

Anti-predator strategies of free-ranging Campbell's monkeys

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Summary

Habitat type, predation pressure and reproductive interests are all thought to determine the anti-predator behaviour of non-primates, but only few systematic studies exist. Here, we experimentally elicited anti-predator behaviour in six different groups of forest-living Campbell's monkeys, using visual and acoustic models of leopards, crowned eagles, and snakes. Individuals produced a variety of anti-predator behaviours, depending on the type of predator and whether or not it was visible. Adult males generally behaved conspicuously, either by attacking eagles or producing threat behaviours at a distance to leopards. Adult females remained cryptic to eagles, but joined their male in approaching leopards. To snakes, both males and females responded strongly to familiar Gaboon vipers, but far less to unfamiliar black mambas. Finally, if a predator could only be heard, both males and females produced fewer alarm calls and often changed their vertical position in the canopy (upwards for leopards; downwards for eagles), despite all predator vocalisations being presented from the ground. We concluded that Campbell's monkeys display sex-specific anti-predator behaviours, which are largely driven by the predators' hunting techniques, mode of predator detection and the forest habitat structure.

Keywords: anti-predator behaviour, predation, field experiments, sex differences, forest guenons.

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Introduction

Predation is a powerful evolutionary force, which has led to a large range of adaptations that help animals to protect and defend themselves (Struhsaker, 1967; Edmunds, 1974; Evans et al., 1993a; Fichtel & Kappeler, 2002; Whittingham & Evans, 2004). Whatever the mechanisms are, the habitat appears to have had a major impact on the evolution of the different adaptations. Fieldwork on savannah-living species has shown, for example, that vervet monkeys (*Chlorocebus pygerythrus*: Seyfarth et al., 1980a) and other prey animals, such as ungulates (Leuthold, 1977; Fischhoff et al., 2007), mostly respond with escape behaviour when spotting a predator. However, more recent studies on forest animals have suggested that escape behaviour may not be the only or most adaptive response. In forest habitats, monkeys obtain protection from aerial predators due to canopy cover and, thus, often respond with cryptic behaviour (Zuberbühler et al., 1997; Miranda et al., 2005). Moreover, hunting monkeys in a forest environment is difficult for felids and snakes because monkeys are better adapted to locomotion in the arboreal environment. Forest primates operate in three-dimensional space, which affords a much more complex set of anti-predator responses than in a savannah-type habitat (Enstam, 2007). At the same time, the forest also provides ambush predators with a plethora of hiding spots (Boinski et al., 2003). In dense habitat, foraging animals must compensate such increases in predation risk due to poor visibility by being more vigilant, in contrast to animals living in more open habitat (birds: Quenette, 1990; Devereux et al., 2006; primates: Rose, 1998). For communicating danger, vocal signals are more useful for species living in forest habitats while gestures and other types of visual signals may be more suitable in open habitats (Seyfarth et al., 1980a; Alvarez, 1993; Zuberbühler et al., 1997).

Anti-predatory strategies are not only determined by the habitat, but they often also depend on the type of predator (Evans et al., 1993b; Macedonia & Evans, 1993; Palleroni et al., 2005). A manifestation of predator-specific defence behaviour is the predator-specific alarm calling produced by many species, which usually trigger adaptive responses in recipients. Several species of birds and mammals produce distinctive vocalizations in response to particular classes of predators (Seyfarth et al., 1980a,b; Gyger et al., 1987; Cheney & Seyfarth, 1990; Evans et al., 1993a; Zuberbühler et al., 1997; Kirchhof & Hammerschmidt, 2006). Often, the vocal behav-

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our reveals a species' ability to discriminate between threatening and non-threatening stimuli, including large birds (Seyfarth et al., 1980b) or different snakes (Ramakrishnan et al., 2005). Distinct reactions to aerial and terrestrial predators (as well as to the corresponding alarm call types), mostly vertical locomotion or change in gaze direction, have been reported in several animals living in open habitats (vervet monkeys: Seyfarth et al., 1980a,b; deer (*Odocoileus virginianus*): Gese & Grothes, 1995) and in the forest (white-faced capuchins (*Cebus capucinus*): Digweed et al., 2005; saddleback and moustached tamarins (*Saguinus fuscicollis* and *S. mystax*): Heymann, 1990; Peres, 1993; buffy-headed marmosets (*Callithrix flaviceps*): Ferrari & Ferrari, 1990).

