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Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*

Abstract One of the most prominent behavioural features of many forest primates are the loud calls given by the adult males. Early observational studies repeatedly postulated that these calls function in intragroup spacing or intergroup avoidance. More recent field experiments with Diana monkeys (*Cercopithecus diana*) of Ta Forest, Ivory Coast, have clearly shown that loud male calls function as predator alarm calls because calls reliably (1) label different predator classes and (2) convey semantic information about the predator type present. Here, I test the alarm call hypothesis another primate, the Campbell's monkey (*C. campbelli*). Like Diana monkeys, male Campbell's monkeys produce conspicuous loud calls to crowned hawk eagles (*Stephanoaetus coronatus*) and leopards (*Panthera pardus*), two of their main predators. Playback experiments showed that monkeys responded to the predator category represented by the different playback stimuli, regardless of whether they consisted of (1) vocalisations of the actual predators (crowned hawk eagle shrieks or leopard growls), (2) alarm calls to crowned hawk eagles or leopards given by other male Campbell's monkeys or (3) alarm calls to crowned hawk eagles or leopards given by sympatric male Diana monkeys. These experiments provide further evidence that non-human primates have evolved the cognitive capacity to produce and respond to referential labels for external events.

Introduction

Vervet monkeys (*Cercopithecus aethiops*) are known to produce acoustically distinct alarm calls in response to leopards, eagles or snakes (Struhsaker 1967). Field playback experiments demonstrated that these alarm calls were alone sufficient to elicit adaptive anti-predator responses from recipients in the same way as the corresponding predator normally would (Seyfarth et al. 1980). When hearing recordings of conspecifics' eagle alarm calls, for example, monkeys looked up into the sky, apparently searching for an eagle. Because the vervets' alarm calls refer to external objects, similar to the way in which human words refer to external objects, they have been called semantic (Seyfarth et al. 1980; Seyfarth and Cheney 1992; but see Evans 1997).

In the meantime, little research has been conducted on other simian alarm call systems. We do not know, therefore, whether the vervet alarm call behaviour, the associated mental capacities and the general theories about non-human primate communication that have been developed from the vervet behaviour are supported by data from other species. Recent work on wild Diana monkeys (*C. diana*) in Ta forest, Ivory Coast, however, suggests that communication about predator classes may be a common feature of primate alarm-calling behaviour. In this species, both males and females produce acoustically distinct alarm calls to crowned hawk eagles (*Stephanoaetus coronatus*) and leopards (*Panthera pardus*) two of their main predators (Zuberbühler et al. 1997). Further experiments suggested that Diana monkeys have a rather sophisticated understanding of the meaning of their own alarm calls. When primed with a playback of a

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conspecific's leopard alarm calls, for example, recipients no longer responded to a subsequent playback of leopard growls, a normally extremely powerful stimulus. Instead, they seemed to have already anticipated the presence of the leopard. If animals were primed with a playback of a conspecific's eagle alarm calls, however, the response to leopard growls was as strong as under unprimed conditions. Since they could not have anticipated the presence of a leopard, the strong response seemed to reflect their surprise when hearing the growls. These and other data were taken to imply that non-human primates are able to form mental representations of different predator categories when hearing conspecific or heterospecific alarm calls (Zuberbühler et al. 1999a; Zuberbühler 2000a, 2000c, 2000d). A related study showed that when giving alarm calls to a leopard or a crowned hawk eagle, Diana monkeys did not respond to the predator's imposed threat (meaning its nearness or direction of attack), but callers reliably labelled the predator's biological category (Zuberbühler 2000b).

Campbell's monkeys (*C. campbelli*) resemble Diana monkeys in a number of ways. Both species live in West African rainforests (Wolfheim 1983), are closely related phylogenetically (Napier and Napier 1985) and live in small one-male groups with several adult females and their offspring (Galat and Galat-Luong 1985). The males of both species produce loud and conspicuous calls in response to a number of disturbances, including the presence of a predator. The two species improve their antipredation strategies by frequently forming mixed species associations and by responding to each other's alarm calls (Zuberbühler 2000c). Early observational studies repeatedly postulated that these loud male calls function in spacing, for example by providing an acoustic 're-union point' for other group members after a disturbance (Struhsaker 1969; Gautier and Gautier 1977). The Diana monkey work, however, is somewhat at odds with the spacing hypothesis, because male calls reliably label different predator classes (Zuberbühler 2000b) and because calls convey information about the predator type present (Zuberbühler et al. 1999a).

