Published in Animal Behaviour, Vol. 78, Issue 1, 2009, p. 35-44
which should be used for any reference to this work

The alarm call system of female Campbell's monkeys

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ARTICLE INFO

Keywords:
alarm call
Campbell's monkey
Cercopithecus campbelli
evolution of language
predation
referential
semantic

Field studies on male forest guenon alarm-calling behaviour have revealed a number of intricacies about how these primates use vocalizations to protect themselves from predation. In these species, the vocal behaviour of adult females is often different from that of the males, but little systematic work has been done. Here, we describe the alarm call system of female Campbell's monkeys, *Cercopithecus campbelli*, in their natural forest habitat in western Ivory Coast. We found that in response to disturbing events, females produced three basic alarm call types, 'wak-oos', 'hoks' and acoustically variable 'trill' calls, consisting of repeated and rapidly ascending (RRA) pulses, which varied systematically in the temporal and frequency domains. Using observational and experimental data we were able to demonstrate that the RRA calls consisted of four acoustic variants, which could be associated with specific contexts, allowing listeners to draw inferences about the type of disturbance experienced by the caller. We also compared the alarm call behaviour of free-ranging individuals with published results from captivity. As predicted, captive individuals failed to produce predator-specific alarm calls, but they also produced an RRA variant in response to humans that was absent in the wild. We discuss the relevance of these findings in terms of their broader potential impact on evolutionary theories of primate communication.

Most forest guenons show a marked age–sex difference in their vocal behaviour (Gautier & Gautier 1977). Adult females and their subadult offspring typically produce a diverse repertoire of close-range vocal signals, which serve various functions during their daily activities (see Gautier 1975, 1978 for examples in the wild and Lemasson et al. 2004; Lemasson & Hausberger 2004 for captive Campbell's monkeys, *Cercopithecus campbelli campbelli*). The single adult males of forest guenon groups, in contrast, behave in markedly different ways. They rarely participate in any of these vocal interactions, but instead produce a small range of low-pitched and high-amplitude calls that carry over considerable distances through the dense forest vegetation. These male loud calls are typically given in response to disturbances, but sometimes also without any apparent reason. The calls tend to affect the locomotor behaviour of conspecifics, and a range of studies has shown that they can convey something about the call-eliciting external referent, usually some sort of a disturbance such as the presence of a predator (Zuberbühler 2000c, 2001; Arnold & Zuberbühler 2006a, 2008; Arnold et al. 2008).

While the vocal behaviour of guenon males is relatively well studied for a number of species, comparably little progress has been made with the females and subadults. In most species, female calls are soft low-amplitude signals, audible only over relatively short distances. This makes systematic recording difficult, unless the animals are well habituated to the presence of human observers and regularly forage in the lower forest canopy. Studies on captive Campbell's monkeys have reported considerable acoustic diversity in the vocal behaviour of adult females, with much of the observed variation caused by changes in the social and ecological environment (Lemasson et al. 2003, 2004, 2005; Lemasson & Hausberger 2004). Similarly, studies on Diana monkeys, *Cercopithecus diana diana*, in the Taï Forest of Ivory Coast demonstrated that adult females produced acoustically distinct alarm calls to different

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predators (Zuberbühler et al. 1997), while their contact calls varied acoustically depending on context (Uster & Zuberbühler 2001).

In this study, we investigated the alarm-calling behaviour of free-ranging Campbell's monkey females of Taï Forest, Ivory Coast. The species has already been investigated before, although the attention has been on the adult males (Zuberbühler et al. 1999; Zuberbühler 2000b, 2001, 2002; Wolters & Zuberbühler 2003). Adult males produce a range of basic call types in response to external events, such as falling trees, leopards, *Panthera pardus*, and crowned eagles, *Stephanoaetus coronatus* (Zuberbühler 2003). These calls are meaningful in the sense that nearby listeners respond to them as if they had witnessed the call-eliciting event themselves, a phenomenon that also crosses species barriers (Zuberbühler 2000c; Rainey et al. 2004a, b). Another relevant finding was that Campbell's monkey males combine different call types into structured sequences that can function as carriers of meaning (Zuberbühler 2002; K. Ouattara A. Lemasson & K. Zuberbühler, unpublished data), a behaviour also seen in wild putty-nosed monkeys, *Cercopithecus nictitans* (Arnold & Zuberbühler 2006a, b, 2008; Arnold et al. 2008).

Given the general significance that vocal signals have for primates when interacting with their predators (e.g. Seyfarth et al. 1980) and in light of previous results from captivity and the wild, we predicted that female Campbell's monkeys produced predator-specific alarm calls, even though previous research efforts have not revealed any interesting patterns (Zuberbühler 2001). We were also interested in how the vocal behaviour of free-ranging monkeys compared to what has already been described in captivity (Lemasson 2003; Lemasson et al. 2004).

To address these points, we monitored the adult females of six Campbell's monkey groups in the Taï Forest, two of which were fully habituated to human observers. Data were collected both during the females' responses to naturally occurring disturbances and by simulating the presence of natural predators with customized visual and acoustic predator models.

METHODS

Study Groups

Data were collected in the Taï National Park of western Ivory Coast in a study area adjacent to the Taï Monkey Project Research Station (5° 50′N, 7° 21′W) between January 2006 and September 2007. Two Campbell's monkey groups had been followed by researchers and field assistants for more than 10 years. Group members were fully habituated to the presence of observers and individually known. The responses of some females of four additional semihabituated groups to predator models were added to the database. Study groups consisted of one adult male and three to seven adult females with their offspring.

Natural Calling Behaviour

Natural calling events were recorded from the two habituated groups. For this purpose, a focal animal was selected by the observer (K.O.) and subsequently monitored for a 15 min period between 0800 and 1700 hours GMT. During each period, all her vocalizations, as well as her general behaviour (travel, forage, rest, groom, aggression), and any unusual event immediately preceding a vocalization were recorded. If an unusual and relevant event occurred at other times, such as detection of a predator, calls from all group members were collected using ad libitum sampling (Altmann 1974). The total observation time was about 2000 h. Focal animal samples amounted to a total of 193 h, during which we also recorded three leopard encounters (0.016/h) and 11 crowned eagle encounters (0.057/h). In addition, a field assistant also observed the monkeys independently for an additional 800 h during which he recorded six eagle and two leopard encounters.

Recordings were made with a Sony TCD D100 stereo cassette recorder and a Sennheiser ME88 microphone. If necessary, spoken comments were made simultaneously, using a Lavallier microphone, and later transcribed. With this protocol, about 2000 alarm calls were recorded from the different females of all groups. A large majority of alarm calls were given in response to one of the following events: (1) presence of a predator (leopard, crowned eagle), (2) male Diana monkey alarm call to a predator, (3) sudden appearance of a flying animal (e.g. bird, flying squirrel), (4) sudden movements by the observer, (5) risky locomotion by the caller within the canopy (descending from tree; jumping to another branch).