The size relations between predator and prey may also influence a prey's response (Evans et al., 1993; Zuberbühler et al., 1997). The typical hunting technique of a predator plays a well-documented role. For example, for predators relying on attacking their prey by surprise some primates appear to communicate directly to the predator by signalling their detection and futility of further hunting (Zuberbühler & Jenny, 2002; Zuberbühler, 2003). In contrast, chimpanzees (*Pan troglodytes*) do not rely on surprise hunt but pursue prey monkeys in the trees for which they need to locate them accurately (Boesch, 1994). Thus, conspicuous alarm calling may simply trigger pursuit and monkeys often remain silent in the presence of chimpanzees (Zuberbühler, 2000a).

Predation is thought to be a primary cause for the evolution of sociality (Alexander, 1974; van Schaik, 1983). Apart from basic group-size related benefits, gregarious animals sometimes engage in organised cooperative defence behaviours (monkeys: Cheney & Seyfarth, 1980; sciurids: Macedonia & Evans, 1993; cetaceans: Palacios & Mate, 1996). An interesting example concerns the evolution of sentinel systems as documented in a number of species (monkeys: Uster & Zuberbühler, 2001; birds: Wright et al., 2001; suricates: Manser et al., 2002). Also, in many species, including primates (brown capuchin (*Cebus apella*) or white-fronted capuchin (*C. albifrons*): van Schaik & van Noordwijk, 1989) and birds (red-winged blackbirds (*Agelaius phoeniceus*): Yasukawa et al., 1992; mountain bluebirds (*Sialia currucoides*) Gibson & Moehrensclager, 2008), the anti-predator behaviour is sex-specific. Males typically engage in more vigilance or more risky behaviours (approaching, counter-attacking) than females (*Cercopithecus pogonias* and *C. cephus*: Gautier et al., 1983; *C. diana*: Zuberbühler et al., 1997).

One plausible reason for this has to do with the sexual dimorphism observed in these species (e.g., male Diana monkeys are almost twice as big as females, Kingdon, 1997).

Most of the previous studies using predator presence simulation focussed either on visual (Ramakrishnan et al., 2005; Coss et al., 2007; Arnold et al., 2008) or acoustic models (Zuberbühler et al., 1997, 2000a,b, 2001; Manser et al., 2002) to test the reaction of animals to their main predator. Yet, the two modes of detection may differ in important ways because they induce different levels of threat. Visual models are considered to be more dangerous because they simulate the presence of a nearby predator that is likely to be hunting already (Schel et al., 2009).

Here, we report on the anti-predator behaviour of free-ranging Campbell's monkeys (*Cercopithecus c. campbelli*). The species is interesting because many of the variables discussed before have relevance, such as a dense forest habitat with high degree of arboreal locomotion (Mc Graw, 1996), different types of natural predators (Jenny & Zuberbühler, 2005; Shultz & Thomsett, 2007), complex social life (Lemasson et al., 2006; Buzzard & Eckardt, 2007) and sexual dimorphism (males, 5.5 kg; females, 3.5 kg; Glenn & Bensen, 1998). Males and females also differ in terms of their vocal behaviour (Zuberbühler, 2001; Lemasson & Hausberger, 2004; Ouattara et al., 2009 and data not shown).

Campbell's monkeys are found in the Taï National Park of Ivory Coast, one of the last remaining blocks of the once vast Upper Guinea forest. The Taï forest has a rich fauna and its primate inhabitants are confronted with all their natural predators, including crowned eagles (*Stephanoaetus coronatus*), leopards (*Panthera pardus*), chimpanzees and human poachers (*Homo sapiens*). A variety of snakes are present, and one of them, the Gaboon viper (*Bitis gabonica*), is particularly dangerous due to its powerful venom, large body size and ultra-cryptic behaviour. We describe the Campbell's monkeys' anti-predator behaviour to these natural predators, using experimental techniques. We were particularly interested in the way the monkeys used their habitat in the predation context, in the effects of predator type and modality of predator detection, as well as the roles taken by each sex in dealing, vocally (in terms of alarm call rate) and non-vocally, with the different predator contexts. Most previous studies using visual models with wild primates have focused only on alarm calling behaviour (Coss et al., 2007; Arnold et al., 2008; Wheeler, 2008) without reporting on the associated anti-predator behaviours (but see van Schaik & van Noordwijk, 1989). Our general predic-

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tions were that the monkeys would select anti-predator strategies suitable to the forest habitat, take into account the different predator types and their associated hunting techniques, the momentary degree of threat, as well as their own vulnerability. In particular, based on the sexual dimorphism and previously described sex differences in guenon behaviour (Gautier & Gautier-Hion, 1977; Lemasson et al., 2006), we predicted that the single male would play a more active role in predator defence.

