

## Predator-detering alarm call sequences in Guereza colobus monkeys are meaningful to conspecifics

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Guereza colobus monkeys, *Colobus guereza*, produce acoustically conspicuous vocalizations, the roars, in response to their main predators, leopards, *Panthera pardus*, and crowned eagles, *Stephanoaetus coronatus*. Roaring alarm utterances generally consist of the same basic call types but differ in overall structural composition. Leopards trigger roaring alarms containing many roaring sequences of only a few calls each, while eagles trigger few sequences with many calls each. To investigate whether conspecifics extract meaning from these structural differences, we played back leopard and eagle alarm call sequences and compared the monkeys' responses in terms of their locomotor, gaze and vocal behaviour with their responses to the corresponding predator vocalizations. Locomotor responses did not differ between playback conditions; movement was always towards the simulated caller with no clear patterns in the vertical plane. Gaze direction, however, was highly predator specific. When hearing leopard-related stimuli, monkeys were significantly more likely to scan the area beneath them than when hearing eagle-related stimuli, which caused more scanning above. Vocal response rates to conspecific alarms were generally low but comparable with rates to the corresponding predators. If monkeys called, however, they produced the matching call sequences. Overall, our results showed that Guerezas discriminated between predator alarm call sequences produced by unfamiliar conspecifics and responded to them in predator-specific ways. Since the sequences were composed of the same basic call types, we concluded that the monkeys attended to the compositional aspects of these utterances.

One view in animal communication studies is that the vocalizations produced during predator encounters merely reflect location, identity, sex, body size or internal state of the caller, but nothing about the experienced event (e.g. Morton 1977; Owren & Rendall 2001). Yet, a number of studies have challenged this stance by showing that alarm calling in primates and other animal species can be the product of more complicated cognitive processing, sometimes as part of specific biological functions such as conspecific warning or predator deterrence (e.g. Seyfarth et al. 1980; Woodland et al. 1980; Zuberbühler et al. 1997, 1999; Manser et al. 2002; Zuberbühler 2003, 2009).

Conspecific warning has been observed in different degrees of contextual specificity. Some prey species respond with distinct alarm calls to the behaviour of the predator, such as the speed of its approach (Griesser 2008). As a consequence, identical signals can be produced in response to a variety of predators, allowing

recipients to make inferences about the degree of danger and urgency of response (Robinson 1980; Macedonia & Evans 1993; Blumstein 1995). In contrast, some other species, such as East African vervet monkeys, *Cercopithecus aethiops*, produce discrete alarm calls to distinct predator types. Here, recipients can infer the predator category from the calls alone even in the predator's physical absence (e.g. Seyfarth et al. 1980; Cheney & Seyfarth 1990; Macedonia 1990; Marler et al. 1992; Zuberbühler et al. 1997; Zuberbühler 2000a, b, 2001; Fichtel & Kappeler 2002; Manser et al. 2002; Seyfarth & Cheney 2003; Kirchhof & Hammerschmidt 2006). Such observations are interesting from an evolutionary perspective because of the parallels with symbolic reference in human language (e.g. Seyfarth et al. 1980; Macedonia & Evans 1993).

However, the debate about referential signals in animal communication is far from settled. An alternative explanation is that such findings are the result of receiver biases, caused by the mere acoustic characteristics of a signal, not by any mental representations or memories associated with them (e.g. Morton 1977; Fichtel et al. 2001; Owren & Rendall 2001; Rendall 2003). An extreme version of this position is that receivers are mere

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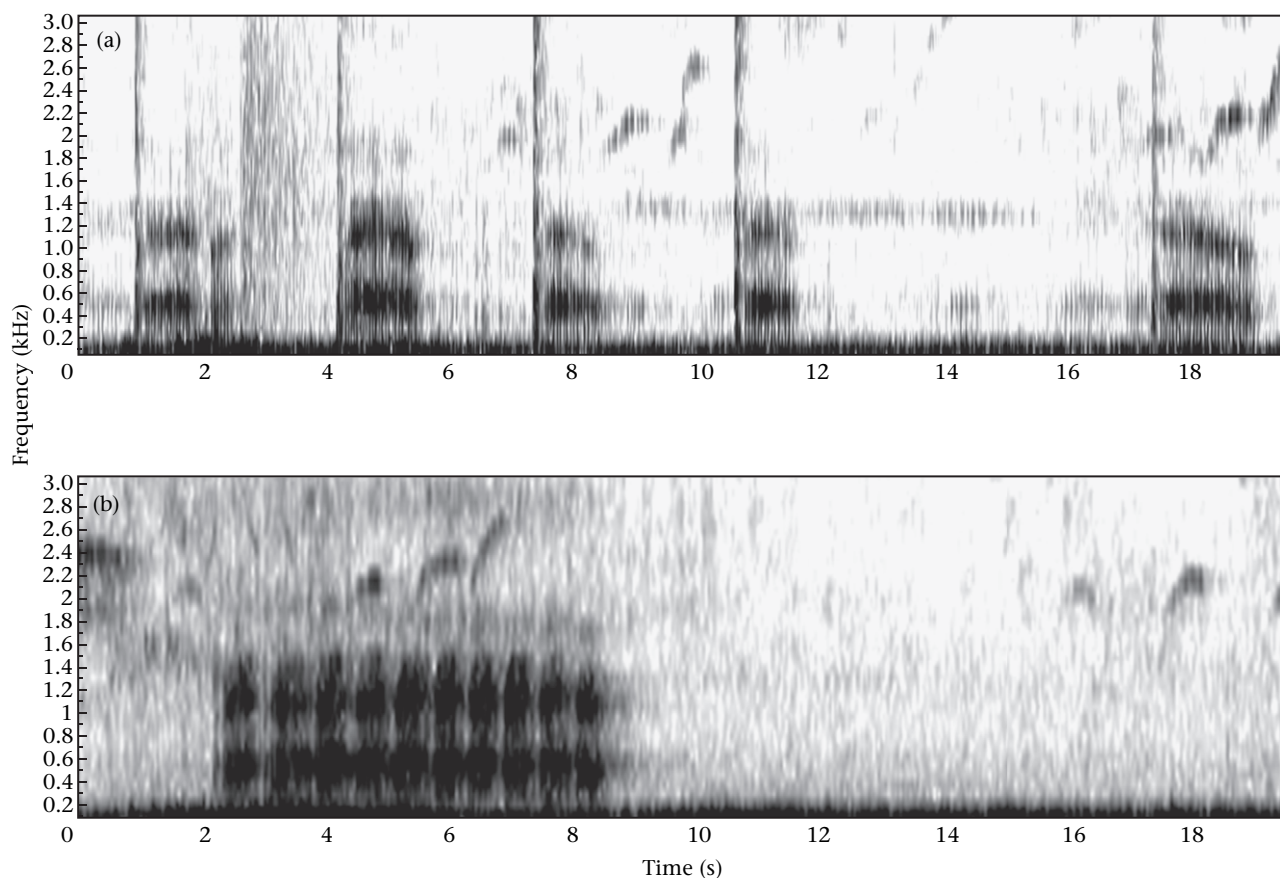
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automatons whose responses can be triggered by specific physical stimuli. A less extreme version is that different acoustic morphologies have different effects on the psychology of the receivers, and that calls merely induce different degrees of arousal rather than mental representations of the event usually associated with the different calls (Rendall et al. 2009). Another point is that conspecific warning may not be the evolved function of alarm calls, and that signallers may be targeting the predator, while conspecifics are mere eavesdroppers of such interactions (e.g. Zuberbühler et al. 1999). In this view, the form and patterning of alarm signals are determined by the sensory bias of the predator, regardless of conspecific receivers (e.g. Marler 1965, 1967; Rundus et al. 2007). Under this hypothesis, signals are arbitrary for conspecifics in terms of their morphology, although receivers can form associations with specific contexts, that is, they can become meaningful to them. This is especially well illustrated by various cases of interspecies communication. For instance, African hornbills, such as *Cerato-gymna elata* or *C. atrata*, are capable of discriminating the alarm calls of Diana monkeys, *Cercopithecus diana*, to crowned eagles, *Stephanoaetus coronatus*, and leopards, *Panthera pardus*, even though monkeys clearly have no intention of informing them (Rainey et al. 2004a, b).