This study investigated whether Campbell's monkeys are able to produce acoustically distinct alarm calls to different predators and whether these calls function as warning signals to indicate the presence of a certain predator class. For this, callers must be shown to really label the actual predator category and not, for example, respond to the threat imposed by a predator. Threat-governed alarm call systems have been described for a number of animal species, for example California ground squirrels (*Spermophilus beecheyi*). In this species, individuals produce two acoustically distinct alarm calls, the 'whistles' to raptors and the 'chatter-chat' alarms to terrestrial predators (Owings and Virginia 1978; Owings and Leger 1980). However, these calls are not labels for raptors and terrestrial predators because the squirrels give 'whistles' whenever a predator arrives suddenly and there is little time for escape. 'Chatter-chat' alarms, on the other hand, are given to predators that have been spotted at a distance. Typically, these predators are mammalian carnivores but it is not unusual for the squirrels to give 'chatter-chat' alarms to a distant hawk (Leger et al. 1980). The predators of monkeys in the Ta forest also differ in their hunting techniques, and hence so do the threats imposed on the monkeys. Crowned hawk eagles, for example, suddenly attack through the canopy (Gautier-Hion and Tutin 1988), while leopards approach slowly or hide on the ground (Zuberbühler et al. 1999b). Hence, in observational studies, predator category and imposed threat will naturally be confounded, which makes it difficult to decide to which dimension the monkeys are actually responding when giving alarm calls. In the first experiment, therefore, I simulated the presence of either a crowned hawk eagle or a leopard by playing back typical vocalisations of these two predators. At the same time, I manipulated the predator's apparent threat by varying the distance of the speaker. Second, for alarm calls to function as warning signals for predators, conspecifics must be shown to react to a specific alarm call as they would to the corresponding predator. I predicted that Campbell's monkeys would show the same vocal response to playbacks of predator vocalisations as to playbacks of alarm calls originally given to that predator. I tested the responses of Campbell's monkeys to playbacks of both conspecific Campbell's and sympatric Diana monkey alarm calls to either a leopard or an eagle.

Methods

Study site and species

Field playback experiments were conducted in the Ta National Park, Ivory Coast, between June 1995 and February 1999. The study area consisted of approximately 50 km² of primary rain forest surrounding the field station of the Centre de Recherche en Ecologie (5°50′ N, 7°21′ W) about 25 km south-east of the township Ta. Campbell's monkeys live in one-male groups with several adult females and their offspring. They occupy stable home ranges of approximately 60 ha throughout the study area (R. Noë, unpublished data). By selecting groups that were found at least 1 km apart from each other, I ensured that a particular group was only tested once for a given playback stimulus. The vocalisations of the single adult male are very loud and conspicuous and acoustically different from those of the other group members. Thus the males' vocal behaviour could be studied without making direct visual contact with the group. Male Campbell's monkeys produce two different kinds of alarm calls: (1) attacks of the crowned hawk eagle elicit short alarm calls with a low dominant frequency and little frequency transition over the call, and (2) leopards elicit alarm calls of a longer duration that start with a higher dominant frequency and show a falling frequency transition over the duration of the call. Figure 1 (audio clips S1, S2) illustrates representative exemplars of the Campbell's monkey alarm calls given to two predators.

Materials and data collection

In conducting playback experiments, I systematically searched the study area for monkey groups. Groups were selected from within the 50-km² study area, containing at least 50 different Campbell's monkey groups. Once a group was located, typically by hearing their vocalisations, I determined their geographical location on a
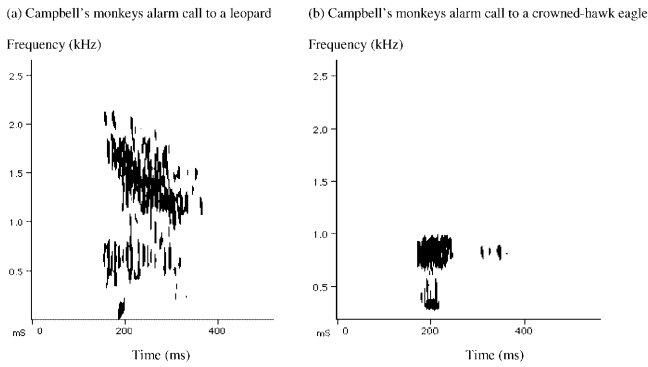
Fig. 1 Spectrograms of the alarm calls of two male Campbell's monkeys to real predators: leopard (**a**) and crowned hawk eagle (**b**) (256-point Fourier transformation, Hanning window function, 684 Hz analysis resolution, 10.77 Hz spectral resolution, 4096 points window length, 0.72 ms temporal resolution)