Predator Experiments

We studied the females' alarm call behaviour more systematically by presenting visual predator models (leopard, crowned eagle and Gaboon viper, *Bitis gabonica*) and acoustic predator models (leopard and crowned eagle), five types of stimuli in total, which allowed us to investigate the monkeys' natural response to these predators more systematically. Each stimulus type was presented once to six of seven different groups. From the moment of detection, we determined the first call uttered by an adult female and we monitored the vocal response of all adult females for the first 3 min. Both acoustic and visual predator models have been used successfully before in primate alarm call studies, and these studies have shown that both modalities work equally well to simulate predator presence (Cheney & Seyfarth 1985; Hauser & Wrangham 1990; Zuberbühler 2003; Coss et al. 2007; Arnold et al. 2008).

The following conditions had to be met before an experiment could be conducted. First, the observer had to establish contact with the group for at least 30 min during which no alarm calls were produced by any group members. Second, focal animals had to be less than 10 m off the ground to ensure sufficient recording quality, although the usual recording distance from the habituated individuals was typically 5 m or less. Third, in visual trials, the predator model had to be positioned by a field assistant on the projected travelling route so that only a member of the study group detected the model first. Campbell's monkeys often associate with other monkey species, and if a member of another primate species detected the model first, the trial was discounted.

For eagle trials, the model was positioned in the canopy at an elevation of 2–3 m; for leopard and snake trials, the model was presented on the ground. Eagle shrieks were recorded in the study area by K.Z.; leopard growls were purchased from the National Sound Archive, London (see Zuberbühler et al. 1997 for spectrographic representations of the playback stimuli). All acoustic stimuli were broadcast with a Sony WMD6C professional Walkman connected to a Nagra DSM speaker-amplifier. Stimulus amplitude was adjusted so that the calls sounded natural to a human observer at a distance of about 20 m. Previous research has shown that the amplitude of predator vocalizations had no effect on the monkeys' alarm call responses, provided they were presented within a natural range (Zuberbühler 2000a).

Acoustic Analyses

Pilot observations indicated that adult female Campbell's monkeys produced at least three basic and acoustically distinct alarm calls to external disturbances, and these calls could be

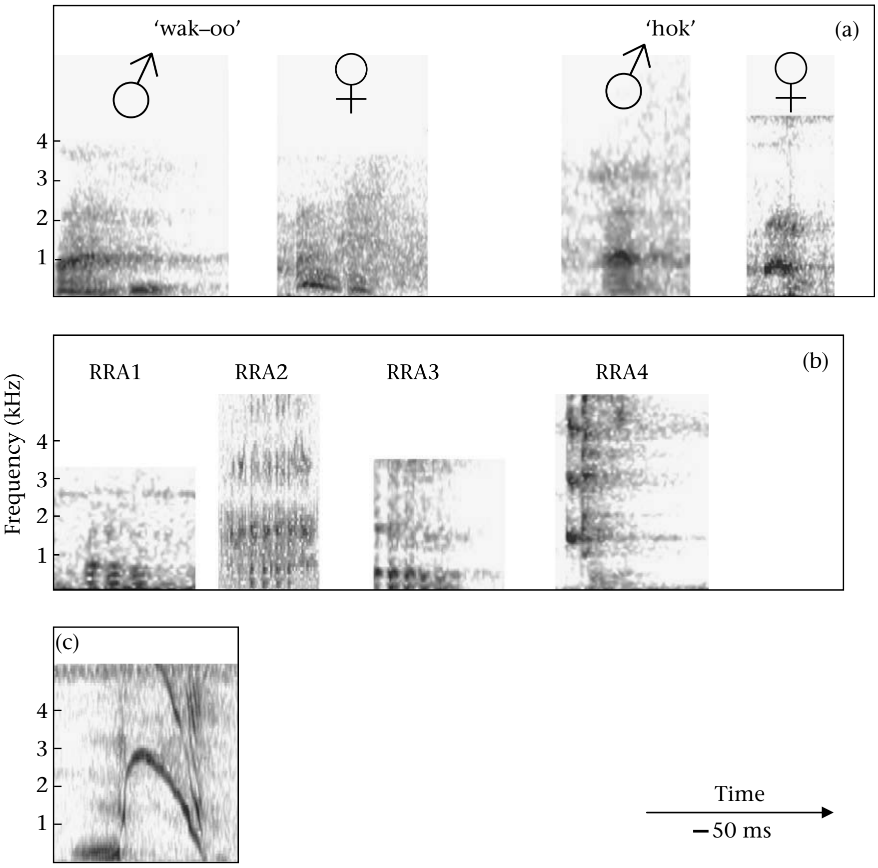

Figure 1. Spectrographic representations of call types: (a) 'wak-oo' and 'hok' alarm calls produced by adult male and females, (b) acoustic variants of female RRA alarm calls, (c) female contact call (CH). RRA2 was never heard in the wild population; the call depicted was recorded in captivity. RRA3 and RRA4 calls have never been recorded in captivity. CH and RRA1 calls were recorded both in captive and wild populations. In (b) the RRA2 call was amplified relative to the other calls.

easily distinguished by ear. The first two were given to aerial dangers and resembled some of the male loud calls in their basic acoustic features (Zuberbühler 2001; K. Ouattara, A. Lemasson & K. Zuberbühler, unpublished data). One of them, the 'wak-oo', consisted of two components, 'wak' and 'oo', which were separated from each other by about 0.06 s. A second one, the 'hok' consisted of a single utterance with little frequency modulation (Fig. 1a).

All spectrographic displays and basic acoustic analyses were conducted using Raven (Cornell Laboratory of Ornithologis, Ithaca, NY, U.S.A.) and ANA (Richard 1991) to extract a number of basic acoustic parameters. Statistical analyses were conducted with Minitab 15 (Minitab Inc., State College, PA, U.S.A.) and Statistica 7 (Statsoft, Tulsa, OK, U.S.A.). Figure 2 illustrates the main parameters extracted from the third basic alarm call type given by the females, a repetitive rapidly ascending call, or 'RRA' call.

The RRA calls have been described extensively in previous captive work (Lemasson 2003; Lemasson et al. 2004). This call is commonly produced in response to disturbances and exhibits considerable acoustic variation, which can be discriminated by ear (Lemasson et al. 2004) and described in terms of a number of basic acoustic measures (Fig. 1b). The females also produced a large range of contact calls (CH: 'combined harmonic calls'), whose acoustic structure is characterized by an arched frequency modulation. These calls are typically produced during peaceful affiliative interactions or while approaching another group member, usually as part of a vocal exchange (see Struhsaker 1970 for a field study and Lemasson et al. 2003, 2004, 2005; Lemasson & Hausberger 2004 for captive studies; Fig. 1c).