Methods

Study site and subjects

The study site consisted of a large grid area located in the Taï National Park (5°50'N, 7°21'W), Ivory Coast. The study area has been used extensively for a range of other behavioural studies of the Taï Monkey Project (McGraw et al., 2007; McGraw & Zuberbühler, 2008). Data for this study were collected between March 2006 and September 2007 from two habituated and five semi-habituated groups of Campbell's monkeys. All seven groups consisted of one adult male, 3 to 7 adult females, and 5 to 7 juveniles and infants. Among Taï forest guenons, Campbell's monkeys spend the highest amount time in the understory below 5 m with 15% of their daily activities on the ground (McGraw, 2000; Buzzard, 2006; 21 months of observation by KO). At the time of the study, human observers had visited the two habituated groups regularly for over eight years (e.g., Buzzard, 2004). The number of adults within these two groups remained stable during the duration of the study.

Field experiments

We tested the monkeys' responses to six stimuli, including four visual and two acoustic models. Visual models were a leopard (adult weight approx. 45 kg), a crowned eagle (approx. 5 kg) and a Gaboon viper (approx. 2 kg), which represented three main predators of these monkeys (Zuberbühler, 2001; Foerster, 2008). We also tested a black mamba (*Dendroaspis polylepis*, approx. 1.6 kg; Gray, 1842). This second snake species was chosen because of its comparable size with the Gaboon viper and because it could represent a danger for monkeys due to its powerful venom, although it has not been reported in the Taï forest. The two acoustic models were playback of leopard growls and crowned eagle shrieks. Ideally, we would have also included

chimpanzees since they are a significant monkey predator in Tai. However, due to their unique cooperative hunting behaviour (e.g., Boesch, 1994), this would have required staging an entire hunting party, something that is not practical with models. We, thus, focussed on the three predator types that usually hunt singly and by stealth.

To exclude habituation effects and to avoid pseudo-replication, only one trial was performed for each stimulus type per group. Six of the seven study groups received all conditions, including the two habituated groups. One habituated group experienced a male takeover during the second half of this study and the new male habituated quickly to our presence. We decided to test the new male as well, with the effect that the other members of this group experienced all predator stimuli twice, so we only analysed the behaviour of the new male during these second exposures.

The leopard, eagle and Gaboon viper models were custom-made replicas of real animals (Fig. 1). The black mamba model was a commercially available plastic model (Fig. 1). All models corresponded roughly to the predators' natural adult size. Playback stimuli consisted of a 15-s series of eagle shrieks, recorded in the study area, and a 15-s recording of leopard growls, purchased from the National Sound Archives, London. Playback stimuli were broadcast with a Sony WMD6C Professional Walkman connected to NAGRA DSM speaker-amplifier. The stimulus amplitude was adjusted so that the calls sounded natural to a human observer at a distance of about 20 m from the speaker. Previous work has shown that stimulus amplitude had no relevant effects on how monkeys responded to their predators (Zuberbühler, 2000a,b). The same leopard and eagle playback stimuli were used to test the six groups.

Before each trial, the following conditions had to be in place to minimise intervening effects and to ensure that the monkeys perceived the models as real predators: (a) the study group had to be aware of the observer's presence for at least 30 min; (b) no alarm call could have been given in the previous 30 min; (c) the model had to be positioned in the direction of the group's projected travelling path, but away from other groups of monkeys. We only conducted experiments if our focal group was not associated with another species. In some rare cases (10%), another monkey group was in the vicinity, but then we positioned the model or the playback equipment so that the focal group was likely to detect the predator model first. The observer (KO) always stayed with the group while a field assistant concealed the loudspeaker or visual model; (d) eagle models had to be positioned at 2–3 m above the

