

# Responses to leopards are independent of experience in Guereza colobus monkeys

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## Summary

How primates learn to recognise the predatory species from their animate world is a largely unresolved problem. We conducted predator encounter experiments with wild Guereza colobus monkeys of the Sonso area of Budongo Forest, Uganda. The monkeys are hunted by crowned eagles and chimpanzees, but not leopards, which have been locally extinct for decades. Despite their unfamiliarity with this predator, monkeys reliably produced appropriate anti-predator behaviour to leopards, which was indistinguishable from that of a neighbouring population, where leopards are present. In both populations, monkeys produced the same vocal responses and predator-specific alarm calls, although leopard-naïve monkeys were more inclined to approach when hearing a leopard than monkeys that were familiar with this predator. Control experiments showed that the monkeys' response pattern was not due to the effects of unfamiliarity or conspicuousness of the experimental stimuli. Natural selection appears to have endowed these primates with a cognitive capacity to recognise direct signs of leopard presence as inherently dangerous requiring specific anti-predator responses.

*Keywords:* *Colobus guereza*, predation, alarm call, leopard, predator experience.

## Introduction

Predation is one of the selective forces that have shaped the evolution of animal behaviour. For primates in particular, leopard and snake predation have been implicated as important selection pressures shaping their cognitive capacities and behaviour (Zuberbühler & Jenny, 2002; Isbell, 2006). Many primate species possess specialised anti-predator techniques that enable them

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to cope with their predators and control mortality risks. One such technique is the production of alarm calls. Alarm calls can be beneficial for a caller in a variety of ways, for example by interfering with a predator's hunting behaviour and by warning individuals valuable to the caller (Zuberbühler, in press). Often, animals produce more than one alarm call type when interacting with different predator types. In some cases, this allows receivers to select the most appropriate anti-predator response by inferring the type of predator the caller has encountered (e.g., Seyfarth et al., 1980; Slobodchikoff et al., 1991; Zuberbühler, 2000, 2001; Kirchhoff & Hammerschmidt, 2006).

Alarm calls are not adaptive in all circumstances, however, particularly when interacting with predators that do not rely on ambush. Predatory chimpanzees (*Pan troglodytes*), for example, are capable of pursuing monkeys through the canopy, and an adaptive strategy to these predators is to remain vocally and visually cryptic (Zuberbühler et al., 1997). Rapid and accurate predator recognition lies at the core of these decisions, and natural selection should favour mechanisms that facilitate this process.

Three basic processes may be at work in helping individuals to respond appropriately to predators. Firstly, prey animals may possess an inherited predisposition to respond to certain animals with anti-predator behaviour. This type of mechanism should be common in solitary species where individuals are unable to benefit from social learning. However, empirical evidence for this mechanism also exists for social species in the form of individuals displaying appropriate anti-predator behaviour in the absence of any prior predator experience (Vitale et al., 1991; Brown et al., 1992; Coss & Ramakrishnan, 2000; Barros et al., 2002). For example, snake models trigger appropriate anti-snake behaviour in predator-naïve tufted capuchins (*Cebus apella*) and crab-eating macaques (*Macaca fascicularis*; Vitale et al., 1991), and, similarly, felid predator models can induce anti-predator behaviour in captive-born black tufted-eared marmosets (*Callithrix penicillata*; Barros et al., 2002) and bonnet macaques (Coss & Ramakrishnan, 2000).

Secondly, predator-naïve animals may not accurately recognise a predator on their first encounter (Yorzinski & Ziegler, 2007; Friant et al., 2008), but they may be equipped with a particularly efficient learning mechanism, which allows them to learn the features of different predator types with a small number of trials, either by experiencing a direct interaction or by witnessing the anti-predator behaviour of others (Griffin et al., 2000; Berger et

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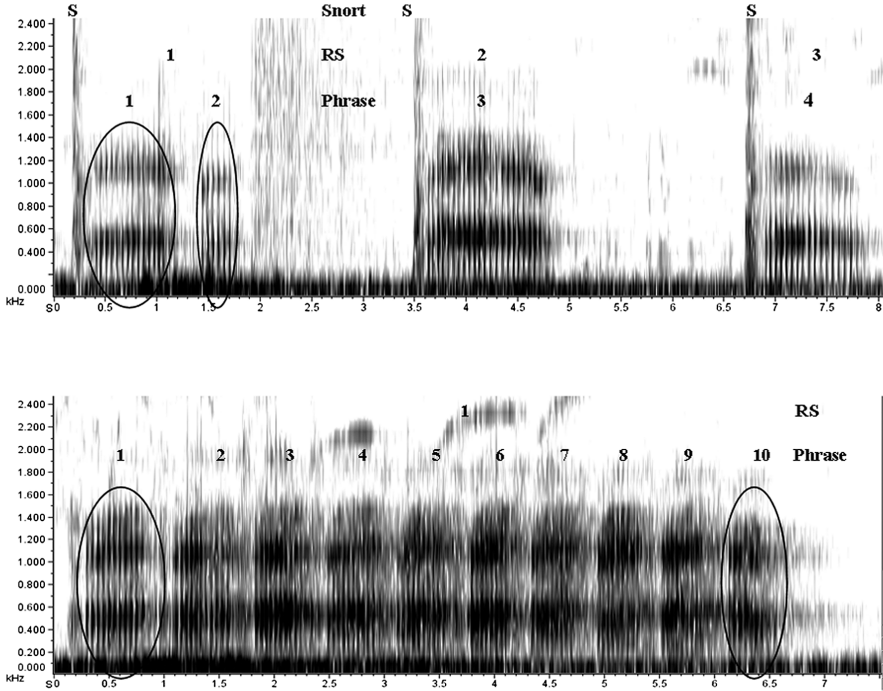
al., 2001; Öhman & Mineka, 2001; Coss et al., 2007). Juvenile rhesus monkeys, for example, can learn to fear snakes after exposure to a video of their mothers responding fearfully to them (reviewed in Griffin et al., 2000; Öhman & Mineka, 2001). Rapid learning also accounts for observations of animals re-acquiring anti-predator behaviour following the re-introduction of a historically important, but previously absent, predator (Berger et al., 2001; Laundré et al., 2001; Gil-da-Costa et al., 2003).

Thirdly, it is conceivable that individuals possess some inherited predator knowledge, but that this knowledge is incomplete and requires experience before appropriate anti-predator behaviour is possible. For example, in tamar wallabies (*Macropus eugenii*) accurate predator recognition in the visual domain appears to be less experience-dependent than recognition in the acoustic domain (Blumstein et al., 2000, 2004), a characteristic also found in other species (Blumstein et al., 2002), including primates (Fichtel & van Schaik, 2006). In some species, synergic effects have been observed. Adaptive responses to unfamiliar predators are sometimes seen in species that are preyed upon by other predators, in contrast to populations that are completely predator-free (Coss, 1999; Blumstein et al., 2004, 2006; Blumstein, 2006).

In previous work we have shown that *Guereza colobus* monkeys (*Colobus guereza*) of Kaniyo Pabidi, Budongo Forest Reserve, Uganda, respond with different types of anti-predator behaviour to the three main predators present at the site: leopards (*Panthera pardus*), crowned eagles (*Stepanoaetus coronatus*), and chimpanzees, both in terms of vocal and locomotor behaviour (Schel et al., 2009; Figure 1; Table 1). For instance, when hearing the calls of a leopard, or another monkey's leopard alarms, adult males respond with their own leopard-specific alarm call sequences. When hearing a crowned eagle, however, or another monkey's eagle alarm calls, then adult males produce eagle-specific alarm call sequences (Figure 1).