Fig. 2 Spectrograms of the playback stimuli used in this study (256-point Fourier transformation, Hanning window function, 684 Hz analysis resolution, 10.77 Hz spectral resolution, 4096 points window length, 0.72 ms temporal resolution)

detailed map of the study area and monitored their vocal behaviour to ensure that they were unaware of my presence. Ta primates are subject to significant predation pressure due to human poaching and unhabituated groups show strong anti-predator behaviour to humans. Typically, after giving a few alarm calls, individuals quickly and silently flee to hide somewhere in the canopy. If this occurred, I did not use the group for further experimentation that day. Otherwise, I silently positioned the speaker in the vicinity of the group, but outside their visual range, which is typically less than 20 m in the Ta forest. No group was tested more than once with a particular playback stimulus (see below), and samples sizes therefore reflect the number of different groups tested.

As outlined above, monkeys might be more at risk of a predator when the predator is close. At the same time, predator threat will depend on the density of the local vegetation and the general illumination of the forest. To experimentally vary the degree of threat I varied the *distance* of the speaker to the group to be either 'close' (about 25 m) or 'far' (about 75 m). For each trial, I determined whether the local *vegetation* was 'dense' (thick undergrowth, upper canopy not visible) or 'open' (little undergrowth, several tree crowns visible) and whether the general *illumination* was either 'dark' (no shadows on ground, sky heavily overcast or twilight) or 'light' (shadows visible, sky only slightly overcast, or direct sunlight). For each playback stimulus, I finally varied the amplitude of the stimulus playback (range 77–99 dB, measured at 1 m from the sound source).

The playback equipment was positioned close to the ground (0–2 m). Both crowned hawk eagle and leopards have been observed to vocalise from the ground, indicating that the experiment simulated a natural situation. I simulated predator presence by playing back either predator vocalisations or monkey alarm calls. These was either (1) the shrieks of a crowned hawk eagle, (2) the growls of a leopard, (3) Campbell's monkey eagle alarm calls, (4) Campbell's monkey leopard alarm calls, (5) Diana monkey eagle alarm calls, or (6) Diana monkey leopard alarm calls. All sounds were recorded in the study area except for leopard growls (National Sound Archive, London). Playbacks of predator vocalisations consisted of a 15-s continuous recording. Playbacks of monkey alarm calls consisted of a natural series of alarm calls over a roughly equal period of time. Each playback tape was edited such that a 5-min period of empty tape preceded the actual playback stimulus. During these 5 min, I positioned myself about 25 m away from the playback equipment and started recording the monkeys' vocal behaviour. Predator vocalisations have been successfully used to simulate predator presence in a number of studies (e.g. Hauser and Wrangham 1990). The spectrographic representations of the playback stimuli depicted in Fig. 2 illustrate that all six playback stimuli differ acoustically from each other (to various degrees), the only resemblance being the predator types that ini-
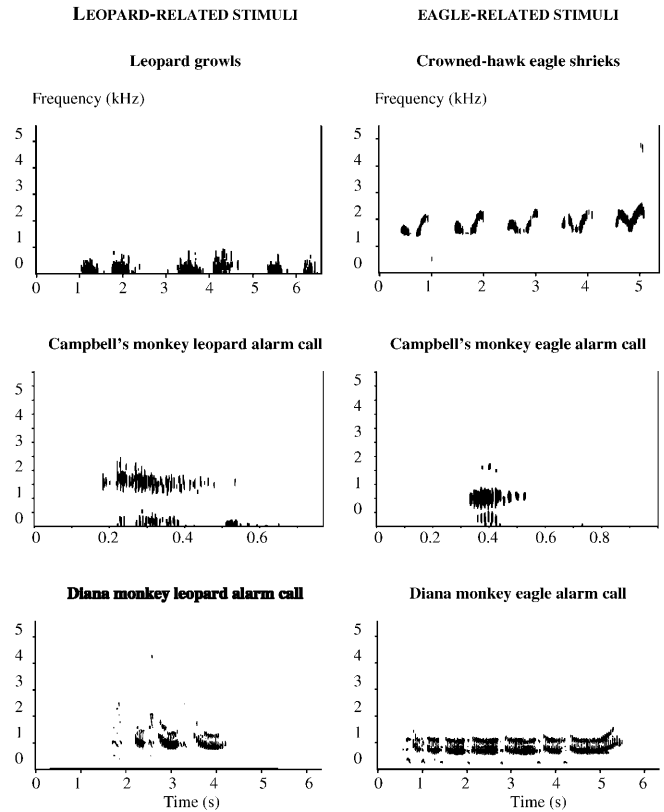
tially caused the calls. In other words, the six different call types used as playback stimuli were all given by (or in response to the presence of) two different predator classes, despite various degrees of acoustic similarity.