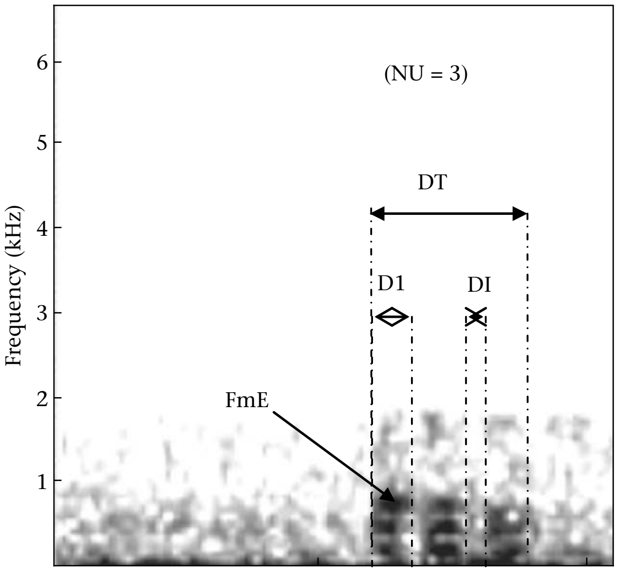

Figure 2. Spectrographic representation of an RRA1 call and illustration of the basic acoustic parameters extracted: NU = number of units, DT = total call duration; D1 = first unit duration, DI = interunit duration, FmE = peak frequency.

Table 1
Acoustic measurements taken from the four basic RRA call variants

Calls	Individual	No. of units	Peak frequency (Hz)
RRA1	Female 1 (N=20)	3±0.10	710±16
	Female 2 (N=20)	3.35±0.15	687±31
	Female 3 (N=20)	3.05±0.17	689±29
	Overall mean	3.13±0.08	693±15
RRA2*	Overall mean (N=25)	5.8±0.28	1917±267
RRA3	Female 1 (N=20)	5.2±0.24	748±22
	Female 2 (N=20)	4.65±0.16	701±15
	Female 3 (N=20)	5.15±0.15	748±8
	Overall mean	5±0.11	732±9
RRA4	Female 1 (N=20)	2.45±0.15	5328±85
	Female 2 (N=20)	2.8±0.11	3420±305
	Female 3 (N=20)	2.65±0.13	2508±113
	Overall mean	2.63±0.08	3752±188

Numbers represent averages calculated from three different females, each contributing equally to each call type. Means are given ± SE.

* Not recorded in Taï, results from five captive females (Lemasson et al. 2004).

Context-specific Use of Alarm Calls

To determine the communicative function of the different female alarm calls, we focused on the very first call given by a female in response to a disturbance. However, females often responded with series of alarm calls that consisted of different call types. Thus, we also determined the number of different calls (contact and alarm calls) produced in the first 1 min and during the first 3 min.

RESULTS

The Alarm Call Repertoire: Observational Data

We were able to record 795 alarm calls from six females of the two habituated groups (group 1: $N = 464$; group 2: $N = 331$). The vast majority of recordings were 'RRA' alarm calls (group 1: 98.3%; group 2: 98.2%), while 'wak-oo' and 'hok' alarm calls were recorded only rarely ($N = 8$ and 6, respectively). The RRA calls were acoustically variable and could be discriminated into four different call variants (RRA1–4) based on their basic acoustic features. We measured the acoustic features of a total of 180 calls (RRA1, RRA3 and RRA4) from three habituated females using spectrograms of maximum quality, that is, 20 calls per female and per call type. All RRA calls consisted of repeated short utterances, separated by about 0.15 s, but they differed significantly in the number of repetitions and in their peak frequency measures (Table 1). RRA1 and RRA3 consisted of lower-pitched units compared to RRA2 and RRA4, while RRA1 had fewer units than RRA3. We failed to record any RRA2 calls in the wild, a call well described in captivity which is relatively soft and audible up to about 5 m (Lemasson 2003; Lemasson et al. 2004).

As we failed to detect a normal distribution, we proceeded with two-tailed nonparametric Kruskal–Wallis tests and Mann–Whitney post hoc tests with Bonferroni corrections. The observed acoustic differences between RRA types were very similar across the three females analysed (Fig. 3). Significant differences were found regardless of female identity in the number of units (Kruskal–Wallis tests: female 1: $H_2 = 43.02$, $N = 60$, $P < 0.0001$; female 2: $H_2 = 37.60$, $N = 60$, $P < 0.0001$; female 3: $H_2 = 40.86$, $N = 60$, $P < 0.0001$; see Table 2 for dyadic comparisons), and peak frequency (Kruskal–Wallis tests: female 1: $H_2 = 42.01$, $N = 60$, $P < 0.0001$; female 2: $H_2 = 39.59$, $N = 60$, $P < 0.0001$; female 3: $H_2 = 40.33$, $N = 60$, $P < 0.0001$; see Table 2 for dyadic comparisons). When comparing females, we found no differences in any of the RRA types regarding the number of units (Kruskal–Wallis tests: RRA1: $H_2 = 4.31$, $N = 60$, $P = 0.11$; RRA3: $H_2 = 4.95$, $N = 60$, $P = 0.08$; RRA4: $H_2 = 4.47$, N = 60, $P = 0.10$). No individual differences were also found in the peak frequencies of RRA1 calls ($H_2 = 0.41$, $N = 60$, $P = 0.80$), but females differed significantly in

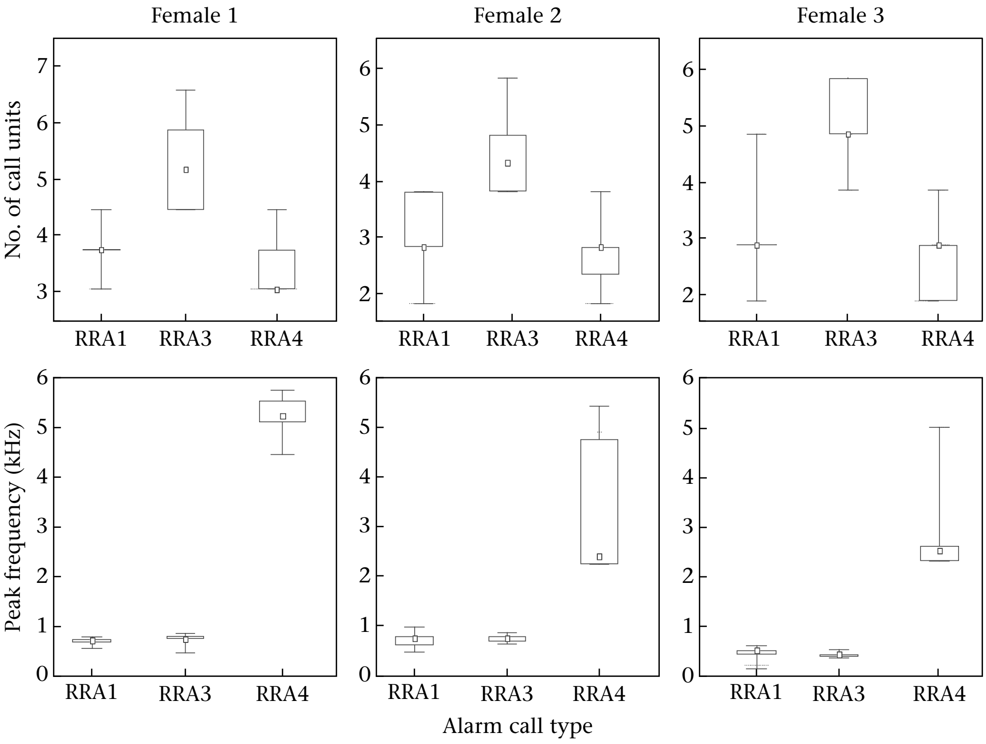

Figure 3. Differences in the acoustic structure of RRA call types. Box plots illustrate the number of subunits and peak frequency of different RRA calls from three different females ($N = 20$/female per call type). Small boxes show the median, large boxes the quartiles and whiskers the range.