During these leopard encounters, the male (sometimes joined by the rest of his group) either approaches or remains stationary in the horizontal plane, and either moves upwards or remains stationary in the vertical plane. In contrast, when spotting a visual leopard model moving on the ground, the males produce the same alarm calls, but consistently approach and follow the predator until it leaves the area. In response to eagle models, they either approach or remain stationary, while the rest of the group remains motionless or moves downwards into cover (Table 1). In response to chimpanzees, the adult male usually remains silent while sometimes moving up in the tree,

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**Figure 1.** Spectrographic representation of the vocal alarm responses of Guerezas at Kaniyo Pabidi. (A) Three Roaring Sequences (RS) consisting of one snort-introduced 2-phrase RS, followed by two snort-introduced 1-phrase RS to an acoustic leopard model. (B) One RS consisting of 10 phrases to an acoustic eagle model. Encircled are the first and last phrases that are produced in the first RS. The x-axis represent the time in s, the y-axis the frequency in kHz.

together with the rest of his group. In this context, the monkeys usually show no preference for a particular direction of movement in the horizontal plane. Table 1 summarises these main patterns.

In the Sonso area of the Budongo Forest Reserve, approximately 50 km southwest of Kaniyo Pabidi, leopards have been absent, probably for at least 45 years (F. Babweteera, personal communication). We took advantage of this ecological anomaly, by investigating how leopard-naïve animals responded to this key primate predator. We conducted predator simulation experiments, by using both acoustic and visual predator models. To control for the effects of novelty, we also conducted a series of control experiments in which we simulated the presence of a non-predator, the African elephant (*Loxodonta africana*) and another African predator, the spotted hyena (*Cro-*

**Table 1.** Overview of the type and number of predator model experiments conducted in Kaniyo Pabidi between 2006 and 2007.

Experimental stimulus	No. of experiments	No. of vocal responses	Response rate (%)	Experiments ( <i>N</i> ) with		Direction of movement in the			Direction of movement in the		
				observed horizontal (H) and vertical (V) movement		horizontal plane ( <i>N</i> )			vertical plane ( <i>N</i> )		
				H	V	Further	Closer	No.	Up	Down	No.
Acoustic predator model type	33	12	36	32	9	3	10	19	4	1	4
Leopard growls											
Eagle shrieks	38	8	21	37	9	4	13	20	0	5	4
Chimpanzee pant hoots	18	0	0	17	16	1	5	11	12	0	4
Visual predator model type	18	17	94	18	18	0	17	1	7	9	2
Leopard model											
Chimpanzee model	12	1	8	12	12	4	3	5	9	1	2

Vocal response rates and the frequencies of the directions of movements in the horizontal and vertical planes are given.

*cuta crocuta*), which is irrelevant for forest monkeys. In the visual domain, we tested the monkeys' responses to a conspicuous object moving on the ground.

## Materials and methods

### *Study sites and subjects*

We conducted experiments in the Sonso area of the Budongo Forest Reserve, Uganda, between September 2005 and September 2006. The Sonso area consists of forest compartments N1, N2, N3 and N4 (Plumptre, 1996), an approx. 9-km<sup>2</sup> area of secondary tropical moist semi-deciduous rainforest (05°49'N, 31°32'E). The Kaniyo Pabidi area of Budongo Forest (01°55'N, 31°43'E) consists of compartments K11, K12 and K13 (Plumptre, 1996), and is classified as primary tropical moist semi-deciduous rainforest. Kaniyo Pabidi is similar to Sonso in most relevant ecological parameters (Eggeling, 1947; Plumptre, 1996; Plumptre et al., 1997), with one exception: whereas both Sonso and Kaniyo Pabidi contain chimpanzees and crowned eagles, leopards are only found in Kaniyo Pabidi (Plumptre, 1996; Schel, 2009). The two forests are separated by a 10 km stretch of open terrain, inhabited by humans, which is thought to prevent migration for most forest species. Although it is impossible to prove the complete absence of leopards at Sonso, there have been no direct sightings or reports of leopard traces in Sonso, despite continuous and intense research activities in the area for the last two decades (Reynolds, 2005). In general, leopard-inhabited forests contain a wealth of cues, including faecal remains, footprints, and conspicuous scratch and scent marks that cannot be overlooked (Jenny, 1996; Zuberbühler & Jenny, 2002), suggesting that if a leopard had frequented our study area this would have been noticed.

Guerezas are arboreal, medium-sized colobine monkeys, living in groups generally consisting of one adult male and about four adult females with their sub-adult, juvenile and infant offspring (Marler, 1969; Oates et al., 1994). Maturing males disperse from their natal group, and sometimes form all-male bands before taking over a group of their own. Guerezas are distributed across equatorial Africa, from Ethiopia to northern Tanzania and west to the Nigeria-Cameroon border (Oates et al., 1994). Over this range, several subspecies of *C. guereza* have been classified, which differ considerably in the

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length and degree of white in the species' characteristic tail-tuft and mantle (Groves, 2007). These subspecies inhabit a diverse range of habitats, such as moist lowland forests, montane forests, riverine forests, dry coastal forests, and gallery forests of the savannah zones (Oates, 1994). Guerezas thrive extremely well in secondary forests, and they are often found at higher densities in heavily logged forest compartments than in unlogged or lightly logged forest compartments (e.g., Plumptre & Reynolds, 1994; Chapman et al., 2000). Accordingly, group densities at Sonso were higher than those in Kaniyo Pabidi (6–10 and 3–5 groups/km<sup>2</sup>, respectively; Plumptre & Reynolds, 1994; Plumptre, 2000; Preece, 2001).

The Guerezas' diet usually contains high quantities of leaves (ranging from 53 to 94%: Oates et al., 1994; Fashing, 2001a,b), providing relatively little energy and requiring long fermentation periods after feeding. The monkeys' highly inactive life-style is likely to be related to the need to cope with these dietary constraints: Guerezas display energy-conserving behaviour, with 57% or more of their time spent resting, around 20% feeding and only 5% moving (cf., Dasilva, 1992; Oates et al., 1994; Fashing, 2001a). In addition, Guerezas' day journey lengths only average about 550 m per day (Oates, 1977; Oates et al., 1994; Fashing, 2001a), and home range sizes are rather small, ranging from 10 to 35 ha, with actively defended core territories of around 1–2 ha in some study populations (Marler, 1969; Oates et al., 1994; but see Harris, 2006; Harris & Chapman, 2007).

*Terminology of Guerezas' vocalizations*

Male Guerezas produce loud and low-pitched roaring sequences in response to predators and also during dawn choruses (Marler, 1972; Oates & Trocco, 1983; Oates et al., 2000; Schel et al., 2009). Roaring sequences are composed of a variable number of individual roaring phrases, that usually consist of about a dozen glottal pulses, which appear in the spectrogram as compound units with an average duration around 700–800 ms (Figure 1a and 1b). The acoustic energy in each roaring phrase tends to appear as two discrete frequency bands on the spectrogram at around 600 and 1300 Hz, representing two formant frequencies (Harris et al., 2006). The first phrase in a roaring sequence can be preceded by one or more snorts, consisting of broadband acoustic energy with a sudden onset, ranging in frequency up to about 4 kHz with the main frequency at around 1 kHz.