Playback stimuli were broadcast with a Sony WMD6C Professional Walkman connected to a Nagra DSM speaker-amplifier. Vocalisations were tape-recorded with a Sony TCM5000EV recorder and a Sennheiser ME88 or ME67 directional microphone. Stimulus intensities were measured with a Radio Shack Sound Level Meter 33-2050, C-weighting, at 1 m distance from the speaker. Spectrograms were made with the software package Canary 1.2.4 (Charif et al. 1995).

Acoustic analyses

Recordings of vocalisations were digitised at a sampling rate of 44.1 kHz with 16 bits accuracy. Quantitative analysis of calls was carried out using a 256-point Fourier transformation with a Hanning window function that resulted in wide-band spectrograms with an analysis resolution of 684 Hz. The accuracy of the spectral parameters was determined by a resolution of 10.77 Hz, implying a window length of 4096 points. The accuracy in the temporal domain was determined by a resolution of 0.72 ms. For illustrative purposes, I did not depict the entire 22-kHz frequency range of the spectrograms if it did not contain any acoustic energy, but calls were never down-sampled. Spectrally, Campbell's monkey alarm calls are best described as having a very low *fundamental frequency* and one prominent band of acoustic energy. This concentration of acoustic energy was termed the *dominant frequency*. The acoustic measurements are defined as follows. *Fundamental*: the fundamental frequency of each call, calculated by counting the number
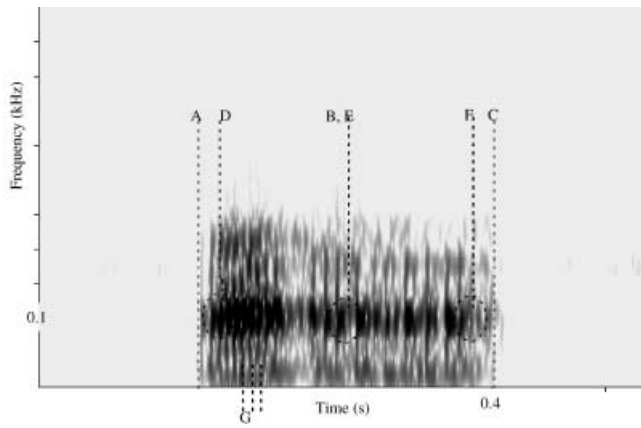
Fig. 3 Spectrogram of a male Campbell's monkey alarm call, showing the acoustic parameters measured. *A* call onset, *B* call middle, *C* call end, *D* DF at call onset, *E* DF at call middle, *F*: DF at call end. *G* striation caused by individual glottal pulses. Early transition: the transitions of the spectral peaks across the call from onset (*D*) to middle (*E*). Late transition: the transitions of the spectral peaks across the call from middle (*E*) to end (*F*) (256-point Fourier transformation, Hanning window function, 684 Hz analysis resolution, 10.77 Hz spectral resolution, 4096 points window length, 0.72 ms temporal resolution)

of striations (i.e. glottal pulses) in the spectrogram over the entire call and divided by the duration of the call. Three different dominant frequency (DF) measurements were taken by determining the frequency at which the highest spectral amplitude occurred in a small range at the beginning, middle or end of the call (see Charif et al. 1995, p. 88) – *DF-onset*: dominant frequency at the beginning of a call; *DF-middle*: dominant frequency in the middle of a call; *DF-end:* dominant frequency at the end of a call. *Duration*: the duration of the call. From the spectral peaks, I calculated the transitions by determining the differences in the spectral peaks in the following way. *Early transition*: the transitions of dominant frequencies across the call from onset to middle. *Late transition*: the transitions of dominant frequencies across the call from middle to end. *Overall transition*: the transitions of dominant frequencies across the entire call. *Suffix*: the presence or absence of a hooting-type element immediately following the call. I chose these particular acoustic parameters and analysis procedures to allow comparisons with a previous study conducted on Diana monkey alarm calls. That study showed that these parameters sufficiently distinguished Diana monkey alarm calls given to crowned hawk eagles and leopards (Zuberbühler 2000b). Figure 3 illustrates how the acoustic parameters were measured.