Table 2
Results of Mann–Whitney test pair comparisons of RRA calls for each female

Individual	Variable	RRA1 versus RRA3	RRA1 versus RRA4	RRA3 versus RRA4
Female 1	Number of units			
	Z	−5.46	2.99	5.38
	P	<0.0001	0.002	<0.0001
	Peak frequency			
	Z	−2.06	−5.43	−5.46
	P	<0.04	<0.0001	<0.0001
Female 2	Number of units			
	Z	−4.47	2.69	5.47
	P	<0.0001	0.007	0.0001
	Peak frequency			
	Z	−0.09	−5.43	−5.43
	P	0.92	<0.0001	<0.0001
Female 3	Number of units			
	Z	−5.22	1.72	3.51
	P	<0.0001	0.08	<0.0001
	Peak frequency			
	Z	−0.77	−5.46	−5.47
	P	0.43	<0.0001	<0.0001

Bonferroni correction implies a significant difference at $P < 0.017$. $N = 20$/female per call type.

the pitch of their RRA3 and RRA4 calls (RRA3: $H_2 = 8.83$, $N = 60$, $P = 0.012$; RRA4: $H_2 = 35.24$, $N = 60$, $P < 0.0001$). For RRA3, the effect was caused by female 1, which differed significantly from females 2 and 3 (Mann–Whitney *U* tests: $Z = 2.56$, $N_1 = N_2 = 20$, $P = 0.010$; $Z = -2.46$, $N_1 = N_2 = 20$, $P = 0.013$) while females 2 and 3 did not differ from each other (Mann–Whitney *U* test: $Z = 0.73$, $N_1 = N_2 = 20$, $P = 0.46$). For RRA4, the effect was also caused by one female who differed from the others (Mann–Whitney *U* tests: $Z = 4.49$, $N_1 = N_2 = 20$, $P < 0.0001$; $Z = 5.43$, $N_1 = N_2 = 20$, $P < 0.0001$), who did not differ from one another (Mann–Whitney *U* test: $Z = 1.58$, $N_1 = N_2 = 20$, $P = 0.11$).

To estimate the accuracy of the call classifications, K.O. categorized by ear a subset of 795 recordings of female alarm calls from six habituated females, three times each. The intraobserver reliability between the three trials was very high, 92–96%, confirming that the acoustic differences between the different call types are salient to humans and classification is therefore very reliable.

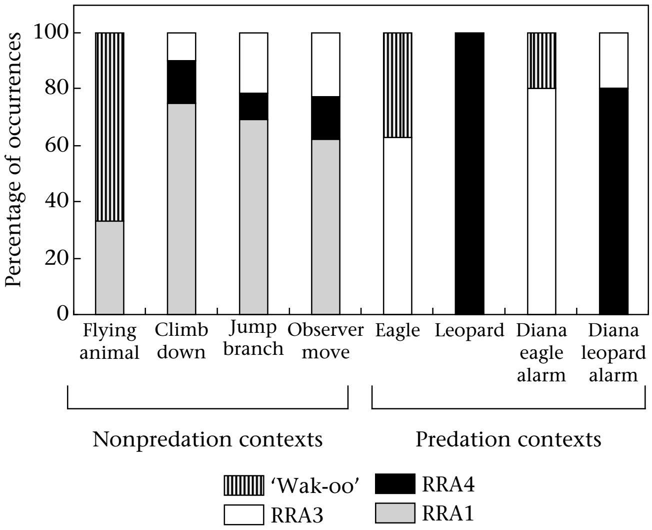

Figure 4. First call types produced immediately after different predatory and nonpredatory disturbances.

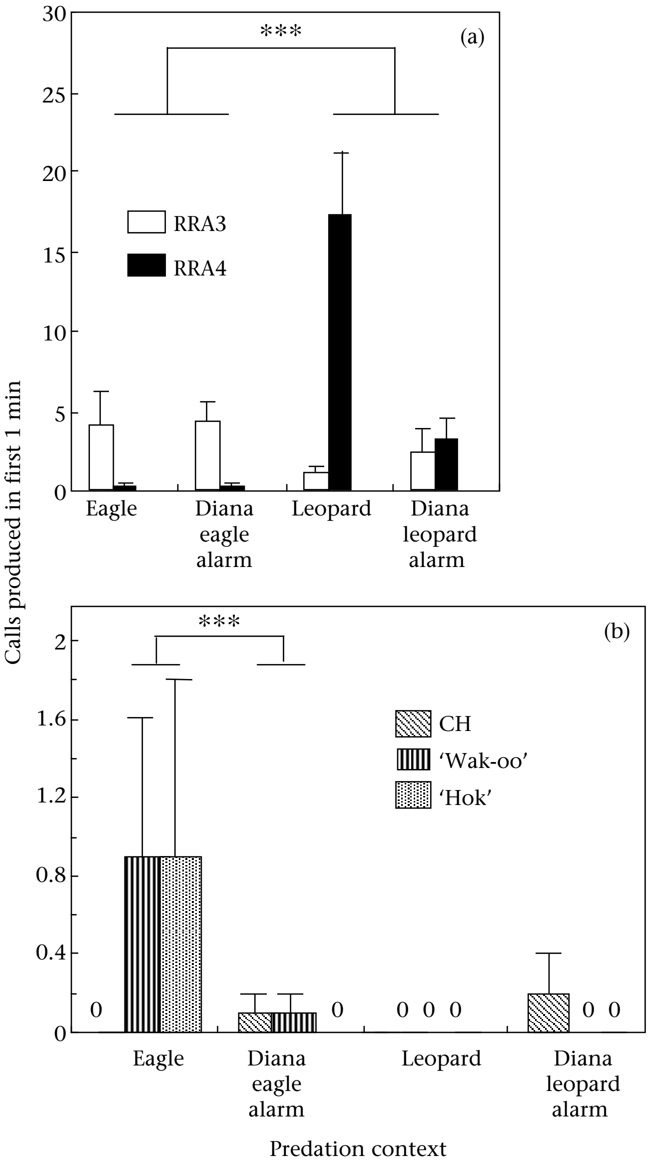

Figure 5. Number of calls produced within the first 1 min after detecting a predator. (a) Frequent call types (RRA3, RRA4). (b) Rare call types ('wak-oo', 'hok' and contact (CH) calls). Means ± SEs are shown. ***$P < 0.001$; Fisher's exact tests.