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(a) Crowned eagle



(b) Leopard



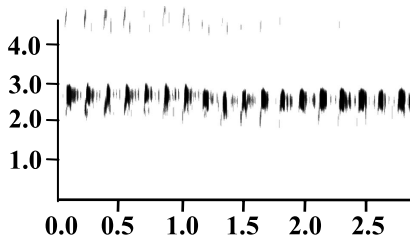
(c) Gaboon viper



(d) Black Mamba



(e) Crowned eagle shrieks



(f) Leopard growls

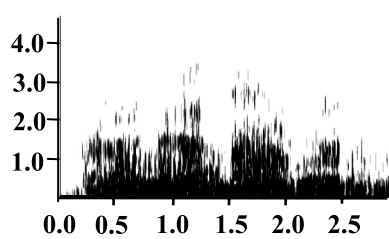


Figure 1. Visual and acoustic models used for field experiments: (a) crowned eagle, *Stephanoaetus coronatus*; (b) leopard, *Panthera pardus*; (c) Gaboon viper, *Bitis gabonica*; (d) black mamba, *Dendroaspis polylepis*; (e) crowned eagle shrieks; (f) leopard growls.

ground; leopard and snake models were presented on the ground; (e) the loudspeaker was positioned at about 1 m from the ground and the sound was played (with a 5-min silent introduction) when the group was at 50 m; (f) the

majority of the group had to be travelling at less than 10 m from the ground. To facilitate detection, the eagle model was moved briefly (via a rope) once the group approached within visual distance. The snake models were moved on the ground (with a 20-m fishing line).

Data collection

After a playback stimulus had been broadcast, or a visual model detected by a group member (usually by fixing its gaze at the model), we monitored focal animals with regards to the occurrence of seven different behaviours (see below) during the first 3 min, using the one-zero sampling method (Altmann, 1974). Focal animals were the adult male and one randomly selected adult female, observed simultaneously, provided we could ensure that they saw the predator model. Observations during natural responses to predators indicated that the first 3-min interval after detection was sufficient to reveal the different anti-predator behaviours produced (see also Coss et al., 2007).

In parallel, we recorded all vocal utterances given in the first minute after detection by all group members. Recordings were used to quantify all alarm calls given by the adult male and all the adult females combined. Caller identification was possible for the adult male, but not for the adult females. Alarm calls (as defined by Lemasson et al., 2004) were digitised and analysed separately (see Ouattara et al., 2009). Audio recordings were made with a Sony TCD-D100 Walkman Digital Audio Tape-recorder and a Sennheiser ME88 microphone and a Lavallier microphone for spoken comments.

Definitions

Ad libitum observation of actual predator encounters (real crowned eagles, $N = 11$; real leopards passing by, $N = 3$) revealed the following seven anti-predator behaviours (Table 1): (1) Attack: run towards the predator and charge it from a distance of about 2 m; (2) Threat: threaten predator (facial gesture threat with moving eyelids and specific posture towards the predator, combined with branch shaking). During threats, individuals kept their gaze fixed on the predator and the body oriented towards it, while maintaining a safe distance of minimum of 10 m; (3) Agitation: succession of several conspicuous fast movements including short-distance jumping and body rotation while changing places on the branch. No particular eyelid threat or body orientation with regards to the predator location was noticed; (4) Vigilant:

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Table 1. Behavioural responses of Campbell's monkeys to visual encounters with real predators ($N = 2$ groups).

Anti-predator behaviour	Crowned eagle		Leopard	
	♂♂	♀♀	♂♂	♀♀
Attack	***	–	–	–
Threat	–	*	***	–
Agitation	***	–	***	**
Vigilant	*	***	***	***
Ascend	***	–	***	***
Descend	–	**	–	–
Hide	–	***	–	–

Crowned eagle: ($N = 11$ encounters): – absent (0 encounters); * rare (1–2 encounters); ** irregular (3–5 encounters); *** common (6–11 encounters); leopard ($N = 3$ encounters): – absent (0 encounters); * rare (1 encounter); ** regular (2 encounters); *** common (3 encounters); no natural encounters with Gaboon vipers were observed.

remaining immobile and adopting vigilance posture; (5) Ascend: suddenly rushing or pouncing upwards for at least 1–2 m, and staying at this height for several minutes, (6) Descend: suddenly rushing or pouncing downwards for at least 1–2 m, and staying at this height for several minutes; (7) Hide: silently retreating to hide in foliage.

Data analysis

For both the adult males ($N = 7$) and adult females ($N = 6$) of each group we scored, for each of the six trial types, whether or not the focal animal displayed each of the seven anti-predator behaviours. Results were analysed using a Generalized Linear Model (GLM, distribution: binomial, link function: logit, type III) (Venables & Ripley, 2002) using the R software package. We first tested the effect of the focal individual's sex and the type of stimuli ($N = 6$) on the occurrence of each behavioural category (we could not test the effect of the interaction between factors because of disconnected data).