Much of the current literature on alarm calling in primates is based on research with Cercopithecines (Zuberbühler 2009), while the alarm call behaviour of the other major group of Old World monkeys, the Colobines, has not received much attention. This is surprising because the vocal behaviour of some colobine monkeys is particularly remarkable and has been a major research focus for other reasons (e.g. Hill & Booth 1957; Davies & Oates 1994; Oates

et al. 2000; *Colobus guereza*: Marler 1969, 1972; Gautier & Gautier 1977; Oates & Trocco 1983; *Colobus angolensis*: Groves 1973; Walek 1978). In recent studies, we have shown that black-and-white colobus monkeys in both East (*Colobus guereza*) and West (*Colobus polykomos*) Africa produced vocal alarms ('roaring') to two of their major predators, leopards and crowned eagles. In response to chimpanzees, *Pan troglodytes*, another serious predator in many parts of Africa, black-and-white colobus monkeys usually remain vocally and visually inconspicuous (Schel & Zuberbühler 2009). Predator roars consist of a variable number of roaring sequences, which are composed of acoustically uniform call units, the roaring phrases. To leopards, individual sequences are generally short, while to crowned eagles they are significantly longer, suggesting that callers potentially convey information about the predatory event at the level of the sequence, rather than at the level of individual calls (Fig. 1).

In Guereza colobus monkeys (further called Guerezas), alarm calling is usually performed by the single adult male of the group, although, occasionally, other animals join in, presumably the caller's subadult sons. In general, however, monkeys are reluctant to respond with alarm calls to predator models, although other forms of antipredator behaviour occur in age-, sex- and predator-specific ways (see Schel & Zuberbühler 2009 for locomotor data in the Kaniyo Pabidi Guereza population in Uganda). In response to acoustic leopard models, adult males usually approach while moving up and down in the vertical plane. Other group members typically move higher up or they remain seated, although sometimes the male is accompanied in his approach by other group members. In response to acoustic eagle models, the males also



**Figure 1.** Spectrographic representation of the vocal responses of (a) a Guereza male responding to a leopard model with an utterance consisting of five snort-introduced short roaring sequences, and (b) a Guereza male responding to an eagle model with an utterance consisting of one non-snort-introduced long roaring sequence.

approach but mainly move upwards in the canopy, again sometimes accompanied by one or more individuals, while other group members typically move down into dense cover or they remain seated.

To test whether the alarm call sequences of Guerezas are meaningful to conspecifics and inform them about predator type, we played back Guerezas' leopard and eagle alarm sequences, originally recorded at the Sonso study area of Budongo Forest Reserve, Uganda, to naïve monkey groups. We compared their responses with those to the corresponding predators, simulated by playbacks of leopard growls and crowned eagle shrieks. Following the protocol of a previous study (Schel & Zuberbühler 2009), we recorded the Guerezas' horizontal locomotor and vocal antipredator responses, which we expected to be adaptive to the predator type for which the alarms are normally produced. Yet, because horizontal locomotor responses of the adult males are largely identical to both predators and because of the different antipredator strategies of the two sexes, we decided to add vertical locomotor responses and the direction of gaze as additional variables. Vertical movements and gaze have traditionally been used in experimental primate field studies as a measure of call discrimination (Seyfarth et al. 1980; Fichtel & Kappeler 2002; Fichtel 2004; Kirchhoff & Hammerschmidt 2006). In our case, we assumed that initial gaze responses were consistent across all group members, irrespective of age/sex class, as the different hunting behaviours of eagles and leopards are likely to generate different expectations in the monkeys (cf. Macedonia & Evans 1993). We expected that eagle-related stimuli would trigger a higher proportion of upward gazes than leopard-related stimuli, and vice versa, in line with the predators' most likely direction of attack. We scored the monkeys' locomotor responses in the vertical plane as an additional measure of their expectations (see Schel & Zuberbühler 2009).

## METHODS

### *Study Sites and Subjects*

Data were collected at the Sonso study site of Budongo Forest Reserve, Uganda (01°42'–01°44'N, 31°31'–31°33'E), in the vicinity of the Budongo Conservation Field Station. We mainly operated within the grid system of the study site, an approximately 9 km<sup>2</sup> area of secondary tropical moist semideciduous rainforest. We occasionally visited areas outside the grid system by following an old logging road or smaller forest transects. Guerezas are highly arboreal medium-sized colobine monkeys, living in groups generally consisting of 8–10 individuals, including one adult male, approximately four adult females, and their subadult, juvenile and infant offspring (Marler 1969; Davies & Oates 1994).

Monkey predators at Sonso include chimpanzees and crowned eagles, but not leopards, which became locally extinct a few decades ago. In previous work we have shown that, despite having no experience with leopards, the Guerezas at Sonso show appropriate antipredator behaviour to leopards, indistinguishable from a neighbouring population that continues to be exposed to leopards (Schel & Zuberbühler 2009).

Between 2005 and 2009, we conducted playback experiments with predator vocalizations and conspecific alarm calls. In 2005, we conducted 26 trials with leopard growls and 17 trials with eagle shrieks, allowing us to record the Guerezas' horizontal locomotor and vocal responses (reported in Schel & Zuberbühler 2009). In 2008 (September–December: A.C.), we additionally filmed the monkeys' vertical locomotor behaviour and gaze directions in response to these stimuli, by targeting groups that had not been tested before. Finally, in 2009 (March–May: A.S.) we collected further data on locomotor and vocal behaviour, but not on gaze

directions. In 2007 (March–September: A.S.) and 2008 (September–December: A.C.), we tested a large number of Guereza groups on their responses to their own alarm calls, focusing on vocal behaviour in 2007 and also on horizontal and vertical locomotor behaviour and gaze direction in 2008. We adhered to a minimum distance criterion of 200 m between trials conducted in the two successive study periods (see below) to keep trials independent from each other.

