

# The Alarm Call System of Two Species of Black-and-White Colobus Monkeys (*Colobus polykomos* and *Colobus guereza*)

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Vervet monkey alarm calling has long been the paradigmatic example of how primates use vocalizations in response to predators. In vervets, there is a close and direct relationship between the production of distinct alarm vocalizations and the presence of distinct predator types. Recent fieldwork has however revealed the use of several additional alarm calling systems in primates. Here, the authors describe playback studies on the alarm call system of two colobine species, the King colobus (*Colobus polykomos*) of Tai Forest, Ivory Coast, and the Guereza colobus (*C. guereza*) of Budongo Forest, Uganda. Both species produce two basic alarm call types, snorts and acoustically variable roaring phrases, when confronted with leopards or crowned eagles. Neither call type is given exclusively to one predator, but the authors found strong regularities in call sequencing. Leopards typically elicited sequences consisting of a snort followed by few phrases, while eagles typically elicited sequences with no snorts and many phrases. The authors discuss how these call sequences have the potential to encode information at different levels, such as predator type, response-urgency, or the caller's imminent behavior.

*Keywords:* *Colobus polykomos*, *Colobus guereza*, alarm calls, predation, referential signaling

Predation is an important evolutionary force that has selected for a wide variety of antipredator tactics (Lima & Dill, 1990; Stanford, 1995, 1998). One regularly employed by many species is the production of vocal signals upon detecting a predator. These signals can function in predator (or "pursuit") deterrence (Woodland, Jaafar, & Knight, 1980; Zuberbühler, Jenny, & Bshary, 1999) and to warn conspecifics about the type of threat present (Seyfarth, Cheney, & Marler, 1980; Struhsaker, 1967; Zuberbühler, 2005). The classic example for conspecific warning is demonstrated by vervet monkeys, which produce acoustically different alarm calls for different predator classes (Seyfarth et al., 1980; Struhsaker, 1967). Subsequent research has shown that the ability to produce

acoustically distinct alarm calls to different types of predators, usually aerial and ground predators, could be widespread in the animal kingdom (e.g., chickens: Evans, Evans, & Marler, 1993; sciurids: Slobodchikoff, Kiriazis, Fischer, & Creef, 1991; Kiriazis & Slobodchikoff, 2006; Greene & Meagher, 1998; primates: Macedonia, 1990; Seyfarth, Cheney, & Marler, 1980; Struhsaker, 1967; Zuberbühler, Cheney, & Seyfarth, 1999; Zuberbühler, 2001; Kirchhof & Hammerschmidt, 2006). However, different predator classes typically also impose differences in response urgency and threat, and some species appear to respond mainly to these variables rather than predator class per se (e.g., lemurs: Fichtel & Hammerschmidt, 2002; Macedonia, 1990; ground squirrels: Leger,

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Owings, & Gelfand, 1980; Owings & Virginia, 1978; marmot *spp.*: Blumstein & Armitage, 1997; Blumstein, 1999; Brant's whistling rat: Le Roux, Jackson, & Cherry, 2001; black-capped chickadees: Templeton, Greene, & Davis, 2005). In some species, both predator type and urgency appear to interact to influence calling behavior (e.g. *surricates*: Manser, 2001; Manser, Bell, & Fletcher, 2001).

In primates, one common finding is that one alarm call type is given to a narrow range of events, typically dangerous raptors, while a second type is given to all sorts of other disturbances, including terrestrial predators, but sometimes also during intergroup encounters (e.g. white-faced capuchins: Digweed, Fedigan, & Rendall, 2005; Fichtel, Perry, & Gros-Louis, 2005; lemurs: Fichtel & Kappeler, 2002; sifakas: Fichtel & van Schaik, 2006).

Another type of system is found in Chacma baboons and sooty mangabeys. Here, individuals produce only one general call type to predators, but there is much acoustic variation and some call variants are also produced in nonpredation contexts. Experiments have shown, however, that receivers are perfectly capable of associating discrete events to such acoustically graded signals, suggesting that discrete call types are not a prerequisite for encoding specific external events (Fischer, Hammerschmidt, Cheney, & Seyfarth, 2001; Range & Fischer, 2004).

Some other primates follow a different strategy and convey predator information by assembling a small repertoire of call types into more complex call sequences (cf. black-capped chickadees, e.g. Templeton et al., 2005). Campbell's monkeys, for example, indicate low levels of threat, or signals aimed at competitors, by adding a pair of boom calls to subsequent loud call series, which are regularly given to predators (Zuberbühler, 2002). Another example comes from putty-nosed monkeys, which produce two basic types of alarm calls to predators. Unlike Diana or vervet monkeys, both calls are regularly given to both leopards and eagles, but the monkeys assemble the two calls into sequences specific to the presence of eagles, sequences specific to the presence of leopards, and sequences that indicate group travel (Arnold, Pohlner, & Zuberbühler, 2008; Arnold & Zuberbühler, 2006a, 2006b, 2008). White handed gibbons, finally, use some of their vocal behavior, the songs, not only in pair bonding but also to indicate the presence of predators, such as clouded leopards or tigers. Experiments have shown that predator-induced songs consist of the same types of notes as normal songs, but they are assembled in subtly different ways. Differences in the arrangement of notes are meaningful to other gibbons, suggesting that this primate is able to use simple combinatorial rules to convey whether or not a caller is singing in response to the presence of a predator (Clarke, Reichard, & Zuberbühler, 2006). An emerging point from these studies is that predation has selected for an astonishing vocal diversity in the primate order and other groups of animals.

In this study, we analyze the alarm calling behavior of two species of a group of primates that have received little systematic attention in terms of alarm calling behavior, although they represent a major group of Old World monkeys, the colobines. The available literature comes mostly from work on Guereza colobus monkeys, a species of black-and-white colobus monkeys that has long been known for its conspicuous calling behavior (Hill & Booth, 1957; Marler, 1972; Oates, Bocian, & Terranova, 2000; Oates & Trocco, 1983). Adult males, sometimes joined by other

individuals, produce a vocal signal termed 'roaring,' which can be heard over long distances of one kilometer and more (Marler, 1972). Individual roaring phrases ("phrases") are rarely produced singly, but given as part of longer sequences (Marler, 1972, 1977; Oates, 1994; Oates et al., 2000; Oates & Trocco, 1983). These signals are given in a variety of contexts, such as before dawn, in response to calls of other males and/or species, and in response to major disturbances, such as falling trees or the presence of predators (Marler, 1972). A second type of acoustic signal used in predatory situations, the 'snort,' is a low-amplitude, a-periodic sound, audible over short distances only. This signal is usually given in response to potential predators on the ground, such as leopards and (exceptionally) chimpanzees and humans (Marler, 1972). Snorts can be given alone, but they usually precede roaring sequences. Although previous studies have recognized that both vocalizations play a role in predatory contexts, the evidence mainly comes from opportunistic observations of encounters between the colobus and potential predators. To date, no systematic studies on the vocal alarm call system of black-and-white colobus monkeys have been carried out.