In these cases, because multiple tests were conducted, a Benjamini & Yekutieli (2001) correction was applied resulting in $\alpha = 0.013$. Then, we conducted 'Post-hoc GLM tests' in both males ($N = 7$) and females ($N = 6$) to compare the occurrence of each behavioural category regarding the type of predator and the modality of detection (1, Leopard vs. Eagle \times Visual vs. Acoustic; 2, Gaboon viper vs. Black mamba; only dyadic comparisons

showing significant differences are presented). Wilcoxon signed ranks tests with the “small sample sizes method” described by Siegal & Castellan (1988) (see Mundry & Fisher, 1998) were used to compare call rates in the different experimental contexts.

Results

Effects of predator type and detection modality

Alarm call behaviour

The predator type influenced significantly the alarm call rates of males and females, but in different ways (Table 2). The single male called significantly more when detecting a leopard or an eagle than a Gaboon viper, with no differences between the former two. Females called significantly more when detecting a leopard than a Gaboon viper or an eagle, with no differences between the latter two. The black mamba model did not elicit any calling in any of the groups. When comparing the monkeys’ responses between visual and acoustic models, both males and females called significantly more when seeing than when hearing the predator (Table 2).

Table 2. Number of calls produced by the single adult males and adult females within the first minute following the detection of different predator models.

Modality	Predator model	Vocal response (<i>N</i> calls)			
		♂♂		♀♀	
		Range	Median	Range	Median
Visual	Eagle (E _V)	20–41	27.0	4–29	11.0
	Leopard (L _V)	11–69	14.0	7–50	34.0
	Gaboon viper (G)	0–19	2.0	4–19	7.0
	Black mamba	0	0	0	0
Acoustic	Eagle shrieks (E _A)	5–24	10.5	2–5	3.5
	Leopard growls (L _A)	4–19	8.0	2–27	4.5

Males: E_V vs. L_V: $p > 0.3$; E_V vs. G: $p < 0.025$; L_V vs. G: $p < 0.025$; E_A vs. L_A: $p > 0.2$; E_A vs. E_V: $p < 0.025$; L_A vs. L_V: $p < 0.025$; $N = 7$ males; Females: E_V vs. L_V: $p < 0.05$; E_V vs. G: $p > 0.8$; L_V vs. G: $p < 0.05$; E_A vs. L_A: $p > 0.6$; E_A vs. E_V: $p < 0.05$; L_A vs. L_V: $p < 0.05$; $N = 6$ groups of females (Wilcoxon signed rank tests, two-tailed).

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Non-vocal anti-predator behaviour

Across experimental conditions, we noted significant differences in the observed behavioural responses. Tables 3 and 4 summarise the behavioural profiles of the adult males and females, respectively, in experimental conditions to the three predator types. GLM analyses revealed that the focal animal's sex, as well as the type of stimuli significantly influences the occurrence of each behavioural category, apart from ascend where no sex influence was found (Table 5).

Table 3. Behavioural responses of adult female Campbell's monkeys to predator models ($N = 6$ groups).

Behaviour	Eagle visual	Eagle acoustic	Leopard visual	Leopard acoustic	Snake (Gaboon)	Snake (Mamba)
Attack	—	—	—	—	—	—
Threat	—	—	****	****	***	—
Agitation	—	—	****	***	***	—
Vigilant	****	***	—	*	—	—
Ascend	—	—	—	****	****	****
Descend	—	****	****	—	—	—
Hide	****	***	—	***	—	—

— absent (0 of 6 trials); * rare (1 of 6 trials); ** irregular (2–3 of 6 trials); *** common (4–5 of 6 trials); **** obligatory (6 of 6 trials).

Table 4. Behavioural responses of adult male Campbell's monkeys to predator models ($N = 7$ males).

Behaviour	Eagle visual	Eagle acoustic	Leopard visual	Leopard acoustic	Snake (Gaboon)	Snake (Mamba)
Attack	***	—	—	—	—	—
Threat	—	—	****	****	****	—
Agitation	****	*	****	***	****	—
Vigilant	—	***	—	*	—	—
Ascend	****	—	—	****	***	—
Descend	—	**	****	—	—	—
Hide	—	*	—	—	—	—

Data from 6 different groups, one group underwent a male takeover, hence $N = 7$ males. — absent (0 of 7 trials); * rare (1–2 of 7 trials); ** irregular (3–4 of 7 trials); *** common (5–6 of 7 trials); **** obligatory (7 of 7 trials).