### *The Minimum Distance Method*

Group densities in Sonso are very high, reaching 6–10 Guereza groups per square kilometre (Plumptre & Reynolds 1994; Plumptre 2000). At the start of our studies in 2005, we systematically mapped all groups encountered. Separate groups, consisting of an adult male and several females with their offspring, could be found as close as 150–200 m apart from each other (A. M. Schel, unpublished data). In line with previous density estimates (Plumptre 2000), we discriminated approximately 60 different Guereza groups in the entire study area (equivalent to about 500–1000 individuals; Marler 1972). In 2008 and 2009, we chose a minimum distance of 200 m from any of the previous 2005 and 2007 test locations. The minimum distance method is a standard procedure that has been used successfully by many other playback studies with unhabituated groups of unknown home ranges (e.g. Zuberbühler et al. 1997). Furthermore, within a specific year (i.e. 2005, 2007, 2008 and 2009), we kept a distance of at least 750 m between adjacent trials conducted on the same day, since some of our stimuli could carry over considerable distances through the forest. On consecutive test days with one particular stimulus type (e.g. leopard growls), we only tested groups that inhabited a different part of the forest relative to the ones tested the day before. These precautions ensured that only a very small fraction of the 500–1000 tested individuals could have heard a particular playback stimulus more than once (for instance young males that migrated to another group). Although the number of potentially affected individuals was very small, the more crucial point is that it is very unlikely that such single experiences will have lasting effects over a period of one to several years, especially considering the large number of predator-related sounds monkeys are exposed to on a daily basis in tropical forest habitats. We therefore concluded that trials conducted across the different study periods could be treated as independent events.

### *Terminology of Vocal Responses*

As mentioned, male Guerezas produce loud and low-pitched vocalizations, 'roaring', in response to predators and as part of spontaneous dawn choruses (Marler 1972; Oates & Trocco 1983; Oates et al. 2000; Schel et al. 2009). Roaring responses consist of either a large or small number of roaring sequences, which are composed of either 'few' or 'many' individual call units, the roaring phrases. The acoustic energy of roaring phrases is concentrated in two discrete frequency bands around 600 and 1300 Hz, representing two formant frequencies (Harris et al. 2006). The first roaring phrase in a sequence can be preceded by one or more snorts, which consist of broadband acoustic energy with a sudden onset, ranging in frequency up to about 4 kHz with the main frequency at around 1 kHz. As described before, the roaring sequences vary in the number of roaring phrases they consist of between predator types (Schel et al. 2009; Schel & Zuberbühler 2009; Fig. 1), whereas acoustic structures of individual roaring phrases are very similar (Schel et al. 2009; Schel & Zuberbühler 2009).

### Experimental Protocol

We systematically searched for Guereza groups throughout the study area, usually by looking for their conspicuous tail tufts or by hearing their soft intragroup vocalizations. When found, we determined their geographical location using a Garmin GPS 76 and a detailed map to ensure that the group had not been tested before (see minimum distance method described earlier). We then monitored the monkeys' vocal behaviour for at least 15 min to ensure they were unaware of our presence. A trial was conducted only if during this period (1) no other animal in the group's surroundings had produced any alarm calls, (2) no predator vocalizations were heard, (3) no predator was seen, (4) the monkeys were unaware of the observers and playback equipment, and (5) no other humans were present in the experimental area. Using Leica Trinovid 10 × 42 binoculars, we determined the sex of all clearly visible focal individuals during each trial, which was possible in about 70% of trials.

### Presentation of playback stimuli

Playback stimuli of leopard growls were edited from a master recording from the British Library of Wildlife Sounds, London (African leopard; BBC master tape number MM 35 © South African Broadcasting Corporation). Eagle shrieks were recorded by K.Z. in the Tai Forest, Ivory Coast, with a Sony Professional Walkman WMD6C and Sennheiser 70 mm microphone (K3U + ME88). We edited playback stimuli of conspecific alarms from original recordings of Guerezas giving alarm calls to leopard growls and eagle shrieks (Fig. 1). All playback stimuli were edited such that they consisted of 5 min of silence followed by approximately 15 s of vocalizations (three different recordings of eagle shrieks, six different recordings of leopard growls, four different recordings of conspecific leopard alarms and four different recordings of conspecific eagle alarms). Methodologically, it would have been ideal to use a unique playback stimulus for every trial, but given the large number of groups tested in this study, this was simply not feasible. Obtaining high-quality recordings from free-ranging crowned eagles, leopards and Guerezas is not a trivial task (see Schel & Zuberbühler 2009; Schel et al. 2009), so that we opted for the next best strategy, that is, to use a smaller number of high-quality recordings that could be used for several groups. For each stimulus type, we were able to use at least three different recordings, which we used to test the different groups in random ways.

In 2005 and 2007, we broadcast all playback stimuli with an Apple iPod Nano mp3 player connected to a Nagra DSM speaker-amplifier. In 2008 and 2009, we broadcast the playback stimuli with an Archos Gmini XS100 mp3 player connected to a Kenwood KAC-52-03 amplifier and a Bose 151 speaker. All playback stimuli were uncompressed. We adjusted the amplitude of the playback stimuli so that they were all broadcast within their natural amplitude range (eagle shrieks within 80–100 dB, leopard growls within 70–90 dB and conspecific playbacks within 60–70 dB). Stimulus amplitude was calibrated with a Radioshack Sound Pressure Level Meter at 1 m from the source in the natural environment. The playback equipment was placed at a distance of ca. 25–40 m from the group, outside their visual range. All stimuli were played back from beneath the monkeys' location in the trees (i.e. either from the ground or from a height of 0–15 m, with the speaker hanging from a branch).

### Locomotor behaviour

In the horizontal plane, we scored whether any of the focal animals moved at least 5 m away from, or closer to, the speaker. In the vertical plane, we scored whether the monkeys moved at least 1 m upwards or downwards from their initial position. These

observations were made with a pair of Leica Trinovid 10 × 42 binoculars and, if conditions allowed, a Panasonic NV-GS17 video recorder with 24× optical/800× digital zoom. Our previous observations had revealed that females showed a more differentiated locomotor response than males (see also Schel & Zuberbühler 2009), suggesting that it would have been appropriate to conduct comparisons within the sexes. As mentioned earlier, however, it was not always possible to identify the sex of the focal individual, but this made it simply more difficult to reject the null hypothesis (no locomotor differences). Statistical comparisons were made with two-tailed Fisher's exact tests, using a Bonferroni-corrected significance level of  $\alpha = 0.025$  (Siegel & Castellan 1988).

### Gaze orientation

We aimed to film one individual of each focal group 1 min before and at least 1 min after playback to determine its vertical gaze orientation to the different stimuli. Video clips were transferred onto a laptop using Windows Movie Maker software. We conducted a frame-by-frame analysis to determine the direction of the first and second look in the vertical plane following each playback. The second look was relevant because it was likely to reveal something about the monkey's expectation after being surprised by alarm calls. Looking directions were separated into 'downwards' and 'upwards' relative to the monkey's horizontal gaze. We could think of no a priori reason to assume sex differences in this variable. As post hoc scoring of video material can be ambiguous, we performed interobserver reliability tests, which generated high Cohen's kappa coefficients (first and second look: 0.80 and 0.92, respectively; Cohen 1960). Comparisons were made with two-tailed Fisher's exact tests, using a Bonferroni-corrected significance level of  $\alpha = 0.025$  (Siegel & Castellan 1988).