According to the procedure outlined above, I analysed a particular male's first three calls recorded with sufficient acoustic quality. All calls were given during the first minute after the beginning of a playback stimulus. For the three calls, I calculated the median for each acoustic variable and then used these median values for statistical analyses.

Pseudo-replication

Pseudo-replication has been recognised as a potential problem in all experimental science, including studies using playback stimuli (e.g. Kroodsma 1986). It occurs when treatments are not repeated or are not statistically independent, for example, when the same subject is tested several times using the same stimulus. I addressed this issue by making different playback tapes for each stimulus type (crowned hawk eagle shrieks: *n*=3, leopard growls: *n*=5, Campbell's monkey eagle alarm calls: *n*=3, Campbell's monkey leopard alarm calls: *n*=2, Diana monkey eagle alarm calls: *n*=4, Diana monkey leopard alarm calls: *n*=3). Each playback tape con-

tained the calls of one individual only. Within treatments, I obtained statistical independence by testing different monkey groups throughout the 50-km² area, such that each group heard a particular playback stimulus only once. It is highly unlikely that recipients knew the callers individually. Again, this simulated a natural event because both Campbell's and Diana monkey males leave their natal group as adults to live either solitarily or associated with other species. Solitary males have been observed to produce alarm calls (unpublished data).

Results

Experimentally elicited alarm calls

To predator vocalisations

Ten different groups of Campbell's monkeys either heard playback of leopard growls (*n*=5) or crowned hawk eagle shrieks (*n*=5). The males responded by producing their loud and low-pitched alarm calls. During the first minute, males produced between 6 and 26 alarm calls (median 13) to leopard growls and between 14 and 68 alarm calls (median 19) to eagle shrieks.

To conspecific alarm calls

To determine whether Campbell's monkeys perceived and responded to the acoustic differences between their own leopard and eagle alarm calls, I played back examples of conspecifics' alarm calls to leopard or eagle and analysed the subjects' vocal response. Ten different groups of Campbell's monkeys either heard a playback of a conspecific male's leopard alarm calls (*n*=5) or eagle alarm calls (*n*=5). The males responded by producing their loud and low-pitched alarm calls. During the first minute, males produced between 11 and 15 alarm calls (median 13) to conspecific leopard alarm calls and between 10 and 44 alarm calls (median 34) to conspecific eagle alarm calls.

To Diana monkey alarm calls

To determine whether Campbell's monkeys perceived and responded to the acoustic differences between sympatric Diana monkeys' leopard and eagle alarm calls, I played back examples of male Diana monkeys' alarm calls to leopard or eagle and analysed the subjects' vocal response. Ten different groups of Campbell's monkeys heard either playback of a male Diana monkey's leopard alarm calls (*n*=5) or eagle alarm calls (*n*=5). Again, the males responded with their own corresponding alarm calls and produced between 5 and 24 alarm calls (median 14) to Diana monkey leopard alarm calls and between 9 and 41 alarm calls (median 17) to Diana monkey eagle alarm calls during the first minute.

An analysis of variance shows that Campbell's monkeys gave significantly more alarm calls in response to playback stimuli that indicated the presence of a

Table 1 Analysis of variance of the number of alarm calls given to six different playback stimuli

Predator information	Sum of squares	df	F-ratio	P
Alarm calls (yes/no)	130.000	1	0.662	0.423
Conspecific calls (yes/no)	5.000	1	0.025	0.874
Referring predator (leopard/eagle)	1,687.500	1	8.590	0.007
Error	5,107.800	26		

Table 2 Univariate analyses of variance of the different acoustic features of Campbell's monkeys alarm calls as a function of immediate threat, caller category, and meaning. Data entries indicate F-values, *asterisks* symbolise level of significance [(*)$P<0.1$, *$P<0.05$, **$P<0.01$. ***$P<0.005$; analysis of variance for $n=30$ data points per acoustic feature; $F_{1,22}$ for all variables]