We investigated the vocal alarm call behavior of King colobus monkeys (*Colobus polykomos*) of Tai National Park, Ivory Coast, as well as that of Guereza colobus monkeys (*Colobus guereza*) of the Budongo Forest Reserve, Uganda. We studied these species' responses to two of their main predators, crowned eagles (*Stephanoaetus coronatus*) and leopards (*Panthera pardus*). These predators are common in the Tai Forest (densities: 1 leopard per 10 km<sup>2</sup>: Jenny, 1996; 1 crowned eagle per 2–3 km<sup>2</sup>: Shultz, 2002) and they have also been observed in the Kaniyo Pabidi area of the Budongo Forest. Chimpanzees (*Pan troglodytes*) cause additional mortality at both sites, but the monkeys generally respond with cryptic behavior to their presence (Zuberbühler, Noë, & Seyfarth, 1997; Schel, 2009). We conducted playback experiments, in which we played back typical vocalizations of leopards and crowned eagles in the vicinity of different monkey groups in order to record and analyze the monkeys' vocal responses.

## Method

### Study Sites and Subjects

The study area in Tai National Park consisted of approximately 100 km<sup>2</sup> of primary tropical evergreen seasonal lowland rain forest (N 5° 50', W 7° 21'). In this area, King colobus groups occur at densities of one or more groups per square kilometer (Zuberbühler & Jenny, 2002). Groups normally consist of one or two adult males, approximately five adult females, and their subadult, juvenile, and infant offspring (Korstjens, 2001; Oates, 1994). In Tai, playback experiments were conducted between 1995 and 1998 and in 2004. The Kaniyo Pabidi study area of the Budongo Forest Reserve (compartments K11, K12 and K13) consisted of approximately 11 km<sup>2</sup> of primary tropical moist semideciduous rainforest (N 01° 55', E 31° 43'). Guereza colobus groups in this area occur at relatively high densities of three to six groups per square kilometer (Plumptre & Reynolds, 1994; Plumptre, 2000). Guereza colobus groups normally consist of one adult male, approximately four adult females, and their subadult, juvenile and infant offspring (Marler, 1969; Oates, 1994). In Kaniyo Pabidi, playback experiments were conducted in 2006 and 2007.

King colobus monkeys and Guereza colobus monkeys are regarded as two separate species belonging to a diverse group consisting of five different black-and-white colobus species: *C. satanas*, *C. polykomos*, *C. vellerosus*, *C. guereza*, and *C. angolensis*. *C. vellerosus* and *C. polykomos* are found in West Africa, whereas the other three species are found in Central- and East Africa (Oates, 1994). Acoustic analyses of roars of these five species by Oates and Trocco (1983) and Oates et al. (2000) suggested that they are grouped in three clusters based on differences in temporal patterning, frequency and modulation of the roars. *C. vellerosus* and *C. guereza* share a recent common ancestor, and *C. guereza* appears to have the largest number of derived features among the members of the black-and-white colobus group. *C. polykomos* and *C. angolensis* seem to be more primitive, but have diverged rather little from each other, whereas *C. satanas* is a form that has not had a recent common ancestry with any other form, but is most closely related to the *angolensis-polykomos* pair. *C. vellerosus* is suggested to be an intermediate form between *C. polykomos* and *C. guereza*.

### General Experimental Protocol

We used matching experimental protocols at both study sites. We systematically searched for monkey groups throughout the study area. Groups were often found resting high up in a feeding tree. Once found, their exact geographical location was determined using a GARMIN GPS 76 and a detailed map to ensure that the group had not been tested before and that experimental groups were separated by a distance of at least one kilometer from each other (average home range King colobus monkeys at Tai 70 ha: Korstjens, 2001; average home range Guereza colobus monkeys at Budongo 10–35 ha: Marler, 1969). We monitored the monkeys' vocal behavior for at least 15 min to make sure that they were unaware of our presence. Using a NAGRA DSM speaker-amplifier, we then broadcast a playback stimulus consisting of 5 min silence followed by 15 s of predator vocalizations, either the growls of a leopard ( $N = 6$  exemplars, National Sound Archive, London) or the shrieks of a crowned eagle ( $N = 3$  exemplars, recorded in the Tai study area). The playback equipment was positioned on or close to the ground (0–2 m) at a distance of circa 20–40 m from the group, outside the visual range of the monkeys residing in the trees.

Although eagles are typically encountered in the lower or upper canopy, they have been spotted on the forest floor, indicating that our experimental paradigm mimicked a possible natural situation. Moreover, other playback studies targeting different monkey species in the Tai National Park and Guereza colobus monkeys in the Budongo Forest Reserve had already shown that monkeys reliably responded to playbacks of eagle shrieks. Crucially, in these experiments the monkeys responded identically to recorded eagle shrieks broadcast from a speaker positioned on the forest floor or within the canopy as well as to shrieks emitted by real crowned eagles (e.g., Zuberbühler, 2001; Zuberbühler et al., 1997; Schel, 2009).

All recordings began circa 5 min prior to playback and lasted at least 15 min, regardless of whether or not the focal animals responded vocally. In 2004, 2006, and 2007 vocalizations were recorded with a SONY TCD D8 DAT recorder connected to a SENNHEISER K6/ME66 directional microphone. These roars

were transferred digitally from the DAT recorder onto a PC at a sampling rate of 48 kHz, 16 bits accuracy with Cool Edit, 2000 (Syntrillium Software Cooperation). An additional  $N = 7$  eagle responses, recorded between 1995 and 1999 in the Tai National Park, were added to the data set for the King colobus monkeys to increase the sample size. These recordings were collected in the exact same way using the same experimental procedures and playback equipment. They were made with a SONY TCM1000EV professional cassette recorder and then digitized using an EDIROL external sound card.

### Terminology

The basic structural features of Colobus roaring have been described for Guereza colobus monkeys by Marler (1972); Oates and Trocco (1983) and Oates et al. (2000). Individual roaring phrases are the result of about a dozen glottal pulses, which appear in the spectrogram as compound units with an average duration of about 700–800 ms. The acoustic energy in each phrase tends to appear as two discrete frequency bands on the spectrogram ( $M \pm SD = 590\text{Hz} \pm 72$  and  $M \pm SD = 1280\text{Hz} \pm 114$ ; Figure 1A).

Individual roaring phrases are assembled into roaring sequences, which together form a bout. A bout is separated from another bout by a nonroaring period of at least one minute. Roaring sequences vary substantially in the number of roaring phrases they consist of, ranging from one or two to 20 or more given in rapid succession with intervals of around 200 ms between them. Roaring phrases can vary in their acoustic structure, especially when comparing the first and last phrase in a sequence. The final phrase in a roaring sequence often is lower pitched, which generates a perceptually conspicuous marker to terminate the sequence (Marler, 1972; Oates & Trocco, 1983). The first phrase in a roaring sequence can be preceded by one or more 'snorts'. Snorts 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.

King Colobus roaring can be described with the same terminology, but in this species individual roaring phrases are the result of about a dozen glottal pulses, which appear in the spectrogram as compound units with an average duration of about 400 ms. Similar to Guereza colobus phrases, the acoustic energy in each King colobus phrase appears on the spectrogram as two frequency bands, but the frequencies are higher, at around 650 Hz ( $M \pm SD = 650 \pm 78$ ), and 1400 Hz ( $M \pm SD = 1390 \pm 93$ ), respectively (Figure 1B; Oates & Trocco, 1983; Schel, 2009).

### Analyses of Vocal Responses

*Structural measurements.* From the vocal responses produced for each predator type, we determined the following six structural parameters using spectrograms generated on RAVEN 1.2 (Cornell Laboratory of Ornithology, Ithaca, New York; Hanning window function; filter bandwidth: 124 Hz; frequency resolution: 86.1 Hz; grid time resolution: 5.80 ms): (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) number of bouts (cf. Oates & Trocco, 1983).