Table 5. Influence of sex and stimulus type on the anti-predator behaviours.

Behaviour	Variable	LR χ^2	df	<i>p</i> value
Attack	Stimulus	22.3	5	<0.001
	Sex	8.9	1	0.003
Agitation	Stimulus	72.7	5	<0.001
	Sex	13.0	1	<0.001
Hide	Stimulus	43.6	5	<0.001
	Sex	29.3	1	<0.001
Threat	Stimulus	97.1	5	<0.001
	Sex	19.6	1	<0.001
Vigilant	Stimulus	41.2	5	<0.001
	Sex	9.8	1	0.002
Ascend	Stimulus	65.2	5	<0.001
	Sex	0.116	1	0.733
Descend	Stimulus	82.4	5	<0.001
	Sex	6.5	1	0.011

Benjamini & Yekutieli (2001) correction for multiple comparisons: critical *p*-value < 0.013.

First, differences were found in the response to leopard and eagle. Males generally showed more agitation to both eagles and leopards (Table 4), while females only did so for leopards (GLM, Factor = predator type, LR χ^2 = 27.9, df = 1, *p* < 0.001; Table 3). Compared to leopards, females instead were vigilant to eagles (Factor = predator type, LR χ^2 = 21.8, df = 1, *p* < 0.001; Table 3). Also, males regularly attacked the eagle model (Factor = predator type, LR χ^2 = 9.9, df = 1, *p* = 0.002; Factor = detection modality, LR χ^2 = 9.9, df = 1, *p* = 0.002) but only threatened the leopard at a distance (Factor = predator type, LR χ^2 = 38.8, df = 1, *p* < 0.001; Table 4).

Second, when detecting these predators in the acoustic mode, both males and females ascend when hearing leopard growls (Factor = predator type, LR χ^2 = 19.4 (male)/16.6 (female), df = 1, *p* < 0.001) and descend when hearing eagle shrieks (Factor = predator type, LR χ^2 = 5 (male)/16.6 (female), df = 1, *p* < 0.001; Tables 3 and 4). Males regularly adopted vigilance postures in response to eagle shrieks and sometimes to leopard growls, but not to any of the visual models (Factor = detection modality, LR χ^2 = 6.1, df = 1, *p* = 0.013). Females regularly moved away to hide in foliage in response to leopard growls and to both acoustic and visual

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eagle models (Factor = predator type, LR $\chi^2 = 16.6$, $df = 1$, $p < 0.001$; Factor = detection modality, LR $\chi^2 = 16.6$, $df = 1$, $p < 0.001$). The only exception was in response to visual leopard models to which they joined the adult males in threatening at a distance. Hence, sex differences were pronounced to eagles and the acoustic leopard model, but not to the visual leopard model.

Third, differences were found in the response to the two species of snake. When detecting a Gaboon viper, both males and females showed more agitation (Factor = predator type, LR $\chi^2 = 19.4$ (male)/10.4 (female), $df = 1$, $p \leq 0.001$), and threatened the predator (Factor = predator type, LR $\chi^2 = 19.4$ (male)/10.4 (female), $df = 1$, $p \leq 0.001$). Moreover, both males and females ascended after detecting a Gaboon viper while only females did so for black mamba (Factor = predator type, LR $\chi^2 = 13.4$ (male), $df = 1$, $p < 0.001$). Males did not show any noticeable reaction to black mamba.

Discussion

Our field experiments revealed that free-ranging forest Campbell's monkeys did not respond with systematic escape responses to eagles and leopards, in contrast to savannah vervet monkeys (Seyfarth et al., 1980a). Instead, they showed a broader range of anti-predator strategies, consisting of cryptic behaviours where animals took advantage of foliage to hide or remain immobile, silent and vigilant, and more aggressive responses during which the predator was threatened or attacked, as described previously for other guenons (Gautier-Hion et al., 1983; Zuberbühler et al., 1997). When escaping, monkeys moved up or down, rather than running away.