Context Specificity of Alarm-calling Behaviour

First calls

When considering the first calls only, we were able to record four different call types (wak-oo, RRA1, RRA3 and RRA4) in context-specific ways (chi-square test: $\chi^2_6 = 58.685$, $P < 0.0001$; Fig. 4). Real leopard encounters were excluded, owing to the small sample size ($N = 3$). Chi-square contributions revealed that the RRA1 variant was produced in nonpredatory disturbances, such as after detection of a flying animal (except crowned eagles), while climbing down a tree, while jumping to another branch, or in response to a sudden movement by the observer. We never heard any of the free-ranging females giving an RRA2 variant. The RRA3 and RRA4 calls were typically given in predatory situations and these calls were produced in predator-specific ways (Fisher's exact test: $P < 0.0001$). RRA3 was regularly given in response to crowned eagles and Diana monkeys' eagle alarm calls, but never in response to leopards and

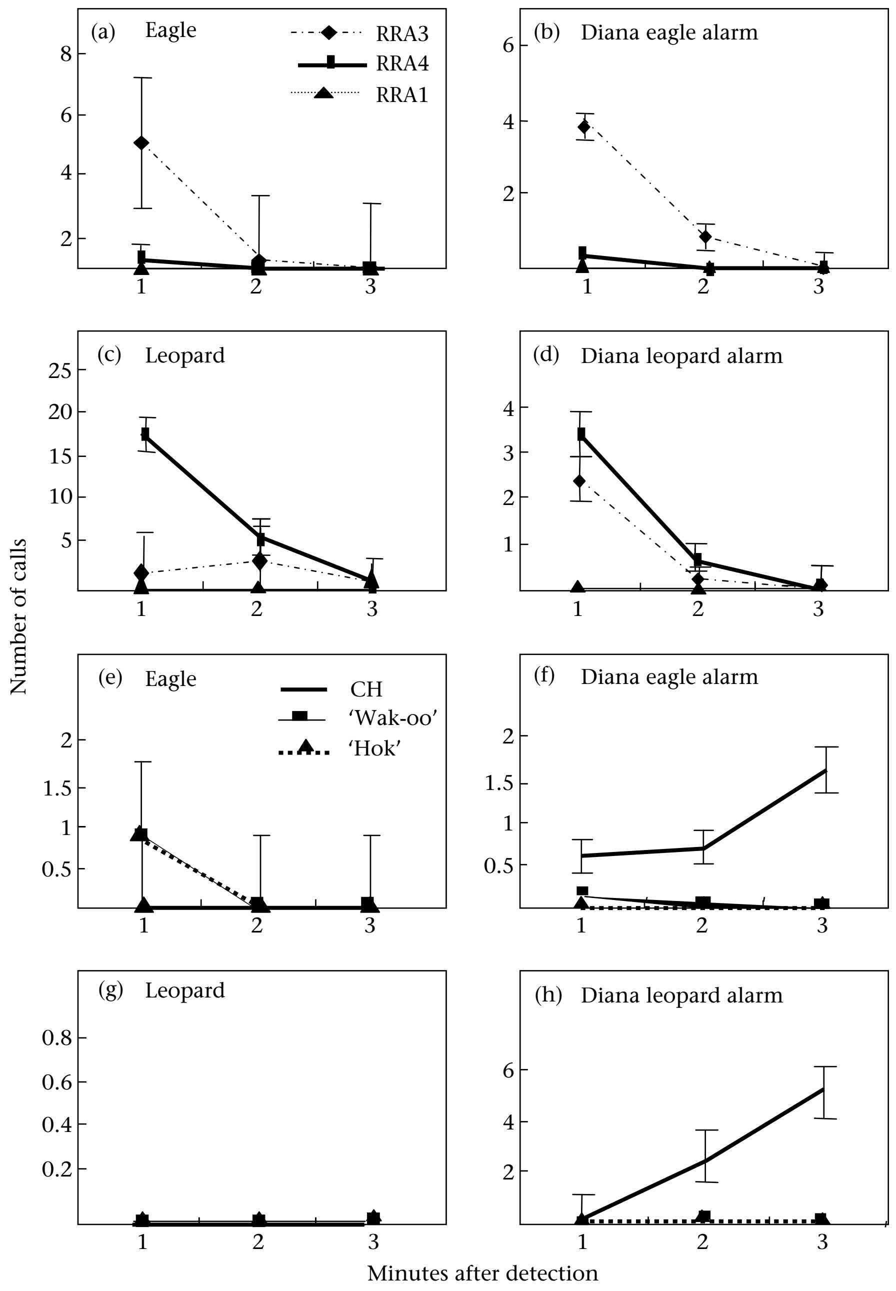

Figure 6. Number of calls produced within the first 3 min after detection of a predator. (a–d) Frequent call types RRA1, RRA3, RRA4. (e–h) Rare call types 'wak-oo', 'hok' and contact (CH) calls. Means ± SEs are shown.

only very rarely to Diana monkeys' leopard alarm calls. RRA4, however, was never given to crowned eagles (or other flying animals), but it was always the first call to leopards, very often the first call to Diana Monkeys' leopard alarm calls, and sometimes the first call to nonpredatory events. The 'wak-oo' alarm call, finally, could be given to any flying animal, including eagles and nonpredatory animals (Fig. 4), particularly if the male had not called yet.

Calls during first 1 min after detection

In the entire first 1 min after detecting a predator, females never produced any RRA1 or RRA2 alarm calls. However, RRA3 and RRA4 alarm calls continued to be strongly associated with detecting a crowned eagle or a leopard, respectively (Fisher's exact test: $P < 0.001$; Fig. 5). 'Wak-oo' and 'hok' calls were only produced in response to direct encounters with crowned eagles and rarely after hearing nearby Diana monkeys' eagle alarm calls (Chi-square test: $\chi^2_1 = 57.83$, $P < 0.0001$; Fig. 5). Females often increased their contact call rates after hearing a Diana monkey giving eagle alarm calls, a behaviour that was not normally observed in other contexts not linked to danger.

Calls during first 3 min after detection

In the first 3 min after detection of a predator, RRA1 and RRA2 continued to remain absent from the females' vocal responses, while RRA3 and RRA4 call rates decreased over time (Fig. 6). In some cases, RRA3 calls were produced in response to Diana monkeys' leopard alarm calls, but rarely in response to a real

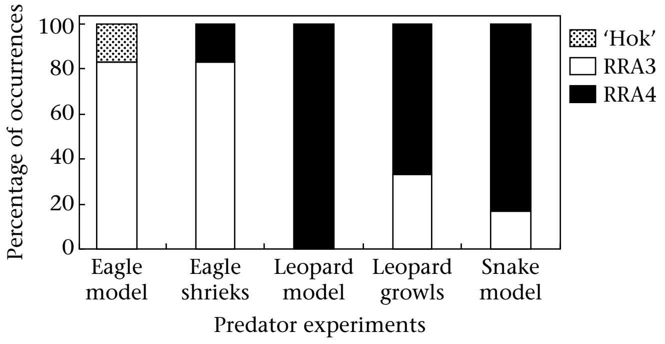

Figure 7. First call type produced immediately after acoustic and visual detection of a predator in the predator experiment.

leopard. K.O. observed subadults giving RRA3 calls to a leopard in both habituated groups, so it is possible that these calls were given by inexperienced individuals. 'Wak-oo' and 'hok' calls were no longer produced during the second and third minutes after eagle encounters, suggesting that these calls are related to urgency. In contrast, contact calls became steadily more common, but only in response to Diana monkeys' alarm calls. Contact calls were not produced after detecting a real predator.