Some of the spectral parameters are likely to be correlated with one another. However, in our analyses we were only interested in

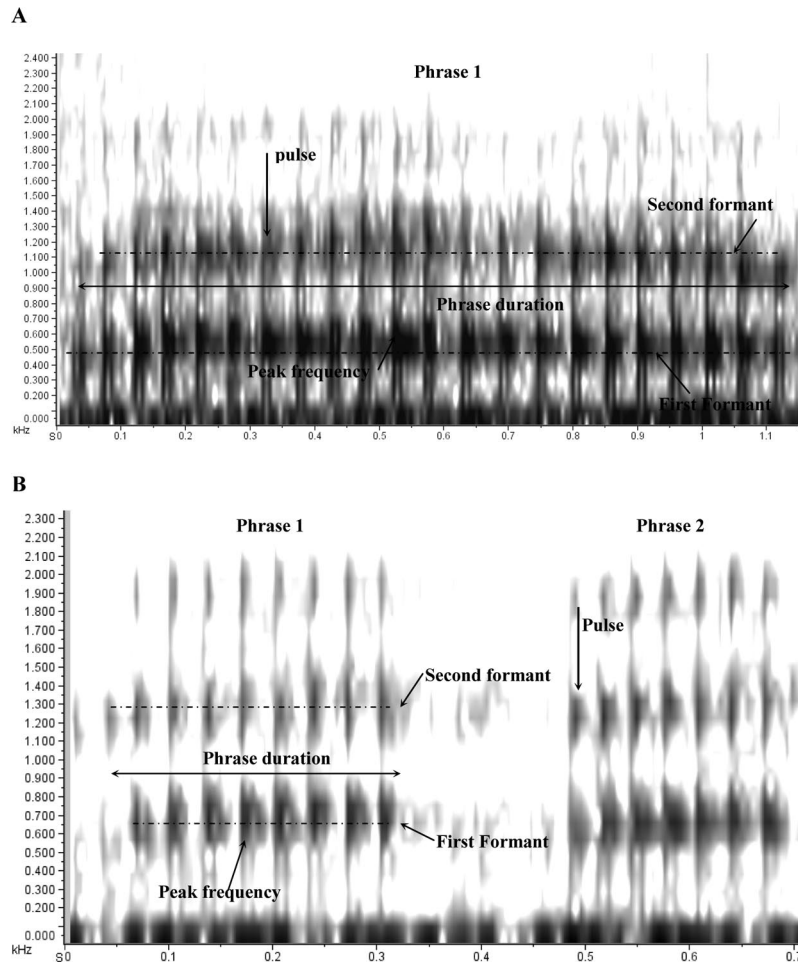


Figure 1. Phrases of A. an individual Guereza colobus male responding to a leopard playback and B. an individual King colobus male responding to a leopard playback, both illustrating the various acoustic variables considered in this study. The x-axis represents time in seconds, the y-axis frequency in kHz.

whether calling responses differed between contexts, not in the minimal number of spectral parameters that sufficiently accounted for any such difference. Thus, we proceeded to report statistical comparisons of all spectral measurements taken. Our overall analysis strategy was to investigate, for each structural and acoustic variable, whether there were any differences as a function of predator type or the position of the phrase within a sequence.

**Spectral measurements.** To compare the acoustic structure of individual roaring phrases given to the two different predator playbacks we measured 7 different acoustic variables (see Figure 1). The following temporal measures were determined using Raven 1.2 (Cornell Laboratory of ornithology, Ithaca, New York; Hanning window function; filter bandwidth: 124 Hz; frequency resolution: 86.1 Hz; grid time resolution: 5.80 ms): (a) *phrase duration (ms)*: time interval from the first to the last produced pulse; (b) *number of pulses per roaring phrase*; pulses were counted by playing back the roar at 10% of the original speed; (c) *fundamental frequency (Hz)*: number of pulses per second. The following spectral measures were extracted using PRAAT 4.3.12 (Boersma & Weenink, 2005). Spectrogram settings: Hanning window shape; window

length = 0.05 s, maximum frequency = 3000 Hz, time step = 0.002 s, frequency step = 20 Hz; Formant settings: burg algorithm; time step = 0.05 s; maximum number of formants = 3; maximum formant frequency = 2700 Hz; window length = 0.025 s., preemphasis from 50 Hz, (cf. Harris, Fitch, Goldstein, & Fashing, 2006): (d) *harmonics-to-noise ratio (HNR, dB)*, defined as the degree of acoustic periodicity; this represents the energy distribution of periodic signals versus noise (e) *first and (f) second formants (Hz)*, representing the first and second peaks in the frequency spectrum, which result from the resonant frequencies of the calls, (g) *peak frequency (Hz)*, defined as the frequency at which maximum acoustic energy occurs in the dominant frequency band of the phrase.

At both field sites, our pilot observations indicated that monkeys predominantly reacted with one bout of roaring to leopard playbacks, consisting of a large number of sequences that typically contained only one or two roaring phrases each. To eagle playbacks, the response was the opposite. Although the monkeys mostly produced only one roaring bout, it generally contained only two sequences but they consisted of a large number of roaring

phrases each. For systematic comparisons, we thus focused our 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).

*Inspection of King colobus' recordings.* In 2004, we tested 18 different groups of King colobus monkeys with playbacks of leopard growls and 24 different groups with playbacks of eagle shrieks. Two eagle trials were discounted as invalid because the monkeys saw the equipment or the observer; one leopard trial was discounted as invalid due to equipment malfunctioning. The response rate to playback of eagle shrieks was relatively low. In only 6 of 22 groups at least one individual responded with alarm vocalizations (response rate = 27.3%). One of these trials had to be discarded for further analyses because of high levels of background noise. To allow meaningful comparisons, we supplemented this small sample with  $N = 7$  eagle recordings collected between 1995 and 1999, yielding a final sample size of  $N = 12$  eagle responses for the structural measurements. The response rate to playback of leopard growls was higher. In 10 of 17 groups at least one monkey responded with alarm vocalizations (response rate = 58.8%). Of these, one trial had to be discarded because of high levels of background noise, yielding a final sample size of  $N = 9$  leopard responses for the structural measurements.

From these data, we were able to obtain reliable spectral data for the first roaring sequences from  $N = 8$  leopard responses and another  $N = 8$  eagle responses. For the second roaring sequence, we had to discard one leopard response due to poor recording quality, yielding a final dataset of  $N = 7$  leopard responses. In 2 of the 8 eagle trials, the animals did not produce a second roaring sequence. In one case, it was not possible to measure the last call of the second roaring sequence, which led to a final sample size of  $N = 6$  first calls and  $N = 5$  last calls for the second roaring sequence in the eagle context. Acoustic analyses of the first and last roars of the first two roaring sequences were made with PRAAT 4.3.12. Additional analyses were conducted with RAVEN 1.2.

*Inspection of Guereza colobus' recordings.* In 2006, we tested 27 different groups of Guereza colobus monkey groups with playbacks of leopard growls and 31 different groups with playbacks of eagle shrieks. In 2007, we tested an additional 9 groups with leopard growls and an additional 9 groups with eagle shrieks. One eagle trial was discounted as invalid because the monkeys saw the equipment or the observer, one eagle trial was discounted as invalid due to equipment malfunctioning, and three leopard trials were discounted as invalid because the monkeys saw the equipment or the observer. Total numbers of valid playback experiments used for overall analyses thus was  $N = 33$  for leopard growls and  $N = 38$  for eagle shrieks.