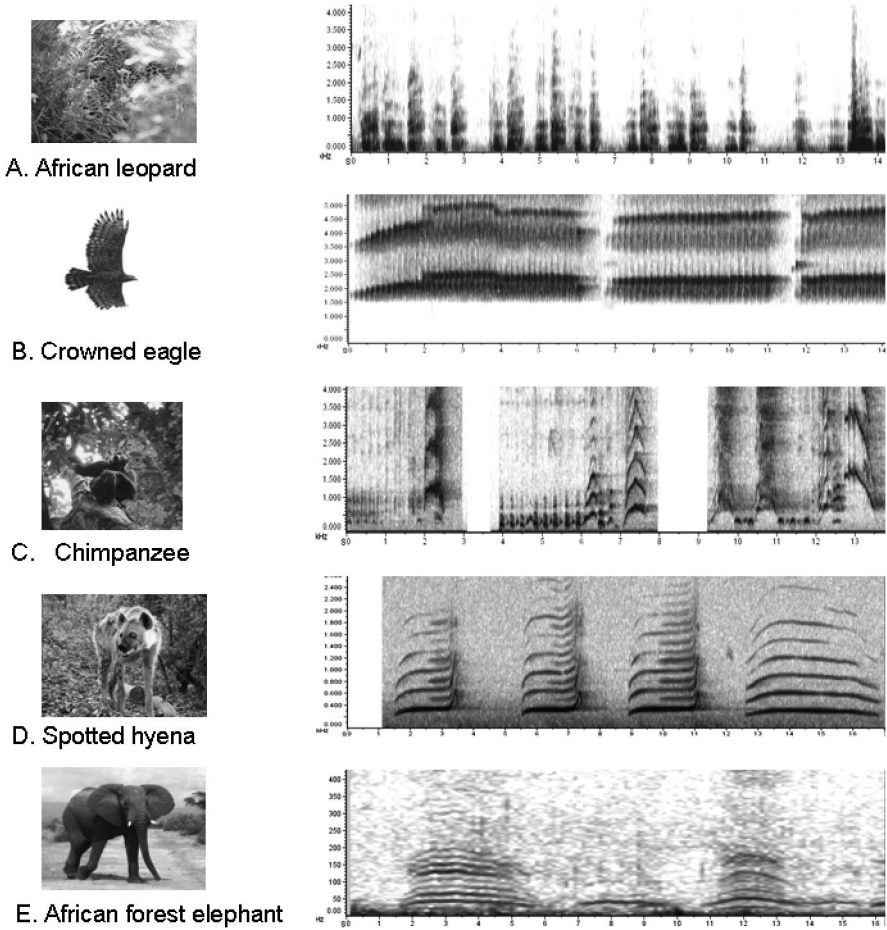
In a previous study, we have shown that roaring sequences produced in predatory situations vary in the number of roaring phrases they consist of, depending on the predator type encountered: sequences consisting of a snort followed by few phrases are typically produced to leopards, while sequences consisting of many phrases without snorts are typically produced to crowned eagles (Schel et al., 2009; Figure 1). The acoustic structure of individual roaring phrases used in the different predator-specific roaring sequences does not differ between contexts, except for the harmonics-to-noise ratio (HNR), which may be related to the monkeys' state of arousal when encountering the different predator types (Fichtel et al., 2001; Rendall, 2003). In contrast, within predator contexts, the first and last phrases of a sequence differ in acoustic structure, with the final phrase in a roaring sequence usually being lower pitched, generating a perceptually conspicuous marker to terminate the sequence.

#### *Acoustic and visual experimental stimuli*

Predator vocalizations used as playback stimuli were purchased from the British Library of Wildlife Sounds, London (African leopard; BBC master tape number MM 35, © South African Broadcasting Corporation) or recorded in Tai National Park, Ivory Coast (eagle shrieks and chimpanzee pant hoots) with a Sony Professional Walkman WMD6C and Sennheiser 70-mm microphone (K3U + ME88) by K.Z. Hyena howls and elephant rumbles were part of the Raven 1.2 software package (Cornell Laboratory of Ornithology, Ithaca, NY, USA; Figure 2).

To simulate the visual presence of a chimpanzee or leopard we used commercially available fur fabric ('fake fur'), which was either uniformly black or leopard-patterned. A sheet with a flower pattern served as a control for an unfamiliar, conspicuous, and animate object of equal size. In all conditions, the fabric was draped over the head, shoulders and torso of a field assistant (GE), who mimicked the size, shape, and posture of the predator as much as possible (Figure 3). The visibility from the middle and upper forest canopy to the forest floor is very poor, so that subjects typically could only see fractions of these predator models presented to them. Previous primate studies already revealed that visual predator models can be powerful in evoking alarm calls from individuals if the fabric resembles a predator's coat pattern, but not if striped or flower-patterned (e.g., Wich & Sterck, 2003; Coss et al., 2005; Arnold et al., 2008).

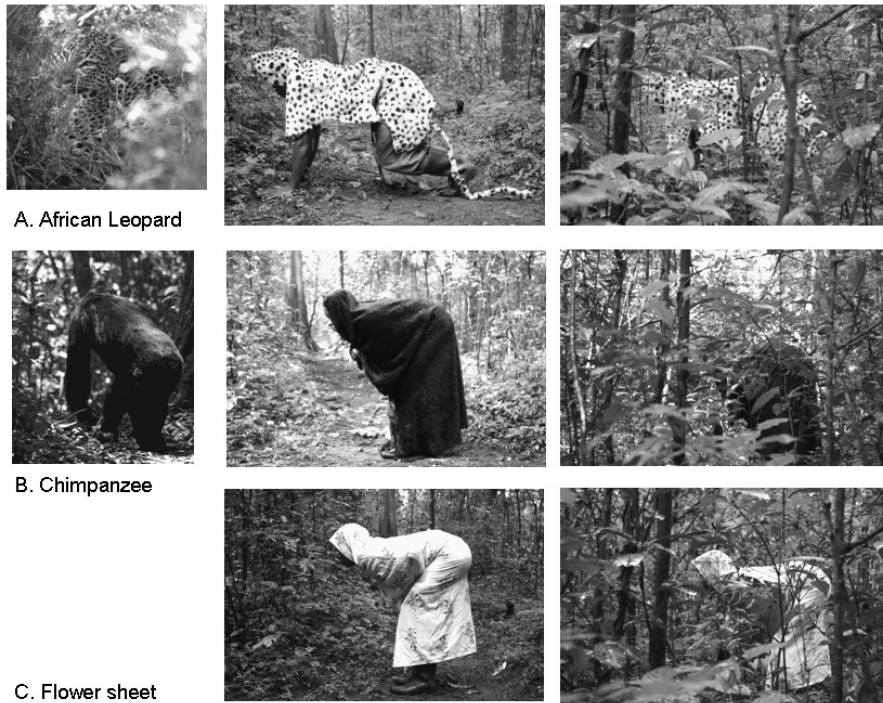
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**Figure 2.** Spectrographic representations of the playback stimuli used in this study. (A) 14 s of leopard growls, (B) 14 s of crowned eagle shrieks, (C) 14 s of chimpanzee pant hoots, (D) 16 s of hyena howls and (E) 16 s of elephant rumbles. The  $x$ -axes represent the time in seconds, the  $y$ -axes the frequency in kHz, except for E, where it represents the frequency in Hz. Photos by A.S., or printed with permission.

*Experimental protocol*

We systematically searched for monkey groups throughout the study area. We usually found them high up in a feeding tree, either by spotting their conspicuous tail tufts, or by hearing their movements or intra-group vocalizations. Once found, we determined their geographical location using a Garmin GPS 76 and a detailed map. To ensure that a group was not tested twice, we



**Figure 3.** (A) African forest leopard in its natural environment, followed by two photographs of the leopard model used in this study. (B) Chimpanzee in its natural environment, followed by two photographs of the chimpanzee model. (C) Control: flower sheet model. Photos by A.S., or printed with permission.

kept a distance of at least 750 m between adjacent locations of experiments conducted on the same day. On consecutive test days with one particular predator stimulus (e.g., leopard growls), we made sure to only target groups inhabiting a different part of the forest as those tested the days before. Once a group was identified we monitored their vocal behaviour for at least 15 min to make sure that they were unaware of our presence. An experimental trial was conducted only if during this period (a) no alarm calls were given in the group's surroundings by other monkeys, duikers, guinea fowls, or other forest animals, (b) no naturally occurring predator vocalizations were heard, (c) no predators were seen, (d) the monkeys did not accidentally detect the observers or the playback equipment and (e) no other humans were present in the experimental area.