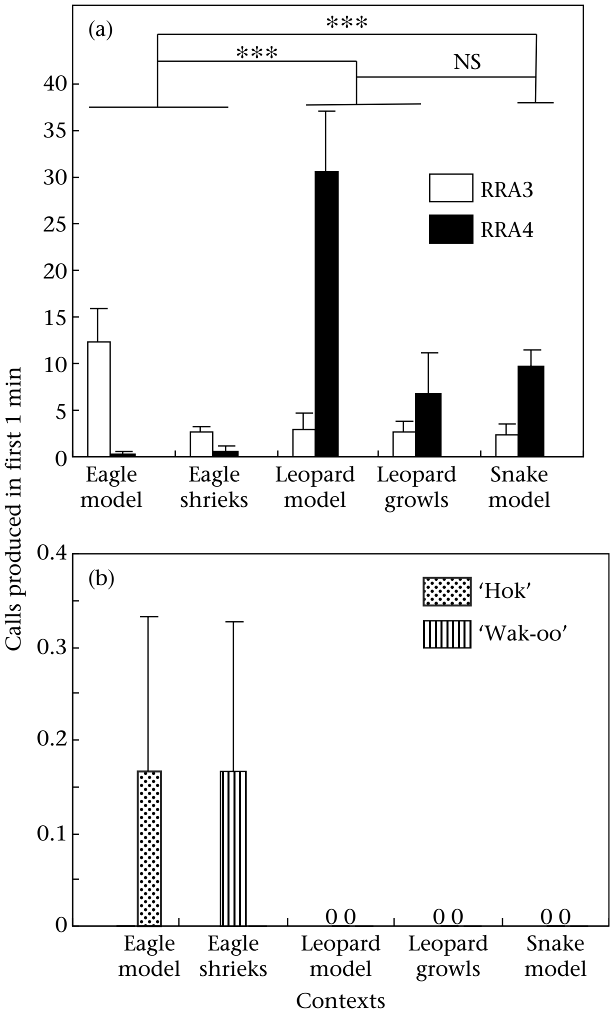

Figure 8. Number of calls produced within the first 1 min after detection of a predator in the predator experiment. (a) Frequent call types (RRA3, RRA4). (b) Rare call types 'wak-oo' and 'hok' calls. Means ± SEs are shown. ***$P < 0.001$, Fisher's exact tests.

Predator Experiments

First calls

After detection of one of the different predator types, 'hok', RRA3 and RRA4 calls differed significantly in the context in which they were produced (chi-square test: $\chi^2_4 = 200.682$, $P < 0.0001$; Fig. 7). As with natural encounters, the models did not trigger any RRA1 or RRA2 calls, but RRA3 and RRA4 calls were given in predator-specific ways (Fisher's exact tests: eagle versus leopard: $P < 0.0001$; eagle versus snake: $P < 0.0001$; leopard versus snake: $P = 0.5$). Some 'hok' alarm calls were given to the eagle model (Fig. 7), but only if the male had not produced his own calls yet, replicating the pattern of 'wak-oo' alarm calls described for natural encounters.

Calls during first 1 min after detection

During the first 1 min the basic pattern remained. RRA3 calls were given to eagle models, while terrestrial predators triggered RRA4 calls (Fisher's exact tests: eagle versus leopard: $P < 0.001$; eagle versus snake: $P < 0.001$; leopard versus snake: $P = 0.21$). In addition, 'hok' and 'wak-oo' alarm calls were only produced for eagles (Fig. 8).

Calls during first 3 min after detection

RRA3 and RRA4 call rates decreased over time to both eagle and leopard models, in both modalities. 'Hok' or 'wak-oo' alarm calls were absent in the second and third minutes after detection (Fig. 9). Contact calls became increasingly more common although this was true only for acoustic predator models. Visual predator models, for some reason, failed to elicit any contact calls at all.

DISCUSSION

Female Campbell's monkeys produced three main types of calls to potentially dangerous events, 'hoks', 'wak-oos' and 'RRA' calls. RRA calls were acoustically variable, and an observer could reliably distinguish four different variants. RRA calls were given to a range of predatory and nonpredatory disturbances, albeit in highly context-specific ways. Two variants, RRA1 and RRA2, had been described for captive individuals in previous research, but only one of them, the RRA1 call, was also given by free-ranging individuals. In this study, RRA1 was given by individuals engaging in dangerous activities or after being startled by sudden movement. RRA2 was never noted in the wild; in captivity it was given to a familiar caretaker or any other human passing by (Lemasson et al. 2004). RRA3 and RRA4 functioned as predator-specific alarm calls, and these calls had not been described in captivity. RRA3 reliably indicated the presence of a crowned eagle, while RRA4 was given to leopards and snakes. The other main alarm call types, the 'hoks' and 'wak-oos', were given to crowned eagles, usually during the early stages of a direct visual encounter and only in cases where the male had not yet given his own alarm calls, similar to what has been found in blue monkeys, *Cercopithecus mitis* (Papworth et al. 2008).

Both wild and captive females produced RRA1 calls in response to similar nonpredatory disturbances. One unusual finding was the striking absence of RRA2 calls in the wild. Of course, it is possible that wild females sometimes produce this call but that they were just not picked up during our recordings. However, individuals of both study groups were very well habituated to human observers and recording distances were regularly less than 5 m (see Methods), suggesting the absence of this call type in the females' repertoire may have been real. Another, although controversial, idea is that the RRA2 call produced by captive individuals is a rare example of a socially transmitted vocal innovation, similar to the pant hoot variants observed in different chimpanzees, *Pan*