Like in Tai, the response rate to eagle shrieks was relatively low. In only 8 of 38 groups at least one individual responded with alarm vocalizations (response rate = 21.1%). In contrast to Tai, however, the response rate to leopards was relatively low as well. In only 12 of 33 groups at least one monkey responded with alarm vocalizations (response rate = 36.4%). In three of these 12 responses to leopard growls, high levels of background noise made it impossible to code the complete vocal reaction, and these recordings had to be excluded from acoustic analyses, generating a final sample size of  $N = 9$  leopard and  $N = 8$  eagle responses for the structural measurements.

For the spectral measurements, one additional leopard trial had to be discarded because of poor recording quality. We were therefore able to obtain reliable spectral data for the analyses of the first roaring sequences from  $N = 8$  leopard responses and another  $N = 8$  eagle responses. In one leopard response, the caller did not produce a second roaring sequence containing a first and last phrase; this individual just continued roaring with one phrase roaring sequences after the initial two phrase roaring sequence. This led to a final sample size of  $N = 7$  leopard responses and  $N = 8$  eagle responses for analyses of the second roaring sequences. Acoustic analyses of the first and last roars of the first two roaring sequences were made with PRAAT 4.3.12. Additional analyses were conducted with RAVEN 1.2.

### Statistical Analyses

A matched-pair design (every group contributing a leopard and an eagle response to the final dataset) would have been an obvious choice for the intended comparisons. However, this approach is usually not practical for fieldwork, especially because the exact ranging behavior of the different unhabituated groups is not known. Moreover, because of the low response rate of these monkeys to eagles and leopards, our experimental protocol was to test each group only once.

We checked for normal distribution both within and between group responses using the SPSS Software Package 12.0. Conditions for parametric analyses were not met and we thus proceeded with nonparametric analyses. Critical  $p$  values were adjusted to  $<0.025$  using a Bonferroni correction if the same dataset was used for two different comparisons. All reported  $p$  values are exact  $p$  values and all testing was two-tailed (Brace, Kemp, & Snelgar, 2000; Hawkins, 2005). 97.5% confidence intervals for means were calculated using the descriptive statistics option in SPSS. Nonparametric effect sizes ( $r$ , Field, 2005) were estimated by dividing the  $z$ -score by the square root of the total number of observations. Values of  $r$  can lie between 0 (no effect) and 1 (perfect effect), with the widely used accepted standards of  $r = .10$  (small effect),  $r = .30$  (medium effect) and  $r = .50$  (large effect).

## Results

### General Response Characteristics in Tai and Kaniyo Pabidi

If more than one individual called in response to the predator playbacks, we used the vocal response of the individual that called first for subsequent analyses; other calling individuals were not used in any analyses. In all trials used for temporal and structural analyses, the calling individuals could be clearly distinguished. As already mentioned, the response rates at both sites were generally low, with slight but nonsignificant differences between the predator types (Tai: leopards: 59%, eagles: 27%,  $p = .06$ ; Kaniyo Pabidi: leopards 36%, eagles: 21%,  $p = .19$ , Fisher's exact test, two-tailed). If calling occurred in response to a predator playback, callers often combined their vocal response with conspicuous visual display behavior, jumping vigorously from branch to branch and thereby approaching the site to inspect the source (Tai: leopard: 9 of 10 trials, eagle: 4 of 6 trials; Kaniyo Pabidi: leopard: 7 of 12 trials; eagle: 6 of

8 trials). In Tai, other group members joined the approaching caller in 4 of 9 leopard trials, but never in response to eagle trials. In Kaniyo Pabidi, the approaching caller was joined in 4 of 7 leopard trials and 5 of 6 eagle trials. In all remaining cases, one or several individuals called, but no one approached.

### *Acoustic Structure of Individual Roaring Phrases*

For the King colobus monkeys, comparisons of leopard responses revealed significant differences between the first and final roaring phrases for both the first and second sequence. Comparisons of eagle responses revealed the same pattern, although differences did not reach significant levels (Tables 1 & 2). For the Guereza colobus monkeys, the same significant differences were found between the first and final roaring phrases in both the first and second sequence, for both leopard and eagle responses (Tables 1 & 2).

Crucially, when comparing roaring phrases *between* the two predator types we found no significant differences in King colobus in any of the spectral parameters. The same was the case for Guereza colobus with the exception of the harmonics-to-noise ratios (HNR), which were higher in response to leopards than eagles. Measurements of all other acoustic variables did not yield any predator-specific acoustic differences (Table 1 & 2). These results suggest that, although both species produced two types of roaring phrases, these were not given in predator-specific ways, but simply indicated the phrases locations within the sequence.

### *Composition of Roaring Sequences*

In contrast to the acoustic features, we found clear differences in the structural composition of the roaring sequences produced in response to eagles and leopards. Most importantly the number of roaring phrases per sequence was significantly smaller in response to leopards than eagles (Tai:  $M_L = 3.8 \pm 2.1$  ( $\pm SD$ );  $M_E = 15.8 \pm 2.6$  ( $\pm SD$ );  $U = 8$ , exact  $p = .000$ ,  $r = .71$ ; Kaniyo Pabidi:  $M_L = 1.4 \pm 1.1$ ;  $M_E = 7.1 \pm 1.2$ ;  $U = 1$ , exact  $p = .000$ ,  $r = .82$ ;  $U$  test, two-tailed). Second, roaring sequences to leopards, but not eagles, were typically preceded by “snorts” (Tai: 9 of 9 leopard trials, 4 of 12 eagle trials;  $p = .005$ ; Kaniyo Pabidi: 9 of 9 leopard trials; 4 of 8 eagle trials,  $p = .029$ ; Fisher’s exact test, two-tailed). Both species produced a higher number of snorts in response to leopard growls than in response to eagle shrieks (Tai:  $M_L = 24.4 \pm 20.6$ ;  $M_E = 4.4 \pm 9.0$ ;  $U = 12$ , exact  $p = .002$ ,  $r = .67$ ; Kaniyo Pabidi:  $M_L = 43.9 \pm 58.3$ ;  $M_E = 3.8 \pm 4.1$ ;  $U = 10.5$ , exact  $p = .012$ ,  $r = .60$ ;  $U$  test, two-tailed). In both species, snorts were also produced to chimpanzees and humans, although the default reaction to these predators was to remain cryptic (Schel, 2009). Furthermore, King colobus males, but not Guereza colobus males, produced longer roars to leopards than to eagles, both in terms of the total duration of calling (Tai:  $M_L = 312.3 \pm 162.9$  s;  $M_E = 77.8 \pm 68.9$  s;  $U = 12.5$ , exact  $p = .003$ ,  $r = .64$ ; Kaniyo Pabidi:  $M_L = 248.7 \pm 284.7$ s;  $M_E = 145.8 \pm 130.1$ s;  $U = 30$ , exact  $p = .587$ ,  $r = .14$ ;  $U$  test, two-tailed) and the total number of roaring phrases produced (Tai:  $M_L = 191 \pm 97.2$ ;  $M_E = 79.2 \pm 68.5$ ;  $U = 19$ ; exact  $p = .013$ ,  $r = .54$ ; Kaniyo Pabidi:  $M_L = 91.0 \pm 138.1$ ;  $M_E = 48.5 \pm 50.6$ ;  $U = 35$ , exact  $p = .945$ ,  $r = .02$ ;  $U$  test, two-tailed). Finally, King colobus males, but not