Acoustic feature	Predator threat				Predator information obtained by	
	Distance (close/far)	Vegetation (closed/open)	Stimulus amplitude (dB)	Conspecific calls (yes/no)	Alarm calls (yes/no)	Predator (leopard/eagle)
Call	0.256	0.006	0.333	0.148	0.631	16.881***
Fundamental	0.016	0.780	0.010	0.365	0.083	4.679*
Dominant frequency						
Onset	1.205	0.035	0.031	2.023	0.001	75.861***
Middle	5.727*	0.847	0.974	1.947	0.032	92.310***
End	0.000	0.069	0.433	3.234(*)	1.152	7.002*
Frequency transition						
Early	0.641	0.158	1.099	0.218	0.061	7.187*
Late	1.742	0.028	0.016	0.398	0.699	7.954**
Overall	0.118	0.017	0.156	0.011	0.382	10.101***
Suffix	5.290*	1.780	0.380	1.498	0.235	4.449*

crowned hawk eagle than to stimuli that indicated the presence of a leopard (Table 1). The identity of the caller (i.e. whether or not they heard the actual predator or a conspecific) had no significant effect; the only significant effect was caused by the predator class responsible for the calls, either in the form of vocalisations of the predators or as alarm calls given to the two predators.

Overall acoustic analyses

Although the alarm calls to crowned hawk eagle and leopards are similar in their overall acoustic structure, they differ from each other in subtle ways as a function of predator category (Fig. 1, audio clips S1, S2). Alarm calls to crowned hawk eagles are shorter, have a lower DF at call onset, and show little frequency transition over the entire call. Leopard alarm calls are longer, start with a higher DF, and show a falling frequency transition over the duration of the call. To quantify these observations, I calculated for each male, the median value of all acoustic parameters from the three calls given in response to a playback, leading to a total sample size of $n=30$ per acoustic variable (6 conditions×5 trials each). When each of the six independent variables was investigated for their effect on the different acoustic measurements, the information content or 'meaning' of the playback stimuli (i.e. whether the calls were caused by an eagle or a leopard) explained the largest amount of variation in all acoustic parameters, as indicated by the r^2 val-

ues (Fig. 4). Univariate analyses of variance revealed that all acoustic parameters showed significant differences as a function of the calls' meaning (Table 2). Discriminant-function analysis indicated that only the independent variable 'meaning' had a significant effect on the acoustic variables considered (Wilks' lambda=0.145, $F_{9,14}=9.199$, $P<0.001$). No significant effects were found for the other variables (conspecific: Wilks' lambda=0.540, $F_{9,14}=1.325$, $P=0.307$; alarm call: Wilks' lambda=0.792, $F_{9,14}=0.409$, $P=0.910$; stimulus amplitude: Wilks' lambda=0.767, $F_{9,14}=0.473$, $P=0.870$; vegetation density: Wilks' lambda=0.813, $F_{9,14}=0.358$, $P=0.937$; illumination of surroundings: Wilks' lambda=0.852, $F_{9,14}=0.269$, $P=0.973$; distance to speaker: Wilks' lambda=0.527, $F_{9,14}=1.397$, $P=0.277$).

Effects of predator distance

Table 2 indicates that the acoustic structure of Campbell's monkey alarm calls was strongly affected by the predator class, i.e. whether the playback stimuli referred to a leopard or an eagle. However, the predators' distance also affected the position of the DF in the middle of the call, because close predators tended to elicit calls with a higher middle DF than distant predators. In addition, close predators were less likely to elicit calls with a suffix than more distant predators (Fig. 4, Table 2), suggesting that the distance of the predator may have some additional effects on the acoustic structure of male Campbell's monkey alarm calls.

Fig. 4 Results of acoustic analyses of the different measurements on the alarm calls of different males. Each data point represents the median value for the measurements taken from three alarm calls from a single male

Discussion

Male Campbell's monkeys produce loud alarm calls to leopards and crowned hawk eagles. These alarm calls can be elicited experimentally by playing back predator vocalisations from a concealed speaker. Although the male alarm calls to leopards and eagles were similar in their overall acoustic structure, they differed for a number of parameters as a function of the predator type (audio clips S1, S2). Alarm calls to eagles were shorter, had a lower DF at call onset, and showed little frequency transition over the entire call. Leopard alarm calls, by contrast, were longer, started with a higher DF, and showed a falling frequency transition over the duration of the call. Campbell's monkeys responded to recordings of conspecific alarm calls as if the corresponding predator were present. Males produced leopard alarm calls when hearing leopard growls or conspecific leopard alarm calls and eagle alarm calls in response to eagle shrieks or conspecific eagle alarm calls, indicating that Campbell's monkeys were able to use their own alarm calls to refer to two different external events. Similarly, when hearing the acoustically different alarm calls of sympatric Diana monkeys, Campbell's males consistently responded to the predator type that had originally elicited the Diana monkey alarm calls, indicating that the acoustic structure of the calls served to access associated mental representations of the predators.