### Vocal responses

Vocal responses to the playback stimuli were recorded 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, Scottsdale, AZ, U.S.A.). Acoustic analyses were performed with Raven 1.2 (Cornell Laboratory of Ornithology, Ithaca, New York) and Praat 4.3.12 (Boersma & Weenink 2005). If more than one individual called in response to the stimulus (e.g. the adolescent son of the adult male), we used the vocal response of the individual that called first for subsequent analyses. To allow for comparisons with previous studies (Schel et al. 2009; Schel & Zuberbühler 2009), we measured the following temporal variables: (1) total duration of the vocal response (s); (2) total number of roaring sequences; (3) total number of roaring phrases; (4) mean number of roaring phrases per roaring sequence; (5) number of snorts; and (6) call rate (phrases/s). The following spectral variables were measured for individual roaring phrases: (1) phrase duration (ms); (2) number of combined pulses per phrase; (3) fundamental frequency (Hz); (4) harmonics to noise ratio (dB); (5) first formant (Hz); (6) second formant (Hz); and (7) peak frequency (Hz). If possible, we conducted all spectral analyses on the first and last phrases of the first two roaring sequences (i.e. four roaring phrases per vocal response). We used two-tailed Wilcoxon signed-ranks tests to compare the spectral characteristics of first and last roaring phrases produced within roaring sequences. For the comparison of spectral and temporal parameters between the predator alarm contexts and between alarm contexts and predator vocalization contexts we used two-tailed Mann-Whitney *U* tests. For all comparisons we used a Bonferroni-corrected critical significance level of  $\alpha = 0.017$  (Siegel & Castellan 1988). Apart from the roaring sequences, we also collected data on other calls produced, especially grunts, tongue-clicks and snorts (Marler 1972; Oates 1977).

## RESULTS

Between 2005 and 2009, we tested 66 different Guereza groups with playbacks of leopard growls and 53 different groups with playbacks of eagle shrieks. The full data set was used to determine the monkeys' locomotor responses in the horizontal domain, although seven leopard and four eagle trials had to be excluded owing to poor visibility. Data on vertical movements were collected in 2008–2009, yielding a final data set of 37 trials for leopard growls and 33 for eagle shrieks, after excluding three leopard and three eagle trials owing to poor visibility. Orienting and gaze responses were collected in 2008, with a final data set of 14 for leopard growls and 13 for eagle shrieks, after excluding three leopard and seven eagle trials owing to poor visibility. Vocal responses to the two predator types were rare (2005:  $N = 11$  groups to leopard growls;  $N = 12$  groups to eagle shrieks; 2008:  $N = 5$  groups to leopard growls;  $N = 1$  group to eagle shrieks). The vocal recordings of the 2009 data set ( $N = 6$  leopard and  $N = 2$  eagle responses) had to be excluded from acoustic analyses owing to a technical problem, yielding a final data set of 16 vocal responses to leopard growls and 13 to eagle shrieks for acoustic analyses.

Between 2007 and 2008, we also conducted 45 valid trials using leopard alarm sequences and 51 valid trials using eagle alarm sequences to determine the Guerezas' responses to their own alarm vocalizations. Data on vocal responses were collected in both 2007 and 2008 ( $N = 11$  vocal responses to leopard alarms and  $N = 5$  vocal responses to eagle shrieks). Data on locomotor behaviour and gaze direction, however, were only collected in 2008, leading to a final data set of 18 responses to leopard alarms and 18 to eagle alarms, after excluding one eagle trial owing to poor visibility. Table 1 summarizes the composition of the full data set.

### Locomotor Responses

After hearing both types of leopard-related stimuli (L growls or L alarms), the focal individuals either remained seated or approached the stimuli in the horizontal plane (binomial test: L growls:  $N_{\text{Move}} = 37$ ,  $N_{\text{Not move}} = 22$ ,  $P = 0.067$ ;  $N_{\text{Further}} = 6$ ,  $N_{\text{Closer}} = 31$ ,  $P = 0.001$ ; L alarms:  $N_{\text{Move}} = 9$ ,  $N_{\text{Not move}} = 9$ , exact  $P = 1.000$ ;  $N_{\text{Further}} = 0$ ,  $N_{\text{Closer}} = 9$ ,  $P = 0.004$ ). In the vertical plane, they either remained seated or they moved up or down (binomial test: L growls:  $N_{\text{Move}} = 22$ ,  $N_{\text{Not move}} = 15$ , exact  $P = 0.405$ ;  $N_{\text{Up}} = 16$ ,  $N_{\text{Down}} = 6$ ,  $P = 0.052$ ; L alarms:  $N_{\text{Move}} = 12$ ,  $N_{\text{Not move}} = 5$ ,  $P = 0.143$ ;  $N_{\text{Up}} = 7$ ,  $N_{\text{Down}} = 5$ ,  $P = 0.774$ ; Table 1, Fig. 2).

**Table 1**

Overview of results of all playback experiments

Year	Stimulus	N	Call	Orient	Approach	Retreat	0	Move up	Move down	0	1st Gaze up	1st Gaze down	2nd Gaze up	2nd Gaze down
2005	L growl	26	11/26	—	15/22	2/22	5/22	—	—	—	—	—	—	—
2008	L growl	17	5/17	15/17	8/15	0/15	7/15	7/15	2/15	6/15	2/14	12/14	1/12	11/12
2009	L growl	23	6/23	—	8/22	4/22	10/22	9/22	4/22	9/22	—	—	—	—
Overall	L growl	66	0.324	0.882	0.525	0.09	0.383	0.438	0.157	0.405	0.143	0.857	0.083	0.917
2005	E shriek	17	12/17	—	10/15	0/15	5/15	—	—	—	—	—	—	—
2008	E shriek	20	1/20	17/20	5/19	0/19	14/19	3/18	3/18	12/18	7/13	6/13	9/13	4/13
2009	E shriek	16	2/16	—	3/15	0/15	12/15	3/15	10/15	2/15	—	—	—	—
Overall	E shriek	53	0.294	0.850	0.367	0.000	0.623	0.183	0.416	0.400	0.538	0.462	0.692	0.308
2007	L alarms	27	6/27	—	—	—	—	—	—	—	—	—	—	—
2008	L alarms	18	5/18	15/18	9/18	0/18	9/18	7/17	5/17	5/17	3/12	9/12	3/12	9/12
Overall	L alarms	45	0.249	0.833	0.500	0.000	0.500	0.412	0.294	0.294	0.250	0.750	0.250	0.750
2007	E alarms	32	3/32	—	—	—	—	—	—	—	—	—	—	—
2008	E alarms	19	2/19	19/19	8/18	0/18	10/18	4/13	1/13	8/13	11/14	3/14	9/14	5/14
Overall	E alarms	51	0.099	1.000	0.444	0.000	0.556	0.308	0.077	0.615	0.786	0.214	0.643	0.357

L: leopard; E: eagle. 0: no movement in horizontal or vertical plane.