Guereza colobus males, produced leopard responses with a higher total number of roaring sequences than those to eagles (Tai:  $M_L = 64.4 \pm 36.4$ ;  $M_E = 11.6 \pm 20.3$ ;  $U = 8$ , exact  $p = .001$ ,  $r = .72$ ; Kaniyo Pabidi:  $M_L = 53.7 \pm 82.6$ ;  $M_E = 13.1 \pm 23.3$ ;  $U = 28$ , exact  $p = .465$ ,  $r = .19$ ;  $U$  test, two-tailed). As mentioned before, the number of bouts produced to leopards and eagles did not differ significantly at both sites (Tai:  $M_L = 2 \pm 1.41$ ,  $M_E = 1.7 \pm 0.98$ ;  $U = 49$ , exact  $p = .728$ ,  $r = .09$ ; Kaniyo Pabidi:  $M_L = 1 \pm 0$ ,  $M_E = 1.1 \pm 0.13$ ;  $U = 31.5$ , exact  $p = .471$ ;  $r = .26$ ;  $U$  test; two-tailed: Figures 2 & 3).

## Discussion

In contrast to other primate species, particularly Diana monkeys, we found no evidence that individual calls (“roaring phrases”) of West African King colobus monkeys varied in their acoustic structure depending on the predator type encountered. Instead, our analyses revealed consistent differences in the structural organization at the level of call sequences: responses to leopards consisted of a small number of roaring phrases per sequence compared to eagle responses. These leopard responses lasted longer, were composed of more sequences, and consisted of a larger total number of phrases than those to eagles. All statistical comparisons were highly significant, with little or no overlap, particularly during the first few sequences. In the closely related Guereza colobus monkeys of East Africa, there were a number of striking similarities, especially with regards to the difference in the number of roaring phrases per sequence as a function of predator context. Other structural differences were species-specific, such as total duration of roaring, total number of roaring phrases, and total number of roaring sequences.

Another shared feature of both King colobus and Guereza colobus was the frequent use of snorts accompanying leopard reactions, but rarely eagle reactions. Snorts were sometimes also given to humans and chimpanzees. Since all playback experiments were conducted from the ground, snorts did not simply indicate danger from the ground, but seemed to be used in more specific contexts, which generally included leopards, humans, and chimpanzees, but not eagles.

Finally, in both King and Guereza colobus, the final roaring phrase produced in a sequence was acoustically different from the preceding ones, demonstrating subtle but consistent acoustic changes throughout a roaring sequence. For the King colobus, effects were highly significant in the leopard context, and the same effect was found in the eagle context. In the Guereza colobus, the differences were also highly significant for both predator types, in line with earlier reports (Marler, 1972). Perceptually, the acoustically distinct last phrases reliably indicate the end of a roaring sequence, but whether this feature possesses signal value, or whether it is a mere by-product caused by relaxation of the animal’s musculature, is a matter of further research.

One minor effect in the acoustic structure of individual roaring phrases concerned the difference in the HNR of Guereza roars. This acoustic variable can be influenced by random factors such as an inadequate closure of the vocal folds, allowing excessive airflow through the glottis, which can cause turbulence during phonation, a-periodic vocal fold vibration, and pitch perturbations (Ferrand, 2002; Shama, Krishna, &

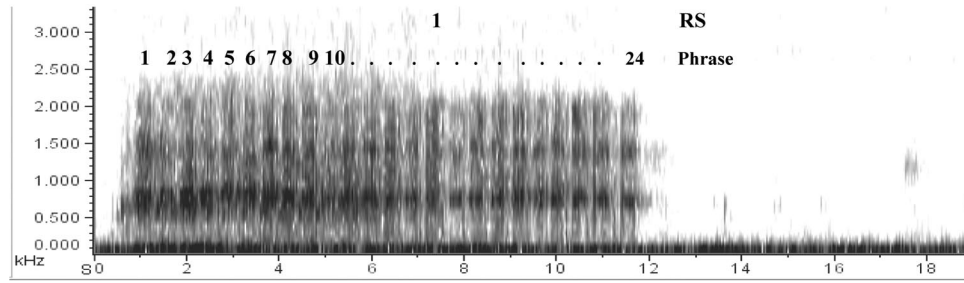


Table 2  
*Statistical Output of Comparisons of Acoustic Measurements of First and Last Phrases Produced Within Predator Contexts and Between Predator Contexts*

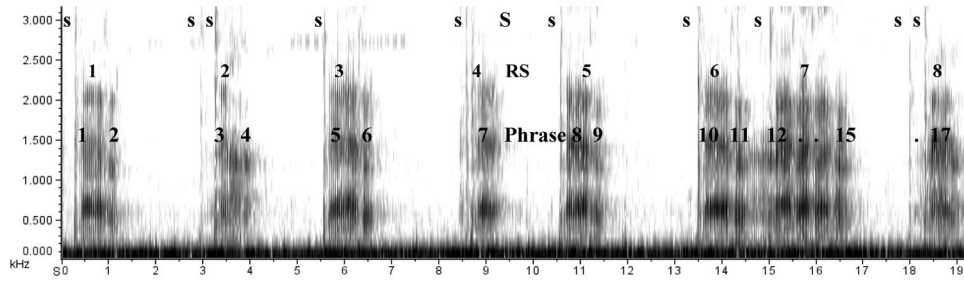
Acoustic variable	Within leopard			Within eagle			Between leopard and eagle contexts									
	(First vs last phrase)			(First vs last phrase)			First phrase			Last phrase						
	<i>C. polykomos</i>	<i>C. guereza</i>		<i>C. polykomos</i>	<i>C. guereza</i>		<i>C. polykomos</i>	<i>C. guereza</i>		<i>C. polykomos</i>	<i>C. guereza</i>					
	exact	<i>p</i>	<i>r</i>	exact	<i>p</i>	<i>r</i>	exact	<i>p</i>	<i>r</i>	exact	<i>p</i>	<i>r</i>				
<b>1<sup>st</sup> RS</b>																
Phrase duration (ms)	<b>0.008</b>	0.63	0.63	0.156	0.38	0.008	0.63	0.63	0.697	0.11	0.161	0.37	0.138	0.04	0.798	0.08
Harmonics-noise ratio (dB)	0.195	0.35	0.35	0.375	0.26	0.250	0.32	0.32	0.152	0.39	<b>0.003</b>	0.71	0.138	0.39	0.038	0.53
First formant (Hz)	0.383	0.25	0.313	0.078	0.46	0.742	0.11	0.11	0.195	0.34	0.130	0.39	0.366	0.21	0.442	0.21
Second formant (Hz)	0.461	0.21	0.109	0.313	0.62	0.844	0.07	0.07	0.798	0.08	0.083	0.45	0.945	0.08	0.442	0.21
Peak frequency (Hz)	<b>0.109</b>	0.42	<b>0.086</b>	0.844	0.08	0.180	0.35	0.35	0.594	0.15	0.505	0.18	0.800	0.48	0.463	0.20
Number of pulses	0.008	0.63	0.008	0.047	0.51	<b>0.008</b>	0.63	0.63	0.978	0.01	0.234	0.31	0.169	0.28	0.722	0.09
Fundamental freq (Hz)	0.016	0.60	0.945	0.242	0.32	0.383	0.25	0.25	0.505	0.18	0.028	0.55	0.731	0.43	0.077	0.45
<b>2<sup>nd</sup> RS</b>																
Phrase duration (ms)	<b>0.016</b>	0.63	<b>0.016</b>	0.031	0.64	<b>0.008</b>	0.63	0.63	0.901	0.44	0.189	0.36	0.295	0.32	0.694	0.12
Harmonics-noise ratio (dB)	0.578	0.18	0.438	0.188	0.43	0.945	0.04	0.04	0.130	0.44	<b>0.002</b>	0.75	0.755	0.11	<b>0.002</b>	0.77
First formant (Hz)	0.813	0.09	0.938	0.313	0.33	0.844	0.07	0.07	0.442	0.28	0.694	0.12	0.945	0.04	0.189	0.36
Second formant (Hz)	0.375	0.27	0.938	0.05	0.64	0.945	0.04	0.04	0.798	0.04	0.463	0.21	0.445	0.11	0.867	0.06
Peak frequency (Hz)	<b>0.063</b>	0.54	<b>0.297</b>	0.125	0.51	<b>0.008</b>	0.63	0.63	0.059	0.08	0.554	0.16	0.383	0.26	0.930	0.03
Number of pulses	0.016	0.63	0.016	0.063	0.58	<b>0.008</b>	0.63	0.63	0.285	0.40	0.29	0.29	0.644	0.14	0.710	0.11
Fundamental freq (Hz)	0.578	0.18	0.688	0.14	0.313	0.844	0.07	0.07	0.105	0.12	0.232	0.33	1.000	0	0.351	0.25