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*Presentation of acoustic stimuli*

We edited the acoustic stimuli such that they consisted of 5 min silence prior to the test stimulus, which consisted of approx. 15 s of continuous vocalizations. To avoid pseudo-replication (McGregor, 2000; Kroodsma et al., 2001), we engineered several exemplars for each of the stimulus types (leopard growls ('L'):  $N = 6$ , eagle shrieks ('E'):  $N = 3$ , chimpanzee pant hoots ('Ch'):  $N = 6$ ; hyena howls ('H'):  $N = 4$ ; elephant rumbles ('El'):  $N = 4$ ). All playback stimuli were broadcast with a Panasonic SL-SX320 CD player connected to a Nagra DSM speaker-amplifier. The volume of the CD player was kept constant, while the amplitude of the Nagra amplifier was adjusted such that all playback stimuli were broadcast within a natural amplitude range (leopard growls 70–90 dB, eagle shrieks 80–100 dB, chimpanzee pant hoots 90–100 dB). Stimulus amplitude was measured with a Radio Shack Sound Pressure Level Meter at 1 m from the source, in the natural environment in which the playback was broadcast. For each trial, the playback equipment was usually positioned close to the forest floor (0–2 m) at a distance of circa 20–40 m from the group, outside the monkeys' visual range. Before conducting a trial, the observer found a suitable hiding place from which the group could be observed. Recordings of the monkeys' vocal and locomotor responses started about 3 min before a playback, and lasted for approx. 5 min after the monkeys' alarm call responses had ceased.

*Presentation of visual stimuli*

One successful procedure for testing primates' responses to the sight of predators is to position a visual model in their anticipated travelling path (e.g., Arnold et al., 2008). However, Guerezas have an unusually inactive lifestyle (Oates et al., 1994), and group progressions are rare. To increase the chance of spotting our visual models, we, therefore, simulated the presence of a moving predator (cf. Wich & Sterck, 2003; Arnold et al., 2008). This was done by a field assistant (GE) slowly approaching the group in a crouched position, covered by one of the different fabrics (Figure 3). This methodology and the monkeys' general locomotor inactivity prevented us from using visual eagle models.

As soon as GE began to move slowly towards the target group, the observer (AMS) recorded and observed the monkeys from the hiding place. In

case of the leopard model, GE moved on all fours, and in case of the chimpanzee and control model, he moved in a hunched position on two legs. In exceptional cases, GE managed to arrive unnoticed directly under the tree in which the monkeys were residing. He then made some rustling noises while moving to get the monkeys' attention. After detection, he stayed in sight of the group for about 15 min, before slowly moving back towards the observer's hiding place. We started recordings of the monkeys' vocal and behavioural responses from the moment GE moved away from the hiding place until approx. 5 min after the monkeys had ceased to respond.

#### *Locomotor and vocal responses*

For each trial, we scored whether the adult male and any other visible individuals moved, and if this was towards or away from the stimulus. Usually, it was possible to determine the sex of the visible individuals before stimulus presentation, using Leica 10 × 42 BA binoculars. Whenever possible, we noted the movements of all visible group members after stimulus presentation, as observed from the ground. Furthermore, we recorded all vocal behaviour using a Sony TCD D8 DAT recorder connected to a Sennheiser K6/ME66 directional microphone. Vocalizations were transferred onto a PC at a sampling rate of 48 kHz, 16 bits accuracy using Cool EDIT 2000 (Syntrillium Software, Phoenix, AZ, USA). Acoustic analyses were performed using RAVEN 1.2 (Cornell Laboratory of Ornithology) or PRAAT 4.3.12 (Boersma & Weenink, 2005).

#### *Data analysis*

We analysed locomotor data within and between contexts. We first determined whether the monkeys moved or stayed still in response to predator simulation. If movement occurred, we noted its direction in relation to the predator model. We used two-tailed Binomial tests and Fisher exact tests to compare within and between conditions, respectively (Siegel & Castellan, 1988). To be able to compare our data directly with a previous study on the locomotor behaviour of the Kaniyo Pabidi population (Schel, 2009; Table 1), the test probability used during statistical testing was set at chance level ( $p = 0.5$ ), and the critical significance level  $\alpha = 0.05$ .

Sometimes, more than one individual produced loud alarm sequences, possibly the adolescent son of the adult male. If this happened, we analysed

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the vocal response of the individual that called first, which was relatively easy to do. For each vocal response we determined the following six structural/temporal parameters: (a) total duration of the vocal response(s); (b) total number of roaring sequences; (c) total number of roaring phrases; (d) mean number of roaring phrases per roaring sequence; (e) number of snorts; and (f) call delivery rate (phrases/s). We also determined seven spectral variables from individual phrases: (a) phrase duration (ms); (b) number of combined pulses per roaring phrase; (c) fundamental frequency (Hz), calculated as the number of combined pulses per second; (d) harmonics-to-noise ratio (HNR, dB); (e) first formant (Hz); (f) second formant (Hz); and (g) peak frequency (Hz). We focussed all spectral analyses on the first and last phrases of the first two roaring sequences, provided they contained at least two roaring phrases (i.e., four roaring phrases per response; see Schel et al., 2009). We used two-tailed Wilcoxon matched pairs tests to compare the spectral characteristics of first and last roaring phrases produced within a roaring sequence. We used two-tailed Mann–Whitney  $U$ -tests to compare the spectral and temporal parameters between the predator contexts (Brace et al., 2000; Maltby & Day, 2002; Hawkins, 2005).

## Results

### *Locomotor response to acoustic predator models*

In 2005, we tested 28 different colobus groups with playbacks of leopard growls, 19 different groups with playbacks of eagle shrieks, and 23 different groups with playbacks of chimpanzee pant hoots. In 2006, we tested an additional 14 groups with chimpanzee pant hoots. Two eagle trials were discounted because the trial was conducted too close to a previous one, or because the monkeys saw the equipment or observer. Two leopard trials were discounted because there were chimpanzees in the area. One chimpanzee trial was discounted because of equipment malfunctioning. Thus, final sample sizes were:  $N_{\text{Leopard (L)}} = 26$ ,  $N_{\text{Eagle (E)}} = 17$ ,  $N_{\text{Chimpanzee (Ch)}} = 36$ .

In four leopard trials, two eagle trials, and two chimpanzee trials it was not possible to directly observe the animals, which reduced the dataset for locomotor analyses to  $N_L = 22$ ,  $N_E = 15$  and  $N_{\text{Ch}} = 34$ . Overall, monkeys were equally likely to approach a simulated leopard and eagle, but significantly more likely to remain motionless in response to chimpanzees (L:

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$N_{\text{Move}} = 17$ ,  $N_{\text{Not Move}} = 5$ , E:  $N_{\text{Move}} = 10$ ,  $N_{\text{Not Move}} = 5$ ; Ch:  $N_{\text{Move}} = 7$ ,  $N_{\text{Not Move}} = 27$ ; L vs. E: exact  $p = 0.708$ ; L vs. Ch: exact  $p = 0.000$ ; E vs. Ch: exact  $p = 0.003$ ; Fisher's exact tests; Figure 4A). Upon hearing leopard growls, subjects were significantly more likely to approach the simulated predator than to remain motionless ( $N_{\text{Move}} = 17$ ;  $N_{\text{Not Move}} = 5$ , exact  $p = 0.017$ ;  $N_{\text{Further}} = 2$ ;  $N_{\text{Closer}} = 15$ ; exact  $p = 0.002$ ; binomial test). In contrast, after hearing eagle shrieks, the monkeys sometimes moved, but not significantly so ( $N_{\text{Move}} = 10$ ;  $N_{\text{Not Move}} = 5$ , exact  $p = 0.302$ , binomial test). However, if they decided to move, it was always towards the simulated predator, never away from it ( $N_{\text{Further}} = 0$ ;  $N_{\text{Closer}} = 10$ , exact  $p = 0.002$ , binomial test). After hearing chimpanzee pant hoots, the monkeys were significantly more likely to remain seated than to move ( $N_{\text{Move}} = 7$ ;  $N_{\text{Not Move}} = 27$ , exact  $p = 0.001$ , binomial test). If they moved, it was in either direction ( $N_{\text{Further}} = 4$ ;  $N_{\text{Closer}} = 3$ , exact  $p = 1.000$ , binomial test).