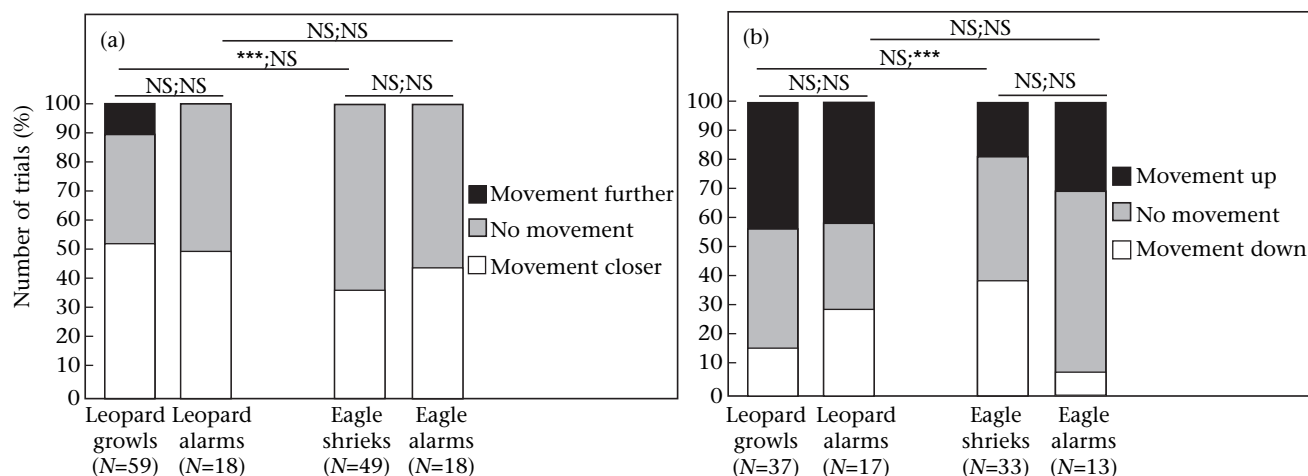
After hearing both types of eagle-related stimuli (E shrieks or E alarms), the focal individuals either remained seated or they approached the stimulus in the horizontal plane (binomial test: E shrieks:  $N_{\text{Move}} = 18$ ,  $N_{\text{Not move}} = 31$ , exact  $P = 0.085$ ;  $N_{\text{Further}} = 0$ ,  $N_{\text{Closer}} = 18$ ,  $P = 0.001$ ; E alarms:  $N_{\text{Move}} = 8$ ,  $N_{\text{Not move}} = 10$ ,  $P = 0.815$ ;  $N_{\text{Further}} = 0$ ,  $N_{\text{Closer}} = 8$ ,  $P = 0.008$ ). In the vertical plane, the monkeys either remained seated or they moved up or down (binomial test: E shrieks:  $N_{\text{Move}} = 19$ ,  $N_{\text{Not move}} = 14$ , exact  $P = 0.487$ ;  $N_{\text{Up}} = 6$ ,  $N_{\text{Down}} = 13$ ,  $P = 0.167$ ; E alarms:  $N_{\text{Move}} = 5$ ,  $N_{\text{Not move}} = 8$ ,  $P = 1.000$ ;  $N_{\text{Up}} = 4$ ,  $N_{\text{Down}} = 1$ ,  $P = 0.375$ ; Table 1, Fig. 2).

Comparing the Guerezas' locomotor responses to conspecific alarms with those to the corresponding predators revealed no significant differences, implying that the response patterns were largely identical (all  $P$  values  $> 0.122$ ; Table 1, Fig. 2). However, across predator conditions, Guerezas were more likely to start approaching leopard growls than eagle shrieks (Fisher's exact test, two-tailed:  $P = 0.012$ ) and moved more often down in response to eagle shrieks than leopard growls (Fisher's exact test, two-tailed:  $P = 0.013$ ), something that was not observed as strongly in response to the conspecific alarm trials (Table 1, Fig. 2).

### Gaze Orientation

In response to both types of leopard-related stimuli, the focal individuals usually turned their head in the horizontal plane towards the speaker (binomial test: L growls: 15/17 trials, 88.2%,  $P = 0.002$ ; L alarms: 15/18 trials, 83.3%,  $P = 0.008$ ). We were able to determine the first vertical gaze direction of at least one individual in 14/17 trials with leopard growls and in 12/18 trials with leopard alarms, and the second vertical gaze in 12/17 trials with leopard growls and in 12/18 trials with leopard alarms. In both contexts, the first and second gazes were usually downwards (binomial test: 1st gaze L growls: downwards: 12/14 trials, 85.7%; upwards: 2/14 trials, 14.3%,  $P = 0.013$ ; 1st gaze L alarms: downwards: 9/12 trials, 75.0%; upwards: 3/12 trials, 25.0%, exact  $P = 0.146$ ; 2nd gaze L growls: downwards: 11/12 trials, 91.7%; upwards: 1/12 trials, 8.3%, exact  $P = 0.006$ ; L alarms: downwards: 9/12 trials, 75.0%; upwards: 3/12 trials, 25%, exact  $P = 0.146$ ; Table 1, Fig. 3).

In response to eagle-related stimuli, the focal individuals usually turned their head in the horizontal direction towards the speaker (binomial test: E shrieks: 17/20 trials, 85.0%,  $P = 0.003$ ; E alarms: 19/19 trials, 100%,  $P = 0.001$ ). We were able to determine both the first and second vertical gaze directions of at least one individual in 13/20 trials with eagle shrieks and in 14/19 trials with eagle alarms. In response to eagle shrieks, the monkeys' first gaze was upwards in 7/13 trials (53.8%) and downwards in 6/13 trials (46.2%; binomial test:



**Figure 2.** Locomotor responses in the (a) horizontal and (b) vertical plane to the different playback 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. \*\*\* $P < 0.001$  (Fisher's exact tests, two tailed).

exact  $P = 1.000$ ), whereas their second gaze was upwards in 9/13 trials (69.2%) and downwards in 4/13 trials (30.8%; binomial test: exact  $P = 0.267$ ; Table 1, Fig. 3). In response to eagle alarms, the monkeys' first gaze was upwards in 11/14 trials (78.6%) and downwards in 3/14 trials (21.4%; binomial test: exact  $P = 0.057$ ), and their second gaze upwards in 9/14 trials (64.3%) and downwards in 5/14 trials (35.7%; binomial test: exact  $P = 0.424$ ; Table 1, Fig. 3).

Comparing the Guerezas' gaze responses to conspecific alarms with those to the corresponding predators revealed no significant differences, implying once more that the response patterns were largely identical (all  $P$  values  $> 0.24$ ; Table 1, Fig. 3). Crucially, across all conditions, monkeys generally looked up in a significantly higher proportion of eagle-related trials compared to leopard-related trials (Fisher's exact test, two-tailed: 1st gaze: L growls versus E shrieks:  $P = 0.046$ ; L alarms versus E alarms:  $P = 0.016$ ; 2nd gaze: L growls versus E shrieks:  $P = 0.004$ ; L alarms versus E alarms:  $P = 0.062$ ; Fig. 3).

