicry of Pacific newts (genus *Taricha*) by the salamander *Ensatina eschscholtzii xanthoptica*. Evolution 62:984–990

Langridge KV, Broom M, Osorio D (2007) Selective signalling by cuttlefish to predators. Curr Biol 17:R1044–R1045

Lappan S (2007) Social relationships among males in multimale siamang groups. Int J Primatol 28:369–387

Lappan S (2008) Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. Behav Ecol Sociobiol 62:1307–1317

Malone N, Okatvinalis H (2006) The socio-ecology of the silvery gibbon (*Hylobates moloch*) in the Cagar Alam Leuweung Sancang (CALS), West Java, Indonesia. Am J Phys Anthropol 129(S42):124

Matsuda I, Tuuga A, Higashi S (2008) Clouded leopard (*Neofelis diardi*) predation on proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. Primates 49:227–231

McDonald JH (2009) One-way ANOVA: planned comparisons of means. In: Handbook of biological statistics 2nd edn. Sparky House Publishing, Baltimore, Maryland pp 137–140

Morino L (2010) Clouded leopard predation on a wild juvenile siamang. Folia Primatol 81:362–368

Norman MD, Finn J, Tregenza T (2001) Dynamic mimicry in an Indo-Malayan octopus. Proc Biol Sci 268:1755–1758

Noser R, Byrne RW (2007) Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, *Papio ursinus*. Anim Behav 73:257–266

Ouattara K, Lemasson A, Zuberbühler K (2009) Anti-predator strategies of free-ranging Campbell's monkeys. Behaviour 146:1687–1708

Owings DH, Coss RG (1977) Snake mobbing by California ground squirrels: adaptive variation and ontogeny. Behaviour 62:50–69

Palombit RA (1994) Extra-pair copulations in a monogamous ape. Anim Behav 47:721–723

Rabinowitz A, Andau P, Chai PPK (1987) The clouded leopard in Malaysian Borneo. Oryx 21:107–111

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

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

Reichard U (1995) Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). Ethology 100:99–112

Reichard U (1998) Sleeping sites, sleeping places, and presleep behaviour of gibbons (*Hylobates lar*). Am J Primatol 46:35–62

Reichard UH (2009) The social organization and mating system of Khao Yai white-handed gibbons, 1992–2006. In: Lappan SM, Whittaker D (eds) The gibbons: new perspectives on small ape socioecology and population biology (developments in primatology: progress and prospects). Springer, Berlin, pp 347–387

Reichard UH, Barelli C (2008) Life history and reproductive strategies of Khao Yai *Hylobates lar*: Implications for social evolution in apes. Int J Primatol 29:823–844

Rödl T, Berger S, Romero LM, Wikelski M (2007) Tameness and stress physiology in a predator-naive island species confronted with novel predation threat. Proc Biol Sci 274:577–582

Savini T, Boesch C, Reichard UH (2009) Varying ecological quality influences the probability of polyandry in white-handed gibbons (*Hylobates lar*). Biotropica 41:503–513

Slobodchikoff CN, Placer J (2006) Acoustic structures in the alarm calls of Gunnison's prairie dogs. J Acoust Soc Am 119:3153–3160

Stone AI (2007) Age and seasonal effects on predator-sensitive foraging in squirrel monkeys (*Saimiri sciureus*): a field experiment. Am J Primatol 69:127–141

Struhsaker TT (1967) Behavior of vervet monkeys (*Cercopithecus aethiops*). University of California Press, Berkeley

Struhsaker TT, Leakey M (1990) Prey selectivity by crowned-hawk eagles in the Kibale forest, Uganda. Behav Ecol Sociobiol 26:435–443

Stuart-Fox DM, Moussalli A, Johnston GR, Owens IP (2004) Evolution of color variation in dragon lizards: quantitative tests of the role of crypsis and local adaptation. Evolution 58:1549–1559

Sunquist ME, Sunquist F (2002) Wild cats of the world. University of California Press, Chicago

Taylor RJ (1979) The value of clumping to prey when detectability increases with group size. Am Nat 113:299–301

Tillmann JE (2009) An ethological perspective on defecation as integral part of antipredatory behaviour in the grey partridge (*Perdix perdix L.*) at night. J Ethol 27:117–124

Treves A (1999) Has predation shaped the social systems of arboreal primates? Int J Primatol 20:35–67

Uhde NL, Sommer V (2002) Antipredatory behavior in gibbons (*Hylobates lar*, Khao Yai/Thailand). In: Miller LE (ed) Eat or be eaten. Cambridge University Press, Cambridge, pp 268–292

van Schaik CP, Hörstermann M (1994) Predation risk and the number of adult males in a primate group: a comparative test. Behav Ecol Sociobiol 35:261–272

van Schaik CP, van Hooff JA (1983) On the ultimate causes of primate social systems. Behaviour 85:91–117

van Schaik CP, van Noordwijk MA, Warsono B, Sutriono E (1983) Party size and early detection of predators in Sumatran forest primates. Primates 24:211–221

van Schaik CP, Preuschoft S, Watts DP (2004) Great ape social systems. In: Russon AE, Begun DR (eds) The evolution of thought: evolutionary origins of Great Ape intelligence. Cambridge University Press, Cambridge, pp 190–209

Waterman JM (1997) Why do male Cape ground squirrels live in groups? Anim Behav 53:809–817

WCS (2001) Status, ecology and conservation of tigers in their critical habitats in thailand. In: Final Report Wildlife Conservation Society (Thailand), April 1st 1999 to September 30th 2001 http://www.nfwf.org/AM/Template.cfm?Section=Home&CONTENTID=8683&TEMPLATE=/CM/ContentDisplay.cfm. Accessed 12 November 2008

Wright PC (1998) Impact of predation risk on the behaviour of *Propithecus diadema ewardsi* in the rain forest of Madagascar. Behaviour 135:483–512

Zuberbühler K (2000) Causal knowledge of predators' behaviour in wild Diana monkeys. Anim Behav 59:209–220

Zuberbühler K, Byrne RW (2006) Social cognition. Curr Biol 16: R786–R790

Zuberbühler K, Jenny D (2002) Leopard predation and primate evolution. J Hum Evol 43:873–886

Zuberbühler K, Jenny D, Bshary R (1999) The predator deterrence function of primate alarm calls. Ethology 105:477–490