Campbell's monkeys responded with predator-specific and highly adaptive behaviour to their natural predators. The response to eagles and leopards generally triggered stronger reactions than snakes, notably in term of male alarm calling behaviour. In this dense forest habitat, monkeys rely heavily on vocal signals and male Campbell's monkeys, like Diana monkeys and some other primates, produce conspicuous loud calls for various dangers, including predators (Zuberbühler et al., 1997; Arnold & Zuberbühler, 2006a,b; Schel et al., 2009). Eagles and leopards, both highly dangerous, did not elicit the same anti-predator reactions in males. Only eagles were attacked, while leopards were usually threatened at a distance. Sometimes these attempts to

repel the predator were done in conjunction with other arboreal primates, such as Diana monkey (Zuberbühler et al., 1997). No monkey will risk a physical interaction with a leopard, but perception advertisement from within the tree canopy is a highly adaptive strategy that tends to drive leopards away (Zuberbühler et al., 1999). The same response (i.e., calling and threatening at a safe distance) has been observed in other monkeys when spotting a terrestrial predator (white-faced capuchins: Perry et al., 2003; Fichtel et al., 2005). Crowned eagles, in contrast, weigh about the same as an adult monkey male and males of many monkey species, but not females, approach and attack this raptor (Gautier-Hion & Tutin, 1988; Zuberbühler et al., 1997). Although predators differ in several other characteristics, the predator's body size may be a key factor in determining the appropriate anti-predator response (Palleroni et al., 2005).

Another interesting finding, concerning the influence of the type of predator, was that the black mamba model failed to elicit noticeable anti-predator behaviour, much in contrast to the Gaboon viper that regularly elicited alarm calls, threats at a distance, and locomotor displays. Gaboon vipers also elicited strong responses in other forest primates, including sooty mangabeys (*Cercocebus atys*: Range & Fischer, 2004; Penner et al., 2008) and chimpanzees (Boesch & Boesch-Ackermann, 2000). Gaboon vipers are found on the ground, where they hide motionless and extraordinarily well camouflaged within the leaf litter (Range & Fischer, 2004; Penner et al., 2008; KO, personal observation, $N = 7$). Although Gaboon vipers have been documented to prey on juvenile guenons (Foerster, 2008), to our knowledge no attempt to eat an adult has been observed in the Taï forest. Campbell's monkeys are among the smallest guenons in Taï forest (Oates et al., 1990) and could, therefore, be potential prey. Campbell's monkeys appear to be aware of their dangerousness and respond with ascending in tree and threatening at a safe distance, a behavioural pattern not observed to the mamba model. The quality of the mamba model was very good (Fig. 1) and it is very unlikely that the monkeys did not recognise it as a snake, also because females responded with ascending. More likely, this behaviour might be a sign of the monkeys' ability to discriminate between different snakes. Taï forest contains more than 40 snake species (Cansdale, 1961; Penner et al., 2008; MO Roedel, personal communication), but a large majority is small and potentially not dangerous for primates. Distinct behaviours according to snake type were also found in wild bonnet macaques (*Macaca radiata*), which displayed caution and

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maintenance of safe distance but produced alarm calling only against Indian python (*Python molurus*) that preys on monkeys (Ramakrishnan et al., 2005). During 21 months of field observations we never observed Campbell's monkeys showing anti-predator behaviour in response to snakes, including green mambas, *Dendroaspis angusticeps*, as well as *Mehelya* sp. and *Oxybelis* sp., other than Gaboon vipers. Although black mambas occur in the Ivory Coast, they exclusively live in dry habitats and do not enter forest habitats, suggesting that the monkeys' default response to unfamiliar snakes is to ignore them. Before drawing definitive conclusion, more tests with other models (e.g., real stuffed snake) and other snake species (e.g., non-native dangerous species and native non-dangerous species) would be needed, including mimicking an attack posture (e.g., typical mamba attack with the body lifted).