### Vocal Responses

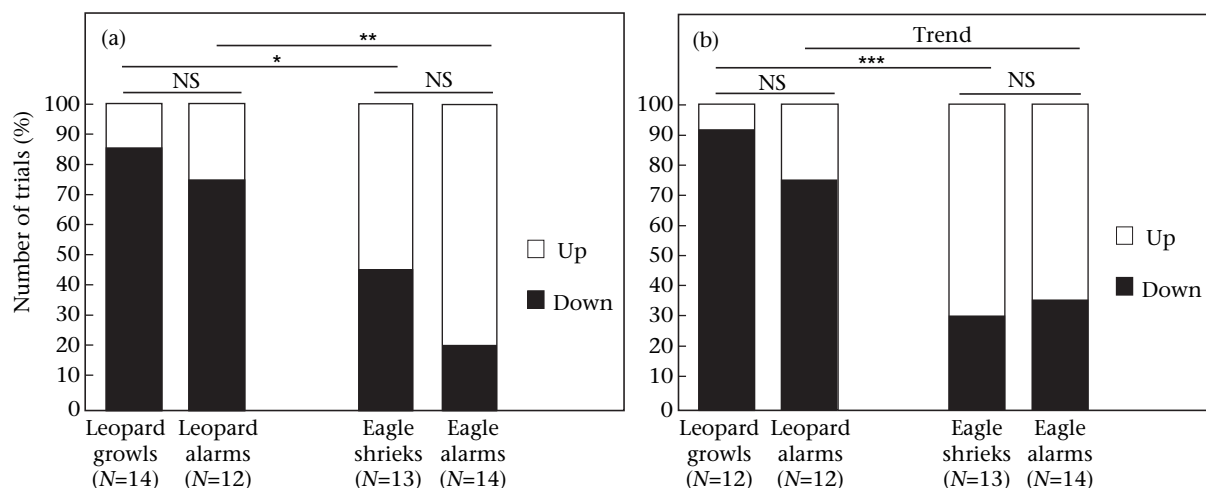
Individuals were reluctant to respond with alarm sequences to all four types of playback stimuli. Response rates to eagle alarm

sequences were lowest (5/51 trials, 9.8%) and significantly different from those to the corresponding predators (15/53 trials, 28.3%; Fisher's exact test, two-tailed:  $P = 0.024$ ). Response rates to leopard alarms were 11/45 trials (24.4%), similar to the response rates to the corresponding predators (22/66 trials, 33.3%; Fisher's exact test, two-tailed:  $P = 0.399$ ; Fig. 4). Grunts, but not tongue-clicks, were produced in 9/51 trials (17.6%) conducted with eagle alarms, and in 8/45 trials (17.8%) conducted with leopard alarms. These proportions were comparable to those in response to actual predator vocalizations (E shrieks: 13.2%,  $N = 7/53$ ; L growls: 9.1%,  $N = 6/66$ ; Fisher's exact tests, two-tailed: L growls versus L alarms:  $P = 0.245$ ; E shrieks versus E alarms:  $P = 0.594$ ).

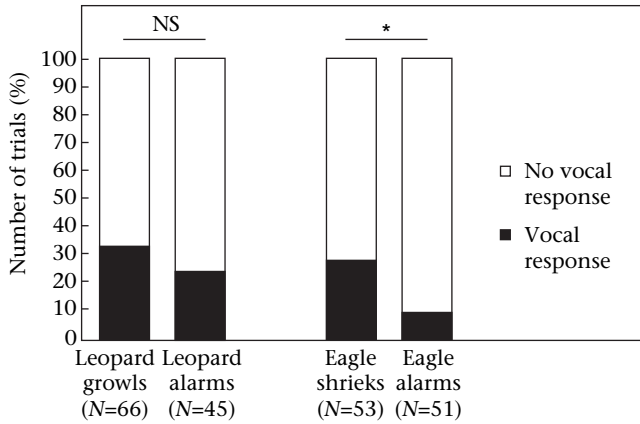
### Acoustic Measurements of Vocal Responses

#### Predator vocalizations

Adding the vocal responses to predator vocalizations collected in 2008 (three leopard responses; two leopard alarms and one eagle alarm recorded in 2008 were discarded owing to background noise) to the 2005 data set (Schel & Zuberbühler 2009) did not change the overall vocal response patterns as described in our earlier reports (Schel et al. 2009; Schel & Zuberbühler 2009). Thus,



**Figure 3.** Gaze direction of the (a) first and (b) second look after playback of the different stimuli. Asterisks refer to the significance of differences between contexts. Trend:  $P < 0.08$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$  (Fisher's exact tests, two tailed).



**Figure 4.** Vocal response rates to the different playback stimuli. Asterisks refer to the significance of differences between contexts. \* $P < 0.05$  (Fisher's exact tests, two tailed).

between the two different predator contexts, there were no consistent spectral differences in roaring phrases produced, but we found consistent differences within predator contexts when comparing the first and last phrases produced in a roaring sequence (Table 2). Furthermore, the structural composition of roars differed significantly between predator contexts, with a large number of short roaring sequences consisting of only a few phrases each produced to leopard growls and a small number of long roaring sequences consisting of many phrases each produced to eagle shrieks (Fig. 1).

#### Conspecific predator alarms

Three of the 11 vocal responses to conspecific leopard alarms only contained snorts, and were discarded from further acoustic analyses. One of the 11 vocal responses to leopard alarms only contained roaring sequences consisting of a snort followed by one roaring phrase. Two of the five vocal responses to conspecific eagle alarms just contained one roaring sequence. Because we were interested in measuring both first and last phrases of the first two roaring sequences for reasons outlined before, our final data set consisted of seven responses to conspecific leopard trials, five containing a first roaring sequence, and three containing a second roaring sequence to conspecific eagle trials.

**Table 2**

Comparison of acoustic measurements of roaring sequences within contexts

Acoustic variable	Leopard growls			Leopard alarms			Eagle shrieks			Eagle alarms		
	FP	LP	<i>P</i>	FP	LP	<i>P</i>	FP	LP	<i>P</i>	FP	LP	<i>P</i>
<b>First roaring sequence</b>												
Phrase duration (ms)	930	274	<b>0.001</b>	1067	281	<b>0.016</b>	757	320	<b>0.001</b>	802	262	0.063
Harmonics to noise ratio (dB)	2.29	2.91	0.090	1.9	2.8	0.250	3.13	2.85	0.820	3.34	2.86	0.625
First formant (Hz)	643	592	0.519	557	584	0.579	659	686	0.465	645	570	0.438
Second formant (Hz)	1401	1510	0.151	1268	1234	0.938	1338	1327	0.413	1236	1249	1.000
Peak frequency (Hz)	524	430	0.226	500	390	0.297	547	522	0.969	576	437	0.125
Number of pulses	17	4	<b>0.002</b>	16	5	<b>0.016</b>	15	6	<b>0.002</b>	13	5	0.063
Fundamental frequency (Hz)	13	16	0.049	15	17	0.047	18	19	0.320	18	18	0.813
<b>Second roaring sequence</b>												
Phrase duration (ms)	898	353	<b>0.001</b>	909	372	<b>0.016</b>	766	417	<b>0.002</b>	934	161	0.250
Harmonics to noise ratio (dB)	3.83	1.68	0.102	2.32	1.19	0.313	2.77	3.7	0.383	4.71	3.1	0.250
First formant (Hz)	597	734	0.206	583	617	0.938	658	727	0.770	589	565	1.000
Second formant (Hz)	1332	1533	0.320	1263	1238	0.469	1422	1445	0.557	1206	1145	0.500
Peak frequency (Hz)	522	471	0.566	537	437	<b>0.016</b>	572	496	0.098	616	597	0.250
Number of pulses	16	6	<b>0.001</b>	13	6	<b>0.016</b>	13	8	<b>0.004</b>	18	3	0.250
Fundamental frequency (Hz)	16	16	0.086	16	18	1.000	18	17	0.301	18	19	1.000