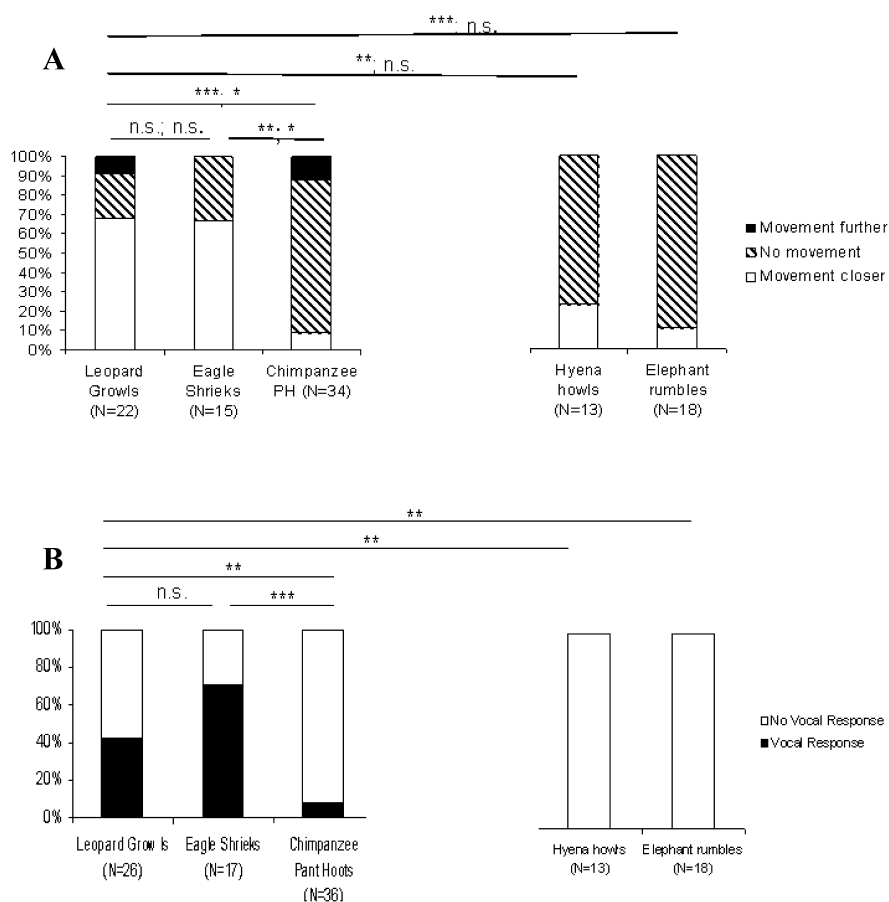
The fact that monkeys responded to leopard growls with anti-predator behaviour, despite their lack of experience, could be explained with novelty. Thus, we conducted a series of control trials with hyena howls ( $N = 13$ ) and elephant rumbles ( $N = 18$ ), two equally loud and conspicuous sounds that the monkeys were not familiar with. After both stimuli, the monkeys usually remained seated (hyena howls (H):  $N_{\text{Move}} = 3$ ;  $N_{\text{Still}} = 10$ , exact  $p = 0.092$ ; elephant rumbles (El):  $N_{\text{Move}} = 2$ ;  $N_{\text{Still}} = 16$ , exact  $p = 0.001$ ; binomial tests). On the few occasions when they moved they always approached, but sample sizes were too small to conduct any meaningful statistical analyses (H:  $N_{\text{Further}} = 0$ ;  $N_{\text{Closer}} = 3$ ; El:  $N_{\text{Further}} = 0$ ;  $N_{\text{Closer}} = 2$ ). Across all novel conditions, Guerezas moved significantly more often in response to a simulated leopard than a hyena or an elephant (H:  $N_{\text{Move}} = 3$ ,  $N_{\text{Still}} = 10$ ; El:  $N_{\text{Move}} = 2$ ,  $N_{\text{Still}} = 16$ ; L:  $N_{\text{Move}} = 17$ ,  $N_{\text{Still}} = 5$ ; H vs. L: exact  $p = 0.004$ , E vs. L: exact  $p = 0.000$ , Fisher's exact tests; Figure 4A). If subjects decided to move, they approached the three stimuli in equal proportions (H vs. L: exact  $p = 1.000$ ; E vs. L: exact  $p = 1.000$ , Fisher's exact tests; Figure 4A).

*Vocal responses to acoustic predator models*

Overall, Guereza colobus were reluctant to produce alarm vocalisations when hearing the vocalisations of one of the three predators. Response rates were highest to eagles (70.6%;  $N_{\text{Vocal Response (VR)}} = 12$ ,  $N_{\text{No VR}} = 5$ ; exact  $p = 0.143$ ; binomial test), followed by leopards (response rate = 42.3%;

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$N_{VR} = 11$ ,  $N_{NoVR} = 15$ ; exact  $p = 0.557$ , binomial test), and chimpanzees (response rate = 8.3%;  $N_{VR} = 3$ ,  $N_{NoVR} = 33$ ; exact  $p = 0.000$ , binomial test). Across conditions, response rates to leopard growls and eagle shrieks were comparable (L vs. E: exact  $p = 0.118$ ; Fisher's exact test), but responses to chimpanzees were mainly cryptic (Ch vs. L: exact  $p = 0.002$ ; Ch vs. E: exact  $p = 0.000$ ; Fisher's exact tests, Figure 4B). The monkeys



**Figure 4.** (A) Locomotor responses in the horizontal plane to the three different acoustic predator models and the two acoustic control stimuli. The first set of asterisks refers to the difference in occurrence of movement between contexts; the second set to the difference in direction of movements between contexts. (B) Vocal response rates to the three different acoustic predator models and the two control stimuli, with exact  $p$ -values. n.s.: no significance; \*, \*\*, \*\*\*: significant difference between the contexts \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p = 0.000$  (Fisher's Exact test,  $\alpha = 0.05$ , two-tailed).

never called in response to hyena howls and elephant rumbles, contrasting significantly with their response to the equally novel leopard growls (H: 0% (0/13); E1: 0% (0/18); L: 42% (11/26); H. vs. L: exact  $p = 0.007$ ; E vs. L: exact  $p = 0.001$ , Fisher's exact tests, two-tailed, Figure 4B).

We were also interested in whether there was any evidence for predator-specific alarm calling. For this purpose, we excluded two vocal responses to leopard growls due to poor recording quality, yielding a final sample size of  $N = 9$  vocal responses. One eagle response was discarded because of high levels of ambient noise produced by other calling individuals, yielding a final sample size of  $N = 11$  recordings. For the spectral measurements, one eagle trial had to be excluded for analyses of the second roaring sequence because the caller produced only one roaring sequence, yielding a final sample size for the second roaring sequences of  $N = 9$  for leopard responses and  $N = 10$  for eagle responses. None of the vocal responses to the chimpanzees was discarded, but due to the small vocal response rate ( $N = 3$ ) no acoustic analyses were performed. The monkeys did not produce any vocal responses to hyena howls and elephant rumbles.

We found consistent differences between the spectral measurements of first and final roaring phrases for both roaring sequences within the leopard and eagle contexts, mirroring the results obtained in the leopard-experienced Kaniyo Pabidi population (Table 2; Schel et al., 2009). When comparing the spectral features of individual roaring phrases between predator types, no consistent patterns were found, in line with our earlier research (Table 2; Schel et al., 2009).