Campbell's monkeys responded in a sex-specific way. In some cases, the adult male and females engaged in joint defence, but more often the two sexes followed their own patterns, with the males, as mentioned above, generally taking the more active and riskier roles. Females, much smaller in size than the adult male, usually behaved differently, preferring cryptic over conspicuous behaviours and often moving away to hide in foliage for both leopard and eagle trials, while the male was exposed by displaying conspicuous behaviour such as counter attack. In our study, although we could confirm that both sexes have each time spotted the predator, we could not control to which extent one sex was reacting in response to the predator or to the other sex's behaviours. Nevertheless, such sex-specific anti-predator behaviours have been reported in other studies on monkey (brown and white-fronted capuchins: van Schaik & van Noordwijk, 1989; common marmosets (*Callithrix jacchus*): Koenig, 1998) but on other animals too, such as white-tailed deer (*Odocoileus virginianus*: Lark & Slade, 2008). In contrast, sex differences were reduced in brown capuchin monkeys living under low predation pressure (Hirsch, 2002) and were not observed in savannah-living vervet monkeys where both sexes appear to react in similar ways with predator-specific responses (e.g., climbing and remaining in tree for ground predator and running and looking up for aerial predator (Seyfarth et al., 1980a)). Interestingly, in some species females are more aggressive than males. This was observed in large ungulates, particularly elk (*Cervus elaphus*) and bison (*Bison bison*), which directed aggressive behaviours more frequently towards coyotes when calves and fawns were present (Gese, 1999).

Whether or not males and females detected the predators in the visual domain also influenced their behaviours, with higher alarm call rates after visual detection of eagles or leopards compared to auditory cues. One could predict that more calls would be given by a group to an acoustic model simply because more individuals would have detected it, but we found the exact opposite. We interpreted alarm calls as responses to either the predator or other callers. Using “phono-responses” is a common strategy in guenons (Gautier & Gautier-Hion, 1977). When hearing a predator’s calls from a hidden speaker, a caller is unable to locate a predator precisely. Whether or not this makes a predator more dangerous is difficult to decide. On the one hand, direct visual contact may indicate more imminent danger but it could also be argued that a hidden predator is inherently more dangerous because its behaviour cannot be monitored. It is possible that monkeys first want to establish visual contact before engaging in the various conspicuous anti-predator behaviours seen to visual models. In line with this argument, males often remain immobile and adopt a vigilant posture in response to acoustic predator models, presumably attending further cues of the predator’s whereabouts. There are a number of other explanations. First, a vocalising predator may not be hunting, in which case the monkeys should be less concerned. Second, the monkeys should be less likely to alarm call because a vocalizing predator probably has not yet detected the monkeys. Third, in our study the acoustic stimuli could be spotted from a larger distance than the visual stimuli and the increased distance could be associated with reduced danger. Fourth, if alarm calls serve to alert conspecifics (e.g., Chapman et al., 1990; Zuberbühler, 2000b), then the benefits are lower if other group members have heard the same thing as the caller, which is different for visual models. Whatever the reason, acoustic predator information appears to predict lower vocal activity than visual predator information.

Once the leopard was visually located, we found similar response patterns from male and female Campbell’s monkeys. Females typically abandoned their default cryptic behaviour to join their male in threatening the leopard from a distance. The high rates of alarm calling observed by both sexes in this context was most likely the result of a general strategy to discourage the predator from further hunting attempts in the monkeys’ home range, as also described in other forest monkeys (Diana monkeys: Zuberbühler et al., 1997; putty-nosed monkeys (*Cercopithecus nictitans martini*): Arnold et al., 2008; black-and-white colobus (*Colobus guereza*): Schel et al., 2009).

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Another effect of the detection modality concerned the vertical movements within the trees. When the predator could not be precisely localised, both males and females climbed higher for leopards and lower for eagles, probably a response to the different hunting strategies of the two predators. Leopards usually hide and attack from the ground, and climbing up will decrease their exposure to surprise attacks. Eagles, in contrast, hunt by sweeping through the canopy or by pouncing on monkeys passing underneath (Shultz & Thomsett, 2007). In either case, attacks mostly happen from above and monkeys respond by climbing lower, away from the likely direction of attack.

In sum, our study points to the flexibility of non-human primates when dealing with predators. It shows that anti-predator responses are not very likely the product of hard-wired behavioural responses to different types of threats, but the results of more complex cognitive processes by which individuals take into account their own vulnerability, the species and behavioural profile of the predator, the degree of threat, the behaviour of other group members, and the specific conditions of the habitat before selecting an appropriate anti-predator response.

Acknowledgements

This work was supported with grants by the European Union (FP6 programme: “What it means to be human” and ESF-Eurocores: “The Origin of Man Language and Languages”), the French Ministry of Foreign Affairs (Egide) and the Centre Suisse de Recherches Scientifiques (CSRS). We are grateful to “Office Ivoirien des Parcs et Réserves” (OIPR) for permission to conduct research in the Taï National Park. We thank all the field assistants of Taï Monkey Project, as well as Martine Hausberger, Jean Emile Gombert and N’goran K. Eliezer for support and discussions.

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