The table shows measurements (medians) and statistical output (exact *P* values) of comparisons between acoustic measurements of first (FP) and last (LP) phrases of the first and second roaring sequences produced within predator and conspecific alarm contexts (Wilcoxon signed-ranks test,  $\alpha = 0.017$ ). Significant *P* values are shown in bold.

**Table 3**

Comparison of acoustic measurements of roaring sequences between contexts

Acoustic variable	LG and ES		LA and EA		LG and LA		ES and EA	
	FP	LP	FP	LP	FP	LP	FP	LP
<b>First roaring sequence</b>								
Phrase duration (ms)	0.288	0.104	0.030	0.639	0.650	0.773	0.743	0.027
Harmonics to noise ratio (dB)	0.960	0.853	0.476	0.886	0.820	0.863	0.613	0.733
First formant (Hz)	0.695	0.379	0.073	0.876	0.142	0.650	0.827	0.267
Second formant (Hz)	0.449	0.288	0.106	0.755	0.028	0.167	0.115	0.320
Peak frequency (Hz)	0.382	0.033	0.500	0.343	0.756	0.695	0.769	0.108
Number of pulses	0.356	0.026	0.116	0.782	0.827	0.670	0.309	0.052
Fundamental frequency (Hz)	<b>0.008</b>	0.065	0.149	0.755	0.270	0.375	0.872	0.601
<b>Second roaring sequence</b>								
Phrase duration (ms)	0.381	0.314	1.000	0.267	0.902	0.592	0.469	0.371
Harmonics to noise ratio (dB)	0.974	0.129	0.262	0.250	0.682	0.913	0.371	0.776
First formant (Hz)	0.107	0.973	0.833	0.833	0.536	0.126	0.077	0.077
Second formant (Hz)	0.456	0.705	0.833	0.183	0.142	0.211	0.161	<b>0.014</b>
Peak frequency (Hz)	0.022	0.709	0.142	0.475	0.821	0.058	0.804	0.773
Number of pulses	0.355	0.173	0.325	0.475	0.950	0.489	0.127	0.605
Fundamental frequency (Hz)	0.080	0.159	0.117	0.367	0.724	0.577	0.373	0.811

The table shows statistical output of comparisons between acoustic measurements of first (FP) and last (LP) phrases of the first and second roaring sequences produced across different experimental contexts (leopard growls (LG), eagle shrieks (ES), leopard alarms (LA) and eagle alarms (EA); Mann–Whitney *U* test,  $\alpha = 0.017$ ). Significant *P* values are shown in bold.

Similar to the responses to predator vocalizations, we found consistent differences in the acoustic structure between the first and last roaring phrases produced within a context. These differences were significant in vocal responses to leopard alarms, and they showed a comparable trend in responses to eagle alarms (Table 2). There were no consistent differences in acoustic characteristics between individual roaring phrases produced to eagle and leopard alarm sequences (Table 3). Apart from this, there were a number of minor differences between calls given in response to actual predator vocalizations and corresponding alarm calls (Table 3).

#### Composition of roaring sequences

A key finding of our previous study was that, in response to their predators, callers produced roars composed of a large number of

roaring sequences containing few phrases each to leopards and roars composed of a small number of roaring sequences containing many phrases each to crowned eagles (Schel et al. 2009). In this study, we found the same pattern in the monkeys' responses to conspecific alarm calls. Responses to other monkeys' leopard alarms were composed of roaring sequences consisting of a few roaring phrases, whereas responses to monkeys' eagle alarms consisted of roaring sequences containing many roaring phrases per sequence (Mann–Whitney  $U$  test, two-tailed:  $U = 2.0$ , exact  $P = 0.003$ ). All other temporal parameters of Guerezas' vocal responses did not differ between alarm contexts (Mann–Whitney  $U$  test, two-tailed: total calling duration:  $U = 20.0$ , exact  $P = 0.572$ ; total number of roaring sequences:  $U = 19.0$ , exact  $P = 0.495$ ; total number of phrases:  $U = 19.0$ , exact  $P = 0.493$ ; call delivery rate:  $U = 10.0$ , exact  $P = 0.074$ ; number of snorts:  $U = 9.5$ , exact  $P = 0.059$ ). In addition, we found no significant statistical differences when comparing the responses to conspecific alarms with responses to predator vocalizations (Mann–Whitney  $U$  test, two-tailed: leopard context: total calling duration:  $U = 21.0$ , exact  $P = 0.052$ ; total number of roaring sequences:  $U = 22.5$ , exact  $P = 0.068$ ; total number of phrases:  $U = 27.0$ , exact  $P = 0.149$ ; number of phrases per roaring sequence:  $U = 41.0$ , exact  $P = 0.780$ ; call delivery rate:  $U = 42.0$ , exact  $P = 0.842$ ; number of snorts:  $U = 20.5$ , exact  $P = 0.046$ ; eagle context: total calling duration:  $U = 22.0$ , exact  $P = 0.583$ ; total number of roaring sequences:  $U = 23.0$ , exact  $P = 0.638$ ; total number of phrases:  $U = 24.0$ , exact  $P = 0.723$ ; number of phrases per roaring sequence:  $U = 21.5$ , exact  $P = 0.526$ ; call delivery rate:  $U = 12.0$ , exact  $P = 0.09$ ; number of snorts:  $U = 15.5$ , exact  $P = 0.163$ ), except for the production of snorts accompanying roaring sequences in the different contexts. Our raw data revealed that 80.0% (4/5 trials) of vocal responses to eagle alarms were accompanied by snorts, something that was not generally observed in response to eagle shrieks (5/12 trials). Snorts were common in response to leopard growls (13/13 trials) and also in response to leopard alarm sequences (10/10 trials).