However, the structural composition of roaring sequences to eagles and leopards differed in a number of ways, as already described for Kaniyo Pabidi (Schel et al., 2009). Most importantly, the number of roaring phrases per sequence was significantly smaller to leopard than eagle stimuli ( $U = 1.000$ , exact  $p = 0.000$ ; Mann–Whitney  $U$ -test). Secondly, the roaring sequences to leopards, but not eagles, were typically preceded by snorts (9 of 9 leopard trials; 4 of 11 eagle trials, exact  $p = 0.005$ ; Fisher's exact test). Across trials with snorts, monkeys produced a higher number of snorts to leopards than eagles ( $U = 0$ , exact  $p = 0.000$ ; Mann–Whitney  $U$ -test). Thirdly, the monkeys produced longer vocal responses to leopards than to eagles, in terms of the total duration of calling ( $U = 5$ , exact  $p = 0.000$ ; Mann–Whitney  $U$ -test), the total number of roaring phrases ( $U = 14$ , exact  $p = 0.006$ ; Mann–Whitney  $U$ -test) and the total number of roaring sequences ( $U = 5$ , exact  $p = 0.000$ ; Mann–Whitney  $U$ -test). The call delivery

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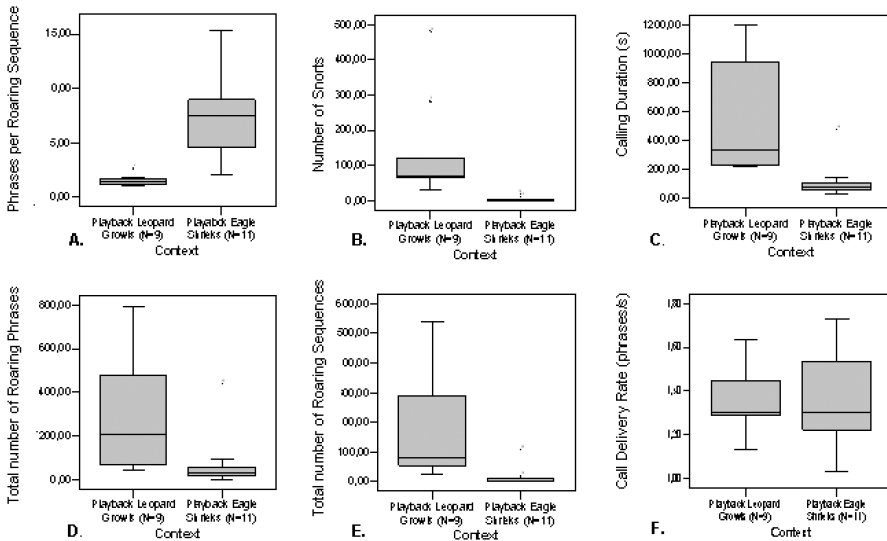
**Table 2.** Measurements (medians) and statistical output (Exact  $p$ -values,  $p$ ) of comparisons between acoustic measurements of first and last phrases of the first and second RS produced within predator contexts (Wilcoxon Signed Ranks Test,  $\alpha = 0.05$ ), followed by statistical output of comparisons between acoustic measurements of first and last phrases of the first and second RS produced across two different predator contexts (acoustic leopard and eagle models; Mann–Whitney  $U$ -test,  $\alpha = 0.05$ ).

Acoustic variable	Median within leopard (first vs. last phrase)			Median within eagle (first vs. last phrase)			$p$ between leopard and eagle	
	First phrase	Last phrase	$p$	First phrase	Last phrase	$p$	First phrase	Last phrase
<b>First RS</b>								
Phrase duration (ms)	857	271	0.004	757	320	0.001	0.656	0.067
Harmonics-noise ratio (dB)	3.74	3.19	0.176	3.13	2.85	0.820	0.645	1.000
First formant (Hz)	621	590	1.000	658.5	686.3	0.465	0.261	0.370
Second formant (Hz)	1412	1487	0.359	1338	1327	0.413	0.261	0.370
Peak frequency (Hz)	522	446	0.547	547	522	0.969	0.340	0.134
Number of pulses	14	4	0.016	15	6	0.002	0.706	0.016
Fundamental frequency (Hz)	13	16	0.297	18	19	0.320	0.047	0.051
<b>Second RS</b>								
Phrase duration (ms)	774	358	0.004	766	416.5	0.002	0.968	0.780
Harmonics-noise ratio (dB)	4.77	1.70	0.148	2.77	3.7	0.383	1.000	0.279
First formant (Hz)	581	734	0.203	658.3	727.1	0.770	0.113	0.720
Second formant (Hz)	1357	1594	0.109	1422	1445	0.557	0.497	0.515
Peak frequency (Hz)	522	471	0.438	572	496	0.098	0.011	0.388
Number of pulses	13	6	0.008	13	8	0.004	0.943	0.385
Fundamental frequency (Hz)	16	16	0.484	18	17	0.301	0.114	0.053

rate was similar between the two contexts ( $U = 47$ , exact  $p = 0.882$ ; Mann–Whitney  $U$ -test; Figure 5).

*Locomotor responses to visual predator models*

In 2005, we tested 11 different Guereza groups with a moving leopard model. In 2006, we tested another 19 groups with the same stimulus, and 34 different groups with a moving chimpanzee model. In the 2006 sample, groups



**Figure 5.** Measurements of temporal response characteristics to acoustic leopard and eagle models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes ( $>3$  box length above box). (A) Number of phrases/RS, (B) number of snorts, (C) calling duration (s), (D) total number of phrases, (E) total number of RS (Hz) and (F) call delivery rate (phrases/s).

previously exposed to the leopard model were not retested. Of the 30 leopard trials, 6 trials were discounted: one because the monkeys saw the observer during the trial, two because chimpanzees were present in the area, and three because of equipment malfunctioning. Of the 34 chimpanzee trials, one trial was discounted because the monkeys saw the observer. The final sample sizes for the visual model experiments, therefore, were  $N_L = 24$  and  $N_{Ch} = 33$ .

After detecting the leopard model, the monkeys were significantly more likely to approach than to stay motionless or move away ( $N_{Move} = 23$ ;  $N_{NotMove} = 1$ , exact  $p = 0.000$ ;  $N_{Further} = 1$ ;  $N_{Closer} = 22$ , exact  $p = 0.000$ ; binomial tests). After detecting the chimpanzee model, the monkeys were also more likely to move, but the direction of movement was not significantly affected ( $N_{Move} = 26$ ;  $N_{NotMove} = 7$ , exact  $p = 0.001$ ;  $N_{Further} = 8$ ;  $N_{Closer} = 18$ , exact  $p = 0.076$ ; binomial tests). Although movement was a common response to both predators (L:  $N_{Move} = 23$ ,  $N_{NotMove} = 1$ ; Ch:  $N_{Move} = 26$ ,  $N_{NotMove} = 7$ : L vs. Ch: exact  $p = 0.12$ ; Fisher's exact test; Figure 6A), the leopard caused significantly more approach than the chim-

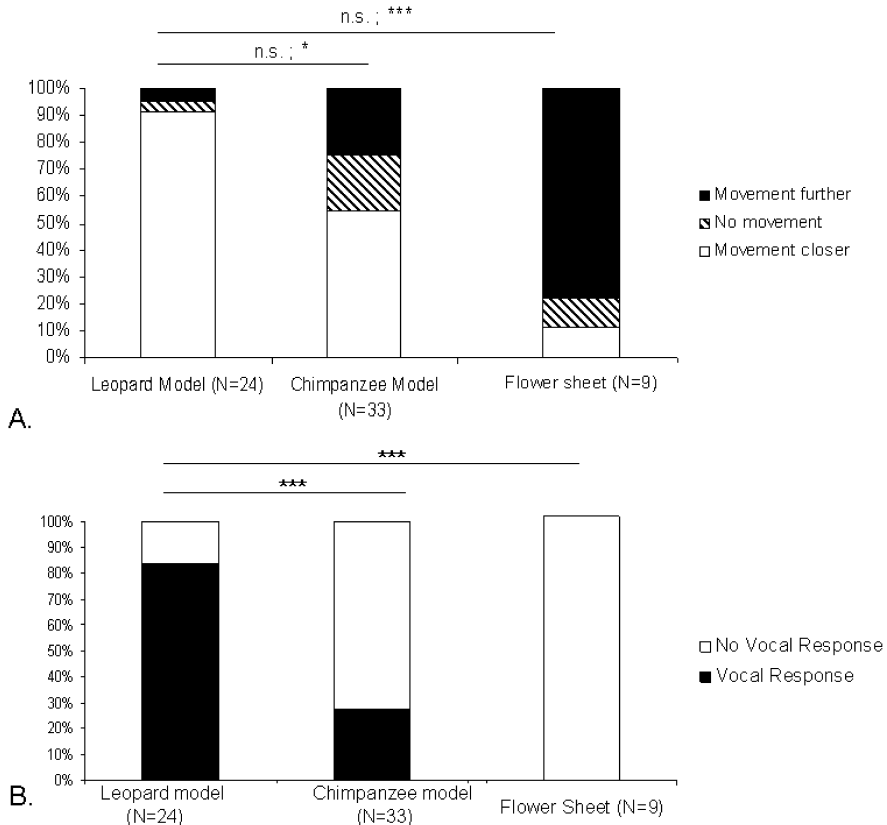
*Leopard responses of naïve Guereza colobus monkeys*