Previous work on savannah-living vervet monkeys has shown that individuals respond to playbacks of their own alarm calls with specific escape responses. Playback of leopard alarm calls, for example, caused animals to run into the trees, as they do when detecting a leopard (Seyfarth et al. 1980). The locomotive behaviour of the Ta monkeys in response to predators is far less distinct. In general, playbacks of either of these two predator vocalisations or the corresponding alarm calls do not usually cause immediate locomotive responses in recipients. Monkeys may increase their scanning rates but they do not usually show any immediate escape responses as has been described for the vervet monkeys (Seyfarth et al. 1980). Two different locomotive patterns can be observed, nevertheless, as responses to these two predators. When hearing eagle-related stimuli, adult male Diana and Campbell's monkeys typically move rapidly towards the hidden speaker, apparently to search for and attack the eagle, while the rest of the group stays behind. When hearing growls of a leopard or the leopard alarm calls of other monkeys, the entire group often approaches the speaker, apparently to search for the presumed leopard (Zuberbühler et al. 1999b). For arboreal forest primates, no distinct escape rules exist for these two predators. Both leopards and crowned hawk eagles can attack from below or above, requiring situationally based decisions that depend on the location and type of the predator, the structure of the habitat, and the monkeys' own position within the canopy. A more effective strategy in the forest habitat, therefore, is the transmission of information about the type and distance of the predator and, if effec-

tive, communicating directly to the predator (if that interferes with its hunting strategy, e.g. signalling detection or readiness to attack). In the open habitat, vocally based anti-predator responses seem to be less important. Interestingly, only one of Seyfarth et al.'s 220 playback trials elicited a vocal response from one of the listeners (R.M. Seyfarth, personal communication). Vervet monkeys that had heard an alarm call first became vigilant or fled to safety, but then waited until they had actually seen the predator before giving alarm calls themselves (Seyfarth et al. 1980). In marked contrast, forest monkeys readily respond with their own alarm calls to playback of conspecific and heterospecific alarm calls.

Males of many primate species produce loud and conspicuous calls that carry over long distances (several hundred metres, personal observation), like those described in this study (e.g. Gautier and Gautier 1977). Typically, these calls have been interpreted to function in intra-specific communication, for example to serve as an acoustic focal point for other group members (Struhsaker 1969), to dissuade conspecific neighbouring groups (e.g. Waser 1975) or to keep away solitary males (e.g. van Schaik et al. 1992). Although male Campbell's monkeys may gain fitness benefits if their calls keep away rival males, this study strongly suggests that Campbell's monkey loud calls function as anti-predator signals. At the same time, these calls do not fit the traditional conception of alarm calls as warning signals (e.g. Maynard-Smith 1965), mainly because softer and less conspicuous calls, like those of the adult females, would fulfil the same purpose in a less costly way (Zuberbühler et al. 1997; Uster and Zuberbühler, in press). The remarkably conspicuous acoustic structure of the male alarm calls may have evolved in the context of predator-prey communication. Both Diana and Campbell's monkey males (but not females) have been observed to attack crowned hawk eagles and approach leopards while giving their loud and conspicuous alarm calls (Zuberbühler et al. 1997). Once detected, leopards tend to give up their hiding position and move to another monkey group, probably because their hunting success depends strongly on prey being unaware of their presence (Zuberbühler et al. 1999b). Perhaps natural selection has additionally favoured these loud and low-pitched calls because they are more effective than softer and higher-pitched alarm calls in driving away predators. Natural selection might also favour males who produce consistent acoustic variation in response to the different predator categories, thereby providing important information for relatives. In species where one escape response protects against all predators (for example, where individuals are safe by running into a burrow), natural selection is unlikely to favour different alarm calls for different predators. However, in species that cannot rely on one or a few simple anti-predator responses, individuals will benefit from signals conveying information about the predator class present. Campbell's monkeys fall into this latter group because their arboreal life in the lower forest strata does not provide them with one safe microhabitat that protects them from

predation. Alarm calls, in other words, become useful as labels for discrete concepts of the different predator classes, including their morphology and hunting behaviour.