## DISCUSSION

A key methodological advance in the study of animal communication has been to compare subjects' responses to their own alarm calls with their responses to the corresponding predators (Seyfarth et al. 1980). If the responses are identical, and adaptive in relation to the predator, then this is usually taken as evidence that the calls convey something about the external event encountered by the caller. Gaze orientation is a particularly useful measure in such studies because it reveals something about the subjects' anticipation of the forthcoming event. In our study, individuals confronted with leopard-related stimuli, either leopard growls or conspecific leopard alarm sequences, were more likely to look downwards during their first two looks than individuals confronted with eagle-related trials, which caused more upward gazes. There were some interesting differences in gaze orientation to conspecific eagle alarms and eagle shrieks. To conspecific eagle alarms, the monkeys mainly looked up as a first response, while looking down was only observed in 21.4% of trials, as expected. To eagle shrieks, looking down as a first response was more common (46.2% of trials) but still less than to leopard growls, although both predator vocalizations were broadcast from below. This difference may have to do with the fact that crowned eagles sometimes hunt in pairs, with one eagle flying through the canopy and another flying overhead (Gautier-Hion & Tutin 1988). Hearing one eagle's shrieks may thus be indicative of a second eagle's presence so that scanning both above and below becomes an adaptive strategy.

Guerezas were generally reluctant to respond with alarm calls to any of the playback stimuli, both predator calls and conspecific

alarm call sequences. Yet, if they responded, they did so in a higher proportion of predator vocalization trials than conspecific alarm trials, especially in the eagle context. Furthermore, if the monkeys responded, the vocal responses to alarm sequences were identical to the ones made by monkeys responding to the corresponding predators in all major variables. The only exception concerned the production of a nonvocal signal, the snorts, which were produced more often in response to playbacks of eagle alarms than eagle shrieks.

In terms of general locomotor responses, we did not observe any significant deviation between the monkeys' standard response to the two predators and the corresponding alarm call sequences. It is also relevant that, even though the alarm calls were essentially given by an unfamiliar male intruder, the callers did not show any of their highly conspicuous display behaviour usually observed during intergroup encounters, such as stiff leg posturing, yawning or bouncing around noisily (Marler 1972; Oates 1977). Because their gaze responses differed between conditions, we rejected the idea that males were simply responding to the presence of a conspecific intruder. More likely, the males reacted to the predator information conveyed by the stimuli.

Why do eagle- and leopard-related stimuli cause these differences in alarm sequences? As mentioned earlier, one explanation is that the calls have evolved as (honest) signals to communicate aggressive motivation to the predator (Zahavi 1977; Zuberbühler et al. 1999). Guerezas actively chase away eagles while producing their impressive roars. In visual predator model experiments, they usually approach and follow a leopard while roaring at it until it is out of sight (A. M. Schel, unpublished data). The long eagle alarm sequences could then function as an indicator of fighting ability and aggressive intent (cf. Harris 2006), while the shorter leopard alarm sequences might primarily function in detection advertisement. Additionally, under this hypothesis the somewhat higher response rates to predator vocalizations (compared to conspecific predator alarms) can be explained with the fact that in such cases predator localization has already taken place. In response to conspecific alarms, it may be adaptive for Guerezas to remain silent and to look for additional cues to locate the predator before giving away one's own position during predator deterrence displays (Searcy & Caine 2003). Nevertheless, although the primary function of these alarm sequences may be in communicating to the predator, our results also show that recipients eavesdrop on these signals and associate them with the predator type for which they are normally produced, as demonstrated by predator-specific gaze direction responses.

An alternative view is that the monkeys' calling behaviour is a mere reflection of the perceived dangerousness of the situation. For example, crowned eagles may be perceived as a more serious threat than leopards, which have been absent from the Sonso area for a considerable time period (Schel & Zuberbühler 2009) and are generally less of a danger for arboreal primates. Under this hypothesis, the long roaring sequences given to eagles are a reflection of perceived high threat, whereas short sequences, given to leopards, are a reflection of low threat. Observations relevant to this question have been made on chimpanzees hunting for colobus monkeys. During a hunt, the chimpanzees usually single out one monkey, which they surround and follow through the treetops. Male Guerezas often attempt to protect their females by chasing away the chimpanzees during direct confrontations in which they actively approach the chimpanzees, while typically producing short roaring sequences (A. M. Schel, personal observation). On two occasions, we observed how an adult male Guereza, captured, wounded and about to be killed by the chimpanzees, also produced short roaring sequences. Although these observations may not be representative for the entire species, it is difficult to

argue that such events could not be perceived as the highest possible degree of danger during a predator encounter. The hypothesis that long roaring sequences indicate high 'perceived threat', therefore, is not supported by these observations. More likely, short roaring sequences refer to significant events on or from the ground, while the long roaring sequences refer to eagle-related events.

We also recorded a number of other sounds produced by the monkeys, notably grunts, tongue-clicks and snorts. Earlier reports have suggested that snorts function as an alarm call in response to ground predators, that is, mainly if given in isolation (e.g. Hill & Booth 1957; Marler 1972). In our study, callers produced snorts to leopard growls, to leopard alarms and to eagle alarms, but usually not consistently to eagle shrieks, even though all four stimuli were played from the ground. In all eagle-related cases, the snorts preceded roaring sequences and were never produced alone, whereas in leopard-related responses snorts were also often produced singly. The function of snorts preceding roaring sequences currently remains unclear. One possibility is that snorts are produced in response to any disturbance coming from below, sometimes including eagles, which are not typical ground predators. By introducing roaring sequences with snorts, callers may indicate to their group members that a specific event is taking place below the group. The prediction here is that alarm sequences (to eagles or leopards) played from above will not elicit any snorts. Testing these possibilities will require further playback experiments, which may be difficult to carry out in light of the Guerezas' highly arboreal lifestyle in the treetops.

Although the default response to conspecific alarms was to remain silent, individuals sometimes produced alarms. When comparing the acoustic structure of these vocal responses with vocal responses to actual predator vocalizations, we found no consistent differences in the major variables, although there were a few subtle acoustic differences, most notably in the details of the second formant frequency of individual calls. It is unclear which kind of psychological factors experienced by the callers could explain these differences (Rendall 2003). One possibility is that, within the same predator class, some situations are perceived as more dangerous than others, but unfortunately we did not measure any suitable independent variables that would allow us to address this hypothesis more systematically. Whether or not these subtle acoustic differences are communicatively important is also unclear and will require further work. Despite this, our key finding was that callers reproduced the alarm call sequences that they heard, suggesting that these were meaningful to them.

In sum, based on the lower vocal response rates to conspecific alarms compared to the corresponding predator vocalizations, we suggest that Guerezas' vocal predator responses have evolved as predator deterrence signals, a function further illustrated by the fact that Guerezas often approach their predators while calling. Natural observations of interactions with predatory chimpanzees argue against the hypothesis that the observed differences in sequence organization are a mere side-product of perceived threat. Our results also show that recipients attribute meaning to these compositional differences. Thus, although not necessarily produced for this purpose, Guerezas' alarm sequences refer to two different external events, the presence of a disturbance on the ground or an eagle. In this species, meaning is conveyed by the call sequences, not the individual calls, a possibly underestimated feature of animal communication (e.g. Zuberbühler 2002; Templeton et al. 2005; Arnold & Zuberbühler 2006, 2008; Clarke et al. 2006). We conclude that Guerezas' alarm sequences evolved to deter predators and function as referential signals by providing vital information to eavesdrop-ping conspecifics.

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