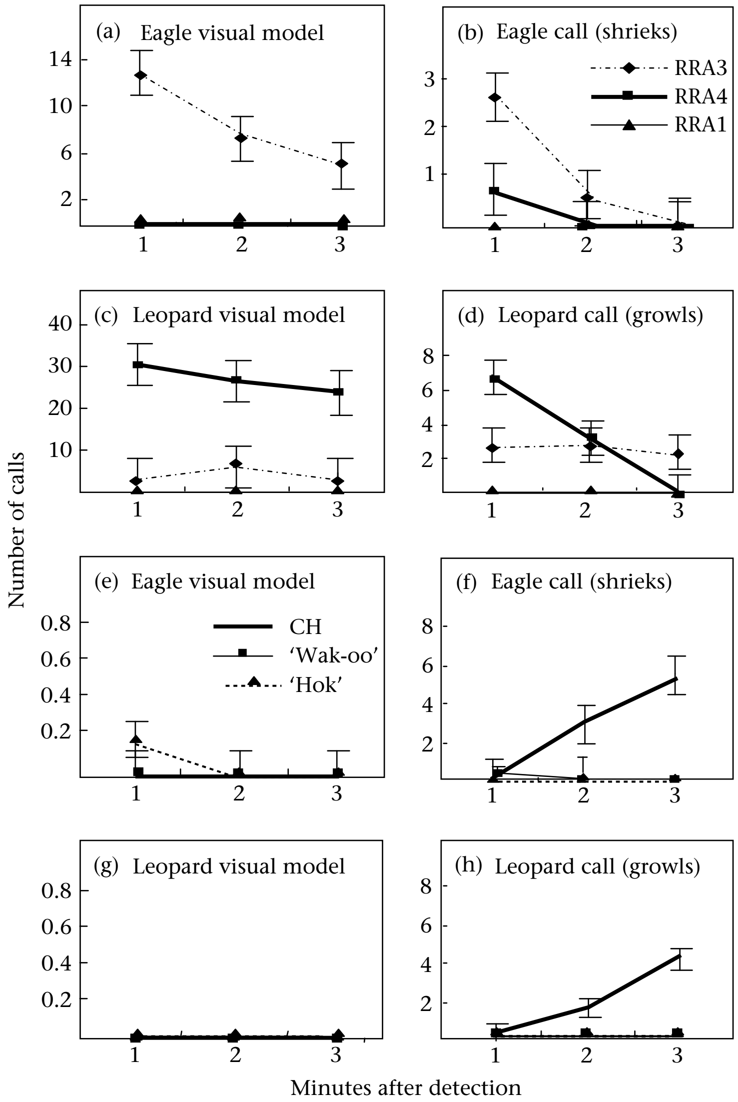

Figure 9. Number of calls produced within the first 3 min after detection of a predator in the predator experiment. (a–d) Frequent call types RRA1, RRA3, RRA4. (e–h) Rare call types 'wak-oo', 'hok' and contact (CH) calls. Means ± SEs are shown.

troglodytes (Marshall et al. 1999). Research on other captive populations would have to be conducted to test this idea. A further possibility is that the call-eliciting context (i.e. a human who sometimes brings food but can also be mildly dangerous) is absent in the wild, although this hypothesis poses problems for explaining the evolution of this call variant. On the other hand, the hypothesis can explain why RRA3 and RRA4 calls to predators were never recorded in captivity. Finally, it is possible that captive adult females simply failed to develop completely and retained parts of their infant vocal repertoire into adulthood (T. Fitch, personal communication). Examining the vocal repertoire of subadult and infant Campbell's monkeys in the wild could test this hypothesis.

In contrast to RRA3 and RRA4, 'wak-oo' calls had been recorded in captivity, but only very rarely. The fact that captive individuals possess a less diverse alarm call repertoire than their wild conspecifics is consistent with the hypothesis that predation is essential for developing or expressing the full vocal capacity that can be achieved by a species (Stephan & Zuberbühler 2008). Work with captive Campbell's monkeys has revealed significant context-specific and socially dependent acoustic variation in their contact calls (e.g. Lemasson & Hausberger 2004; Lemasson et al. 2004, 2005), suggesting that an individual's realized acoustic flexibility is a direct reflection of its communicative needs. As captive animals never interact with predators and probably do not experience situations that require a particular urgent protective response, their alarm call behaviour will also be affected.

Meaning and Function of Campbell Monkeys' Alarm Calls

As mentioned earlier, practised observers can easily discriminate these calls with little difficulty by their auditory features, suggesting that monkeys are likely to be able to do the same, but playback experiments will ultimately have to be conducted to provide conclusive evidence. In particular, it will have to be demonstrated that receivers respond adaptively to the different alarm call types, similar to what has been shown in vervet monkeys, *Chlorocebus pygerythrus*, and other primates (Seyfarth et al. 1980). RRA3 and RRA4, but not RRA1, reliably triggered vocal responses in listeners, suggesting that monkeys were able to discriminate these calls based on their acoustic properties. For now, the conclusion can only be that female Campbell's monkeys are able to produce vocalizations that can convey a range of information about external disturbances that are relevant to other group members, such as whether a predator is present (non-predatory: RRA1 and RRA2; predatory: RRA3 and RRA4) the predator type (crowned eagle: RRA3, ‘wak-oo’, ‘hok’; leopard or snake: RRA4), and possibly the degree of threat (see below). Finally, it is also relevant that in a number of instances RRA3 calls were also given to a leopard, although these were typically young individuals, suggesting that some learning is involved in the acquisition of alarm call behaviour (see also Seyfarth & Cheney 1980).

Predator class was not the only variable that determined the calling behaviour of female Campbell’s monkeys. Our results also showed that calling patterns differed as a function of how the callers learned about the presence of a predator, particularly whether or not they could see the predator, and how much time had elapsed since detection. Contact calls generally became more frequent as time went by, presumably because individuals were trying to re-establish proximity with other group members or because they wished to travel elsewhere. Contact calls were particularly common after hearing the alarm calls of a neighbouring Diana monkey group or after hearing an eagle call, but they were exceedingly rare after a visual encounter with a predator.

‘Wak-oo’ and ‘hok’ calls are interesting because they appear to be given specifically as an immediate response to airborne dangers, often as the very first call in a series. They were more frequent when the eagle could be seen rather than just heard, and typically when the calling females saw the eagle before the adult male or a Diana monkey. One psychologically interesting interpretation is that individuals only produce these predator-specific warning calls if they are the first to spot the danger, not if others have done so already. Again, playback experiments will be needed to address this hypothesis and its alternatives thoroughly.

Referential or Urgency-related?

In the animal communication literature, referential signals are usually defined as ‘encoding information about environmental events’, which is different from encoding individual attributes, such as species, size or motivational state (Evans 1997). According to Macedonia & Evans (1993), a signal qualifies as ‘referential’ if all eliciting stimuli belong to a common category (e.g. ‘leopard’ or ‘ground predator’) and if the signal alone is sufficient to trigger appropriate responses. This view differs from how the term is used elsewhere, particularly in human psychology. Here, the referential act consists of the signaller obtaining and redirecting the receiver’s attention to an external event that is of interest to the signaller, but the means by which this is achieved is somewhat secondary. Referential signalling, in this view, is not equivalent to labelling. Pointing, for instance, would be considered referential, even though the only common feature of the things pointed to (the referents) is that the signaller finds them interesting. Primate alarm calls function in the same way, by referring the attention of the audience to the event the caller finds relevant. Typically such events are urgent in terms of the behavioural reactions they require. Urgency and reference, in other words, are not true alternatives. Our results are consistent with the idea that the alarm call system of female Campbell’s monkeys has the capacity to incorporate information about both predator type and the urgency of the situation.