panzee model (L:  $N_{\text{Further}} = 1$ ,  $N_{\text{Closer}} = 22$ , Ch:  $N_{\text{Further}} = 8$ ,  $N_{\text{Closer}} = 18$ ; L vs. Ch: exact  $p = 0.026$ , Fisher's exact test, Figure 6A). To investigate whether the response to leopards could be explained with stimulus novelty, we conducted a control experiment during which the field assistant approached in the same way, but was covered by a fabric with a flower print of comparable conspicuousness as the leopard fur (Figure 3;  $N = 9$ ). The locomotor responses elicited by the control stimulus ('C') differed significantly from the leopard model. Even though the monkeys started moving in a similar proportion of trials (C:  $N_{\text{Movement}} = 8$ ,  $N_{\text{NoMovement}} = 1$ ; L:  $N_{\text{Movement}} = 23$ ,  $N_{\text{NoMovement}} = 1$ ; C vs. L: exact  $p = 0.48$ , Fisher's exact test), they moved in opposite directions (C:  $N_{\text{Further}} = 7$ ,  $N_{\text{Closer}} = 1$ ; L:  $N_{\text{Further}} = 1$ ,  $N_{\text{Closer}} = 22$ ; C vs. L: exact  $p = 0.000$ , Fisher's exact test; Figure 6A).

*Vocal responses to visual predator models*

In 20 of the 24 groups tested with leopard, at least one individual responded with alarm vocalizations (response rate = 83%;  $N_{\text{Vocal Response (VR)}} = 20$ ,  $N_{\text{No VR}} = 4$ ; exact  $p = 0.002$ ; binomial test). The response rate to the chimpanzee model was much lower, with the monkeys generally remaining silent: in 9 of 33 groups at least one monkey responded with alarm vocalizations (response rate = 27%;  $N_{\text{VR}} = 9$ ,  $N_{\text{No VR}} = 24$ ; exact  $p = 0.014$ ; binomial test). Across predator types, monkeys were much more likely to respond with alarm calls to the leopard than to the chimpanzee model (L: 83%; Ch: 27%, L vs. Ch: exact  $p = 0.000$ ; Fisher's exact test; Figure 6B). The monkeys never vocalized to the control condition, in statistically significant contrast to their response to the leopard model (C: 0% (0/9); L: 83% (20/24); C vs. L: exact  $p = 0.000$ , Fisher's exact test, Figure 6B).

To investigate whether any predator-specific alarm calling occurred, we excluded 3 of the 20 vocal leopard responses from structural analyses because of noise produced by nearby individuals or poor recording quality, yielding a final dataset of  $N = 17$  leopard responses. 12 of the 20 responses were suitable for extracting spectral parameters of the individual phrases; the rest was discarded due to nearby individuals calling, poor recording quality, or the fact that callers did not produce at least 2 phrases. Of the 9 vocal chimpanzee responses, 1 was discarded due to other individuals calling, yielding a sample size of  $N = 8$  for structural analyses. 6 of 9 chimpanzee responses



**Figure 6.** (A) Locomotor responses in the horizontal plane to the two different visual predator models and the visual control stimulus. The first set of asterisks refers to the occurrence of movements between contexts; the second set of asterisk refers to the direction of movements between contexts. (B) Vocal response rates to the two different visual predator models and the visual control stimulus, with exact  $p$ -values. n.s.: no significant difference between the contexts; \*, \*\*, \*\*\*: significant difference between the contexts, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p = 0.000$  (Fisher's Exact test,  $\alpha = 0.05$ , two-tailed).

were suitable to extract spectral parameters; twice the monkeys produced only snorts, once other monkeys called.

There were statistically significant differences between the first and final roaring phrases for both roaring sequences within both leopard and chimpanzee responses (Table 3). Across predators, there were no significant differences in spectral measurements of individual phrases (Table 3).

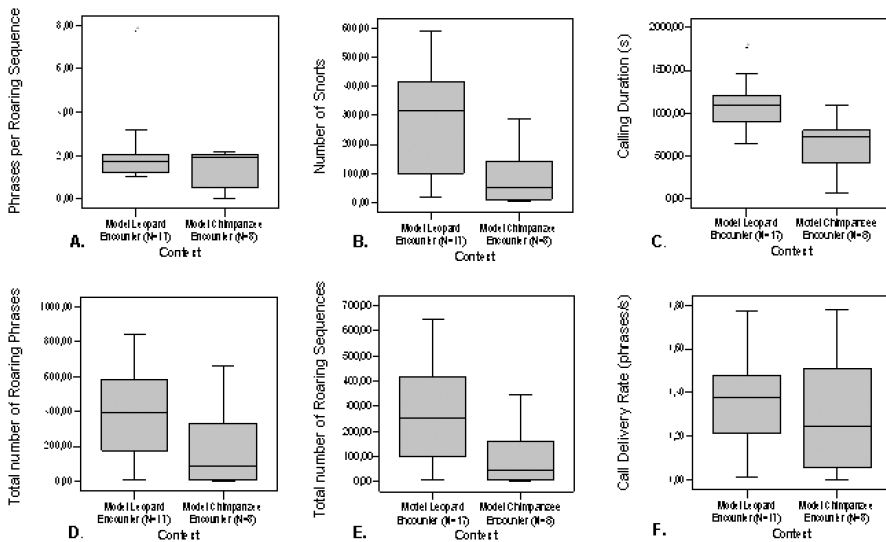
Across predator types, we found three significant differences in the temporal patterning of responses. First, the total calling duration was signifi-

*Leopard responses of naïve Guereza colobus monkeys*

**Table 3.** Statistical output (Exact  $p$ -values) of comparisons between acoustic measurements of first and last phrases of the first and second RS produced within predator contexts (Wilcoxon Signed Ranks Test), followed by statistic output of comparisons between acoustic measurements of first and last phrases of the first and second RS produced across two different predator contexts (visual leopard and chimpanzee models; Mann–Whitney  $U$ -test).

Acoustic variable	Median within leopard (first vs. last phrase)			Median within eagle (first vs. last phrase)			$p$ between leopard and eagle	
	First phrase	Last phrase	$p$	First phrase	Last phrase	$p$	First phrase	Last phrase
First RS								
Phrase duration (ms)	851	312	0.000	1107	478	0.031	0.067	0.157
Harmonics-noise ratio (dB)	4.61	5.79	0.391	4.49	3.83	0.844	0.682	0.385
First formant (Hz)	547	563	0.791	569	561	0.844	0.820	0.892
Second formant (Hz)	1241	1198	0.380	1245	1271	0.844	0.437	0.616
Peak frequency (Hz)	540	499	0.490	540	477	0.031	0.945	0.236
Number of pulses	14	5	0.000	17	9	0.031	0.096	0.155
Fundamental frequency (Hz)	16	18	0.266	16	16	0.438	0.494	0.682
Second RS								
Phrase duration (ms)	893	284	0.000	993	315	0.031	0.125	0.964
Harmonics-noise ratio (dB)	4.68	3.82	0.791	5.08	4.27	0.563	0.221	0.837
First formant (Hz)	571	568	0.519	541	532	0.844	0.335	0.616
Second formant (Hz)	1258	1201	0.424	1276	1214	0.688	0.964	0.964
Peak frequency (Hz)	540	485	0.020	516	456	0.031	0.300	0.086
Number of pulses	14	5	0.000	16	6	0.031	0.347	0.924
Fundamental frequency (Hz)	16	17	0.129	16	18	0.156	0.982	0.494

cantly longer to leopard than to chimpanzee models ( $U = 17$ , exact  $p$ -value = 0.002, Mann–Whitney  $U$ -test). Second, although both predators triggered snorts (17 of 17 leopard trials; 8 of 8 chimpanzee trials, exact  $p = 1.000$ ; Fisher’s exact test), the total number of snorts was higher in response to leopard than chimpanzee models ( $U = 24.5$ , exact  $p$ -value = 0.009, Mann–Whitney  $U$ -test). Third, the total number of roaring sequences was significantly higher to leopard than chimpanzee models ( $U = 32.5$ , exact  $p$ -value = 0.038, Mann–Whitney  $U$ -test). The total number of phrases ( $U = 36$ , exact  $p$ -value = 0.064, Mann–Whitney  $U$ -test) and the call de-



**Figure 7.** Measurements of temporal response characteristics to visual leopard and chimpanzee models. Box plots indicate medians, inter-quartiles and ranges, including outliers (1.5 box length above box) and extremes (>3 box length above box). (A) Number of phrases/RS, (B) number of snorts, (C) calling duration (s), (D) total number of phrases, (E) total number of RS (Hz) and (F) call delivery rate (phrases/s).

livery rate ( $U = 54$ , exact  $p$ -value = 0.432, Mann–Whitney  $U$ -test) were similar between predator types, as were the number of roaring phrases per sequence ( $U = 60$ , exact  $p$ -value = 0.659, Mann–Whitney  $U$ -test; Figure 7).