*Note.* R = Effect sizes, Within-predator context: Wilcoxon Signed Rank Test, two-tailed,  $\alpha = 0.025$ . Between-predator context: Main-Whitney U Test, two-tailed,  $\alpha = 0.025$ . Values in italics signify exact *p*-values of statistic comparisons. Bold values indicate the significant *p*-values.

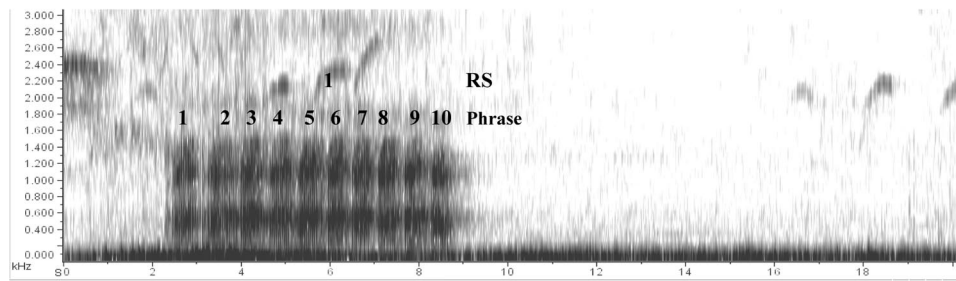
A.



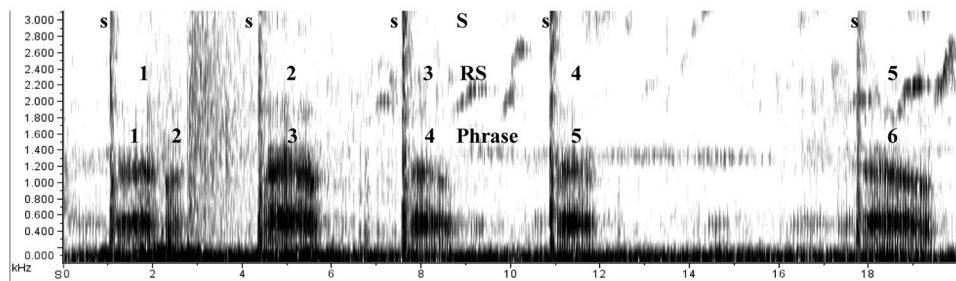
B.



C.



D.



*Figure 2.* Spectrographic illustrations of the main structural differences characterizing the vocal responses to eagles and leopards: Part A depicts a continuous recording of an adult King colobus male responding to an eagle, which consists of a roaring sequence with 24 phrases. Part B depicts a continuous recording of an adult King colobus male responding to a leopard, starting with 6 snort-introduced two-phrase roaring sequences, followed by a snort-introduced four-phrase sequence, followed by a single snort and another snort-introduced one-phrase sequence. Part C depicts a continuous recording of a Guereza colobus male responding to an eagle with a 10-phrase roaring sequence. Part D depicts a continuous recording of an adult Guereza colobus male responding to a leopard, starting with a snort-introduced two phrase roaring sequence, followed by four snort introduced one-phrase sequences. The x-axis represents time in seconds, the y-axis frequency in kHz. “S” stands for snorts, RS for roaring sequence.