Gender Differences in Vocal Behaviour

Our study is in line with earlier work that has highlighted the remarkable acoustic differences between the calls of adult male and female guenons. However, we also noted that some of the female alarm calls (‘hok’ and ‘wak-oo’) appear to be acoustically related to the loud calls given to the male in the same context. We have never recorded these calls in subadult Campbell’s monkeys, suggesting that they are part of the adult repertoire. It is possible therefore that both males and females developed the ability to produce these calls after puberty. Unfortunately, however, the patterns of vocal development of male and female repertoires are not really understood in most primate species, and forest guenons in particular (Gautier & Gautier 1977), a difficult but potentially fruitful area of further research.

Acknowledgments

Research was funded by the European Commission (FP6’ ‘What it means to be human’), by Eurocore (‘the Origin of Man Language and Languages’), the French ministry of foreign affairs (‘Egide’) and the Centre Suisse de Recherches Scientifiques in Abidjan. We are grateful to ‘Office Ivoirien des Parcs et Réserves’ (OIPR) for permission to conduct research in the Taï National Park. Our special gratitude goes to the field assistants of the Taï Monkey Project for all their invaluable help during data collection and their fortitude during years of political unrest in the country.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267.

Arnold, K. & Zuberbühler, K. 2006a. The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. *Animal Behaviour*, **72**, 643–653.

Arnold, K. & Zuberbühler, K. 2006b. Language evolution: semantic combinations in primate calls. *Nature*, **441**, 303.

Arnold, K. & Zuberbühler, K. 2008. Meaningful call combinations in a non-human primate. *Current Biology*, **18**, R202–R203.

Arnold, K., Pohlner, Y. & Zuberbühler, K. 2008. A forest monkey’s alarm call series to predator models. *Behavioral Ecology and Sociobiology*, **62**, 549–559.

Cheney, D. L. & Seyfarth, R. M. 1985. Vervet monkey alarm calls: manipulation through shared information? *Behaviour*, **94**, 739–751.

Coss, R. G., McCowan, B. & Ramakrishnan, U. 2007. Threat-related acoustical differences in alarm calls by wild bonnet macaques (*Macaca radiata*) elicited by python and leopard models. *Ethology*, **113**, 352–367.

Evans, C. S. 1997. Referential signals. In: *Perspectives in Ethology* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 99–143. New York: Plenum.

Gautier, J. P. 1975. Etude comparée des sytèmes d’intercommunication sonore chez quelques cercopithecinés forestiers africains. Thèse d’état, Université de Rennes 1.

Gautier, J. P. 1978. Répertoire sonore de *Cercopithecus cephus*. *Zeitschrift für Tierpsychotogie*, **46**, 113–169.

Gautier, J. P. & Gautier, A. 1977. Communication in old world monkeys. In: *How Animals Communicate* (Ed. by T. A. Sebeok), pp. 890–964. Bloomington, Indiana: Indiana University Press.

Hauser, M. D. & Wrangham, R. W. 1990. Recognition of predator and competitor calls in nonhuman primates and birds: a preliminary report. *Ethology*, **86**, 116–130.

Lemasson, A. 2003. Communication vocale et organisation sociale chez la mone de Campbell (*Cercopithecus campbelli*): partage vocal et relations sociales. Ph.D. thesis, Université de Rennes 1.

Lemasson, A. & Hausberger, M. 2004. Patterns of vocal sharing and social dynamics in a captive group of Campbell’s monkeys (*Cercopithecus campbelli campbelli*). *Journal of Comparative Psychology*, **118**, 347–359.

Lemasson, A., Gautier, J. P. & Hausberger, M. 2003. Vocal similarities and social bonds in Campbell’s monkey (*Cercopithecus campbelli*). *Comptes Rendus Biologies*, **326**, 1185–1193.

Lemasson, A., Richard, J. P. & Hausberger, M. 2004. A new methodological approach to context analysis of call production. *Bioacoustics*, **14**, 111–125.

Lemasson, A., Hausberger, M. & Zuberbühler, K. 2005. Socially meaningful vocal plasticity in adult Campbell’s monkeys (*Cercopithecus campbelli*). *Journal of Comparative Psychology*, **119**, 220–229.

Macedonia, J. M. & Evans, C. S. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, **93**, 177–197.

Marshall, A., Wrangham, R. & Clark Arcadi, A. 1999. Does learning affect the structure of vocalizations in chimpanzees? *Animal Behaviour*, **58**, 825–830.

Papworth, S., Böse, A. S., Barker, J. & Zuberbühler, K. 2008. Male blue monkeys alarm call in response to danger experienced by others. *Biology Letters*, **4**, 472–475.

Rainey, H. J., Zuberbühler, K. & Slater, P. J. B. 2004a. Hornbills can distinguish between primate alarm calls. *Proceedings of the Royal Society of London, Series B*, **271**, 755–759.

Rainey, H. J., Zuberbühler, K. & Slater, P. J. B. 2004b. The responses of black-casqued hornbills to predator vocalisations and primate alarm calls. *Behaviour*, **141**, 1263–1277.

Richard, J. P. 1991. Sound analysis and synthesis using an amiga micro-computer. *Bioacoustics*, **3**, 45–60.

Seyfarth, R. M. & Cheney, D. L. 1980. The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Zeitschrift für Tierpsychologie*, **54**, 37–56.

Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*, **210**, 801–803.

Stephan, C. & Zuberbühler, K. 2008. Predation increases acoustic complexity in primate alarm calls. *Biology Letters*, **4**, 641–644.

Struhsaker, T. T. 1970. Phylogenetic implications of some vocalization of *Cercopithecus* monkeys. In: *Old World Monkeys: Evolution, Systematics and Behavior* (Ed. by J. R. Napier & P. H. Napier), pp. 365–444. New York: Academic Press.

Uster, D. & Zuberbühler, K. 2001. The functional significance of Diana monkey 'clear' calls. *Behaviour*, **138**, 741–756.

Wolters, S. & Zuberbühler, K. 2003. Mixed-species associations of Diana and Campbell's monkeys: the costs and benefits of a forest phenomenon. *Behaviour*, **140**, 371–385.

Zuberbühler, K. 2000a. Causal cognition in a non-human primate: field playback experiments with Diana monkeys. *Cognition*, **76**, 195–207.

Zuberbühler, K. 2000b. Interspecific semantic communication in two forest monkeys. *Proceedings of the Royal Society of London, Series B*, **267**, 713–718.

Zuberbühler, K. 2000c. Referential labelling in Diana monkeys. *Animal Behaviour*, **59**, 917–927.

Zuberbühler, K. 2001. Predator-specific alarm calls in Campbell's guenons. *Behavioral Ecology and Sociobiology*, **50**, 414–422.

Zuberbühler, K. 2002. A syntactic rule in forest monkey communication. *Animal Behaviour*, **63**, 293–299.

Zuberbühler, K. 2003. Referential signalling in non-human primates: cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior*, **33**, 265–307.

Zuberbühler, K., Noë, R. & Seyfarth, R. M. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour*, **53**, 589–604.

Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. 1999. Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology*, **113**, 33–42.