## Discussion

When hearing a leopard, the Guerezas at Sonso responded reliably with approach. If the predator was an eagle, the monkeys were more reluctant to do so and if movement occurred it was always by the adult male approaching the eagle. If the predator was a chimpanzee, the monkeys typically remained motionless. These locomotor responses corresponded well with what has been described in Kaniyo Pabidi where all three main predators are common (Table 1), with one notable difference: whereas the leopard-experienced monkeys of Kaniyo Pabidi were hesitant to start moving after hearing leopard growls, the leopard-naïve monkeys of Sonso consistently approached. The monkeys' vocal behaviour was the same at both sites (Schel et al., 2009;

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Schel, 2009). Stimulus novelty did not explain anything because the monkeys did not vocalise to hyena howls and elephant rumbles, even though both stimuli were loud, conspicuous, and novel to the monkeys, as were the leopard growls in Sonso. Furthermore, at both sites the acoustic structure of vocal responses to leopards and eagles was context-specific, i.e., dependent on the predator type encountered (cf., Schel et al., 2009).

Our preliminary conclusion, therefore, is that experience with leopards is not required for these monkeys to produce predator-specific alarm calling behaviour. Moreover, the fact that naïve monkeys were more likely to approach the leopard, but not other equally unfamiliar loud and conspicuous animal calls, suggests that they recognised leopard growls as a relevant event, requiring further inspection. Approaching and alarm calling, however, are not the default response to any loud, conspicuous and unfamiliar animal sound.

The responses to moving visual leopard models were similar in both populations. At both sites leopards were followed and called at, a perception advertisement strategy that is adaptive to this predator (e.g., Woodland et al., 1980; Zuberbühler et al., 1997, 1999). The significant response differences to leopard and chimpanzee models further support this hypothesis. In response to the control stimulus, equally unfamiliar as the leopard, the monkeys consistently moved away, confirming that the monkeys perceived the leopard stimulus as something that required a specific anti-predator response. Once more, the default response to novel stimuli was not approach and inspection. In further contrast to the leopard model, monkeys never alarm called in the flower sheet control trials. When comparing the acoustic structure of alarm calls to leopards (visual or acoustic models) no differences were found between Sonso and Kaniyo Pabidi. Overall, our results suggest that the Guerezas at Sonso identified leopards as a relevant disturbance. The fact that, from the start, they produced the correct anti-predator behaviour (approach and vigorous calling at close range) suggests that little or no ontogenetic experience is required to develop anti-predator behaviour to leopards.

The monkeys' responses to the chimpanzee model in Sonso are also noteworthy. Although most groups remained cryptic, 9 of 33 males (27%) approached and called. This was different from the generally cryptic response observed when hearing a chimpanzee, as well as from the responses to visual and acoustic chimpanzee stimuli in Kaniyo Pabidi (Table 1). It is possible that the Guerezas at Sonso perceive single, visible, chimpanzees as less

dangerous, and that some males are prepared to signal aggressive intent and readiness to fight. Comparisons with the monkeys' responses to the control stimulus, which never triggered any vocalizations, suggest that the monkeys readily discriminated between the two disturbances. At Sonso, the monkeys have been observed to fight and chase away chimpanzees from their trees while producing their impressive roars, suggesting that our experiments modelled a natural situation. If a male alarm called to a moving chimpanzee model (response rate: 9 of 33 trials), then his vocal behaviour did not differ from that given to a leopard (response rate: 20 of 24 trials), in both acoustic and temporal terms, apart from the fact that responses to leopards were longer and contained more snorts than those to chimpanzees. It is not very likely that these features are sufficient to encode anything about predator type encountered by the caller. Although the Sonso monkeys discriminated leopards from chimpanzees (as judged by the different vocal response rates and locomotor responses), the calling patterns given to them were the same, suggesting that the roaring sequences refer to having spotted a ground predator (that can be repelled with alarm calls). Whether or not Guereza monkeys are able to vocally discriminate between the two ground predators could be addressed with the monkeys at Kaniyo Pabidi, experienced with both chimpanzees and leopards (see Stephan & Zuberbühler, 2008, for a similar example with Diana monkeys).

### *The role of predator experience*

Vocal response rates to leopards were high and largely identical at Sonso and Kaniyo Pabidi, suggesting that both populations recognised leopard growls as something dangerous. The main difference between the two sites was in terms of the high rates of approaching behaviour at Sonso, indicating that the callers were keen to obtain additional information, something that was not normally seen in the leopard-experienced monkeys at Kaniyo Pabidi. Strikingly, visual leopard models led to equally strong anti-predator behaviour at both sites, supporting the hypothesis that predator recognition in the visual domain is less experience-dependent than in the acoustic domain (Blumstein et al., 2000, 2008). Our findings correspond with previous studies investigating the perceptual mechanisms involved in leopard recognition, which found that predator naïve monkeys recognized visual leopard cues without prior experience (Coss & Ramakrishnan, 2000; Coss et al., 2005). However, in these

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studies, the same study subjects could not recognize hetero-specific leopard alarm calls produced by sympatric monkey species living in areas where leopards occur, probably because of their lack of experience with these calls and the predatory events related to them (Ramakrishnan & Coss, 2000).

Leopard predation is an important force of natural selection, which has shaped the vocal and cognitive abilities of primates (Zuberbühler & Jenny, 2002). Guereza monkeys appear to be endowed with the capacity to recognize direct signs of leopard presence without much prior experience. Although we did not specifically test this, other studies suggest that the recognition of indirect signs, such as heterospecific alarm calls, requires learning (Ramakrishnan & Coss, 2000; Zuberbühler, 2000b). In our study, leopards were recognised both in the visual and acoustic domain. In other studies with predator-naïve populations, the typical finding is that recognition is better in the visual than in the acoustic domain (Blumstein et al., 2000). This is explained by the fact that, over evolutionary time, the basic visual characteristics of a predator class (e.g., felid body shape or eye positioning) change less rapidly than their vocalizations (Blumstein et al., 2000). Support for this hypothesis comes from a recent study, which showed that predator-naïve pigtail langurs were unable to recognize vocalizations of different felid predators (Yorzinski & Ziegler, 2007). However, the population under study had been isolated from felid predators for more than 0.5 million years, long enough for significant evolutionary changes to take place (Coss, 1999). The Guerezas at Sonso have been isolated from leopards for as little as 45 years, longer than an individual's lifespan but too short for significant genetic changes to take place. In other species, such short time periods have led to the loss of adaptive anti-predator behaviours, indicating the role of experience (Berger et al., 2001; Laundré et al., 2001; Gil-da-Costa et al., 2003; reviewed in Blumstein et al., 2000, 2004). In our study, the leopard-naïve Guerezas responded appropriately to visual models and generally responded to acoustic models as if they understood the significance of the event. However, callers were still keen to obtain additional information when hearing leopard growls, suggesting that some learning is required despite being endowed with an innate capacity to recognise leopards as a relevant predator.

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