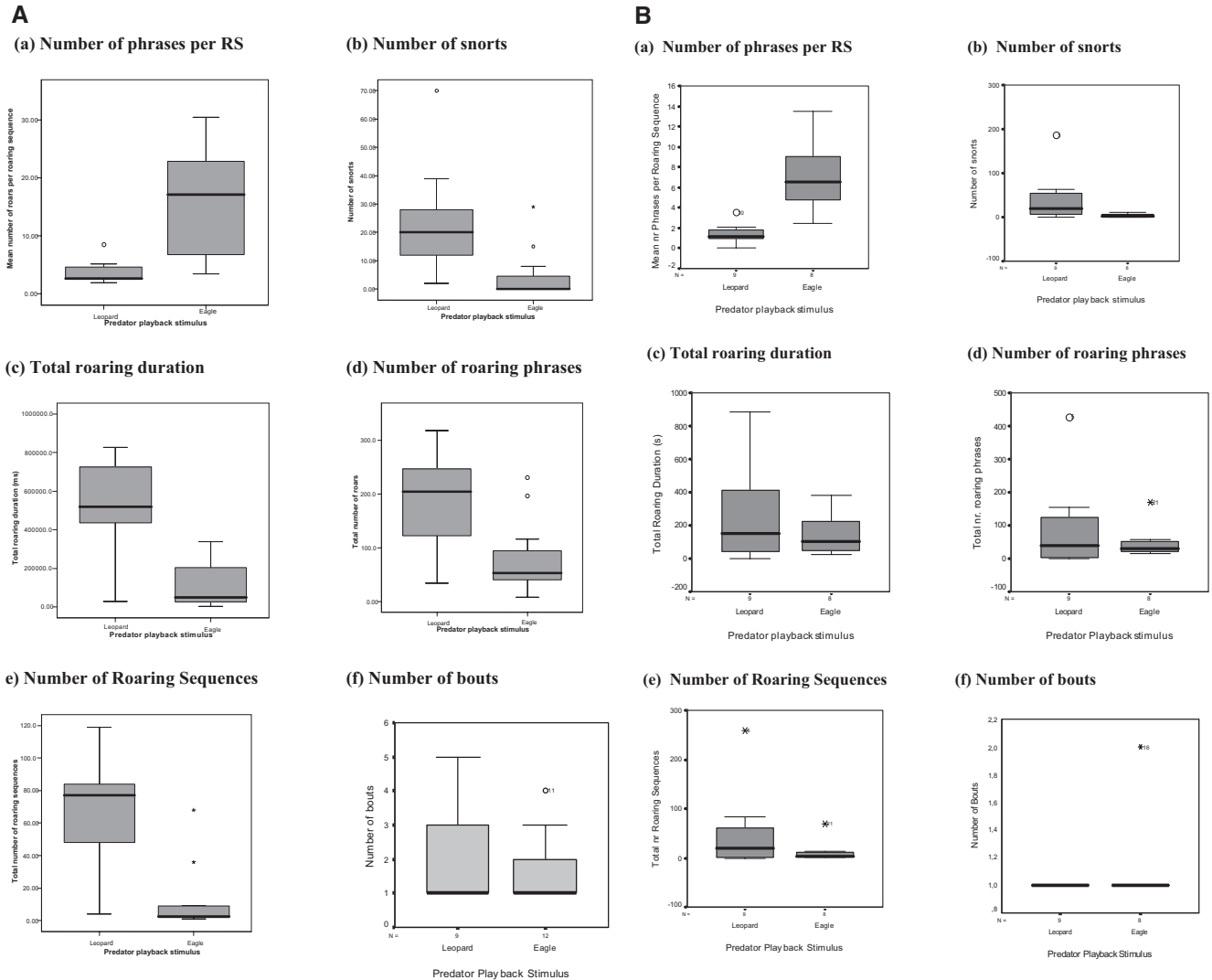


Figure 3. Bar charts representing the main differences in alarm calling behavior of (A) King colobus and (B) Guereza colobus in response to leopards and eagles.

Cholayya, 2007). For the King colobus, the differences in HNR produced between predator types were in the same direction. Most likely, this is a side effect of the differently structured roaring sequences produced to the two predator types. The long roaring sequences produced to eagles may require the monkeys to take in more air before vocalizing compared to when producing the shorter leopard sequences, perhaps causing subtle differences in vocal fold behavior and turbulence when producing individual phrases. It is highly unlikely, however, that this feature alone is conspicuous enough to carry any predator information, especially over longer distances.

Instead, the most salient and consistent differences of King and Guereza colobus predator-specific alarm calling were not found in the acoustic characteristics of individual roaring phrases, but in the number of roaring phrases per sequence, and in the production of snorts accompanying these sequences. Based on the taxonomic studies by Oates and Trocco (1983) and

Oates et al. (2000), we assumed that these features are also shared with *C. vellerosus*, and perhaps also by *C. angolensis* and *C. satanas*, but further studies are needed to confirm this.

### Conspecific Warning

The fact that both monkey species responded with different vocal behavior to the two predator types opens the possibility that black-and-white colobus monkeys provide nearby listeners with information about the type of predator or threat spotted by the caller, a conspecific warning function. In order to determine whether nearby receivers are able to attend to the structural differences, playback experiments must be carried out eventually in which the different alarm vocalizations are played back to nearby conspecifics. In Guereza colobus monkeys, we have carried out such work and found that individuals responded with identical vocal and behavioral reactions to playbacks of

predator vocalizations as to playbacks of the corresponding conspecific predator alarms, (Schel, 2009).

Although predator-specific signaling effectively generates meaningful warning signals for receivers, this may not be the only function. For example, it has been shown that predator-specific alarm calls can also benefit the signaler directly (Cheney & Seyfarth, 1981). Predators often differ with regard to sensory and psychological specializations, which is likely to act as a direct selection factor in the evolution of form and patterning of alarm signals (e.g., Owings & Morton, 1997; Rundus, Owings, Joshi, Chinn, & Giannini, 2007).

In sum, predator-specific vocal behavior allows receivers to make inferences about predator type based on signaling alone, although this may not be the evolved function of predator specific signaling. In line with this, eavesdropping is increasingly recognized as an important mechanism in animal communication (McGregor & Dabelsteen, 1996; Peake, Matessi, McGregor, & Dabelsteen, 2005) and it is entirely conceivable that callers are targeting the predator while conspecifics are merely eavesdropping, suggesting that there is not necessarily symmetry in the mechanisms and functions of signaler and receiver behavior (Owings, 1994).

### *Predator Deterrence*

Another finding of this study was that the overall response rates to the two predator types were relatively low, but not significantly different between predator types (Tai: leopards: 59%, eagles: 27%; Kaniyo Pabidi: leopards: 36%, eagles: 21%). Colobus monkeys generally lead a relatively cryptic life and may thus often be reluctant to engage in conspicuous calling behavior, much in contrast to other primates such as, for example, Diana monkeys (Zuberbühler et al., 1997). In general, conspicuous calling may be a more effective strategy to leopards than to eagles. Forest leopards are surprise hunters that lose much of their dangerousness once detected. A radio-tracking study has shown that leopards move on and leave the area once detected by a group of alarm calling monkeys, suggesting that conspicuous alarm calling has direct benefits for the caller (Zuberbühler et al., 1999). Crowned eagles might be less affected by such behavior. However, they have been observed to flee in response to physical attacks by large monkeys, an antipredator behavior regularly employed by adult male King and Guereza colobus (Schel, 2009). Calling to eagles may thus become more important once the eagle is located, for example to signal aggressive intent, a situation that we were unable to model with the playback experiments.

One way of investigating the relation between alarm call response rates and predator localization is to present visual predator models to monkey groups. Unfortunately, the peculiar activity pattern of black-and-white colobus monkeys (60% of their activity budget is spent resting, 20% feeding and only 5% traveling; Oates, 1977, 1994) makes it difficult to conduct systematic experiments with nonmoving models, such as perched eagle models, as done with other species (Arnold et al., 2008). We did, however, conduct experiments in which we presented the Guereza colobus of Kaniyo Pabidi with a moving leopard model (Schel, 2009). Interestingly, the monkeys responded with alarm calls in a much higher proportion of cases

than after hearing leopard growls. Direct visual encounters with a predator may thus be an important precondition for alarm calling in this species. Observations of natural encounters with crowned eagles very much confirmed this pattern: crowned eagles could often be heard vocalizing at their nests or in social displays, which rarely triggered a vocal response. However, a silent eagle flying through the canopy toward a monkeys group could trigger fierce and aggressive roaring. The monkeys usually combined roaring with pursuing the eagle through the canopy and chasing it away, suggesting that the calls are an integral part of aggressive predator deterrence behavior.

### *Classification of the Black-and-White Colobus Alarm Call System*

(a) *Predator labeling.* For vervet monkeys and some other primates, it has been argued that individuals use their alarm calls to refer to or “label” specific external events, such as the presence of a leopard. Although both colobus monkey species produced at least two acoustically distinguishable call types (two types of phrase variants, snorts), none of them was given exclusively to one predator class. Instead, the monkeys assembled roaring phrases and snorts into longer sequences that differed between predator contexts. Roaring sequences always consisted of variable numbers of phrases, followed by a lower-pitched phrase that marked the end of the sequence. These sequences could be introduced by some snorts. This typically, but not exclusively, occurred if the caller had spotted a terrestrial predator. Overall, the monkeys produce highly patterned and reliable predator-specific alarm call sequences, and these sequences appear to be meaningful to receivers (Schel, 2009).

(b) *Urgency response.* Results might justifiably be interpreted as mediated by basic differences in response urgency, rather than as the product of cognitively more complex mental representations of different predator types. Predator class may only be relevant insofar as they indicate different levels of threat. According to this hypothesis, a predator’s biological class is only one of several variables that feed into the caller’s computations about a predator’s degree of threat. For example, it could be argued that eagles are perceived as inherently more threatening than leopards (which probably do not pose much of a risk as long as the monkeys remain within the main canopy). One prediction from this hypothesis is that two different predator classes should elicit the same response if the perceived threat is equal (e.g., an eagle detected at a safe distance or a leopard detected at close range). In the present study, predator distance varied between trials, but no clear distance-related patterns emerged. There was some indication that the response rate and number of snorts produced to leopards was dependent on the distance and/or modality of the stimulus. The leopard models were presented right under the groups in Kaniyo Pabidi, and evoked many more snorts than playback of the leopard growls from a distance of around 25 m (Schel, 2009).

All predator stimuli were played from the ground, making it difficult to argue that response differences were driven by differences in the direction of threat. Moreover, in one pilot study we conducted five eagle playback experiments in which the speaker was positioned at a height of 15 m within the main tree canopy (Schel, 2009), but this did not yield any vocal responses from the

monkeys either, contradicting the notion that eagles within the canopy are perceived as more dangerous.

We also conducted experiments with chimpanzee vocalizations and chimpanzee models (Schel, 2009) to which the monkeys mainly responded cryptically. If calls were produced ( $N = 4$  to chimpanzee pant hoots and  $N = 8$  to chimpanzee models), calling responses were generally identical to responses to leopard growls and leopard models, although the total duration of calling was higher in response to leopard-related stimuli. Inter-

estingly, we observed two instances during which an injured adult male Guereza colobus monkey was surrounded by hunting chimpanzees. In both cases, the males produced two-phrase roaring sequences, typical of encounters with leopards and chimpanzees. The prediction that two different predator classes can elicit the same response if their perceived threat is equal (in this case, e.g., an eagle pursuing a monkey through the canopy, but also a group of hunting chimpanzees closing in and pursuing a monkey through the canopy) is clearly not supported by

Table 3  
Studies That Investigated the Alarm Call System of Different Mammal Species

Species	Alarm Call System (PRIMATES)				
	Predator labeling	Urgency response	Mixed	Graded	Call sequences
Lemuroids					
<i>Propithecus verreauxi</i>			Fichtel & Kappeler, 2002		
<i>P. v. coquereli</i>			Fichtel & v. Schaik, 2006		
<i>Lemur catta</i>	Macedonia, 1990				
<i>Eulemur f. rufus</i>		Fichtel & Hammerschmidt, 2002	Fichtel & Kappeler, 2002		
<i>Varecia variegata</i>		Macedonia, 1990			
Callitrichids					
<i>Saguinus fuscicollis</i>	Kirchhof & Hammerschmidt, 2006				
<i>Saguinus mystax</i>					
Cebids					
<i>Cebus capucinus</i>			Fichtel et al., 2005, Digweed et al., 2005		
Cercopithecines					
<i>Cercocebus atys</i>				Range & Fischer 2005	
<i>C. aethiops</i>	Struhsaker, 1967 Seyfarth et al., 1980				
<i>C. campbelli</i>	Zuberbühler, 2001				
<i>C. diana</i>	Zuberbühler et al., 1999				Zuberbühler, 2002 Arnold & Zuberbühler 2006, 2008
<i>C. nictitans martini</i>					
<i>Papio c. ursinus</i>				Fischer et al. 2001	
Hylobatids					
<i>Hylobates lar</i>					Clarke et al. 2006
Alarm Call System (NON-PRIMATES)					
Species	Functionally referential	Urgency response	Mixed	Graded	Call sequences
Sciurids					
<i>Cynomys guinisoni</i>	Slobodchikoff et al., 1991 Kiriazis & Slobodchikoff, 2006				
<i>Marmota spp.</i>		Blumstein & Armitage, 1997; Blumstein, 1999			
<i>Spermophilus beecheyi</i>		Owings & Virginia, 1978			
<i>Spermophilus beldingi</i>		Leger et al., 1980			
<i>Tamiasciurus hudsonicus</i>	Greene & Meagher, 1998				
Murids					
<i>Parotomys brantsii</i>		Le Roux et al., 2001		Le Roux et al., 2001	
Herpestids					
<i>Suricatta suricatta</i>			Manser, 2001 Manser et al., 2001		

these anecdotes. In other studies, differences in threat or urgency also only had minor effects on monkeys' alarm calling behavior and usually did not cause alterations of alarm call types (Seyfarth et al., 1980; Zuberbühler, 2000, but see Fichtel & Hammerschmidt, 2002). It therefore seems justified to conclude that differences in threat only had minor effects on calling behavior of black-and-white colobus monkeys, but more systematic future studies might tell a different story.

(c) *Imminent behavior.* Another theoretical position is that different types of alarm calling behavior do not refer to different classes of predators, but are indicative of the behavioral response the caller is about to perform (, e.g., approach the predator, attack the predator, move away from the predator; Smith, 1977, 1996). Predator type and appropriate antipredator behavior are strongly associated, but callers may only be signaling their own forthcoming behavior in these instances, regardless of predator type. It is interesting that the main behavioral responses observed in conjunction with the different vocal responses were rather similar in this study. In 90% of vocal responses to leopards and in 67% of vocal responses to eagles, King colobus males rushed toward the location from where the stimulus was broadcast. This happened in 58% of leopard trials and 75% of eagle trials in Guereza colobus males. Although the behaviors were identical (approaching the speaker), this may have happened for different reasons. King colobus and Guereza colobus have been observed to chase eagles away by running toward them through the dense canopy and roaring fiercely. To leopards, callers also approach but usually keep a safe distance from the ground, probably to monitor the predator and inform it that it has been detected.

(d) *Call combinations.* Finally, the fact that black-and-white colobus monkeys organize their signals into sequences using one or more different vocal signals is not a novel finding (e.g., Arnold & Zuberbühler, 2006a, 2006b; Marler, 1972; Robinson, 1984; Zuberbühler, 2002), but very few systematic studies have been conducted to examine the communicative significance or meaning of such sequencing behavior (Arnold & Zuberbühler, 2006a, 2006b, 2008; Clarke et al., 2006; Zuberbühler, 2002). In line with these recent studies, black-and-white colobus monkeys' roaring phrases appear to serve as units that obtain their meaning only once they are combined into higher-order sequences, a feature already discussed by Marler (1977). The number of roaring phrases given before the final low phrase in each sequence might encode predator type.

In sum, we have shown in this study that these monkeys combine different call types in context-specific vocal responses, relying primarily on perceptual salience of "few" versus "many" in the number of roaring phrases produced before the last low-pitched phrase of a sequence. Whether these differences in call sequencing serve to encode predator type, type of threat, urgency of the situation or the caller's imminent behavior is a largely unresolved matter that requires further empirical work. As so often with field studies, it was not possible to access any of the caller's mental representations, motivations or differences in arousal (see Fichtel, Hammerschmidt, & Jürgens, 2001 for captive squirrel monkeys). Instead, we drew inferences about these possible underlying psychological variables from the observed behavioral patterns in relation to existing models of alarm calling behavior (see Table 3). In our data, monkeys

showed robust responses to different predator types, regardless of differences in threat, and the major way of encoding predator class was by varying the number of phrases to generate roaring sequences and by combining these with or without snorts.

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