In conclusion, this study provides another example of primate flexibility in perceiving and understanding their own and other species' vocal signals (Tomasello and Zuberbühler, in press). As signallers, the alarm calls of both Diana and Campbell's monkeys tend to label the categorical features of the predators, while for recipients, alarm calls refer to the different predator types. These and other studies (e.g. Gouzoules et al. 1984) indicate that non-human primates are capable of mentally representing relevant aspects of their social and ecological environment (Tomasello and Call 1997). Convincing evidence that recipients are indeed responding to the meaning of such calls, and not to such aspects as their emotional intensity, come from habituation experiments in which individuals habituated to some calls show dishabituation only when the meanings of the calls are changed (e.g. Cheney and Seyfarth 1988; Zuberbühler et al. 1999a; Zuberbühler 2000c). Similarly, there is evidence that some primates are able to take into account eliciting causal reasons of calls, both social and ecological, rather than simply and directly responding to the physical attributes of the calls themselves (Zuberbühler 2000a, 2000d; Cheney et al. 1995). Finally, this study supports the notion that the learning skills used in call comprehension show almost unlimited flexibility, since primates can learn to use effectively the calls of various other sympatric species, both primate and non-primate. Diana monkeys, for example, understand the meaning and underlying cause of Campbell's monkeys' alarm calls (Zuberbühler 2000c), guinea fowl alarm calls (Zuberbühler 2000d) and different kinds of chimpanzee screams (Zuberbühler 2000a). Particularly puzzling, in this context, is that comparable data of such referential abilities are not available from any free-ranging ape species, the closest possibility being chimpanzees' differential use of food grunts for different amounts of food (Hauser and Wrangham 1987; Hauser et al. 1993). This seems strange, because chimpanzees are also hunted by leopards (Boesch 1991). Moreover, chimpanzees respond to leopards by producing specific alarm screams (Goodall 1986), which Diana monkeys are able to use to infer the presence of a leopard (Zuberbühler 2000a). Hence, it would be highly surprising if chimpanzees were not also able to understand playbacks of their own alarm calls as well as the various alarm calls of other primate species that reliably predict the presence of a leopard. A simple playback experiment that compares the behavioural responses of wild chimpanzees to either Diana monkey eagle or leopard alarm calls, for example, might answer the question whether wild great apes possess the semantic abilities that they have, so far, demonstrated only in the laboratory (e.g. Premack 1970).

References

Boesch C (1991) The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117:220–242

Charif RA, Mitchell S, Clark CW (1995) Canary 1.2 user's manual. Cornell Laboratory of Ornithology, Ithaca, NY

Cheney DL, Seyfart, RM (1988) Assessment of meaning and the detection of unreliable signals by vervet monkeys. Anim Behav 36:477–486

Cheney DL, Seyfarth RM, Silk JB (1995) The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for causal reasoning? J Comp Psychil 109:134–141

Evans CS (1997). Referential signals. In: Owings DH, Beecher MD, Thompson NS (eds) Perspectives in ethology. Plenum, New York, pp 99–143

Galat G, Galat-Luong A (1985) La communauté de primates diurnes de la fôret de Ta, Côte d'Ivoire. Rev Ecol Terre Vie 40:3–32

Gautier JP, Gautier A (1977) Communication in Old World monkeys. In: Sebeok TA (ed) How animals communicate Bloomington, Indiana University Press, Indiana, pp 890–964

Gautier-Hion A, Tutin CEG (1988) Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. Folia Primatol 51:149–151

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge, Mass

Gouzoules S, Gouzoules H, Marler P (1984) Rhesus monkey (*Macaca mulatta*) screams: representational signalling in the recruitment of agonistic aid. Anim Behav 32:182–193

Hauser MD, Wrangham RW (1987). Manipulation of food calls in captive chimpanzees: a preliminary report. Folia Primatol 48:24–35

Hauser MD, Wrangham RW (1990). Recognition of predator and competitor calls in nonhuman primates and birds: a preliminary report. Ethology 86:116–130

Hauser MD, Teixidor P, Field L, Flaherty R (1993) Food-elicited calls in chimpanzees: effects of food quantity and divisibility? Anim Behav 45:817–819

Kroodsma DE (1986) Design of song playback experiments. Auk 103:640–642

Leger DW, Owings DH, Gelfand DL (1980). Single note vocalizations of California ground squirrels: graded signals and situation – specificity of predator and socially evoked calls. Z Tierpsychol 52:227–246

Maynard-Smith J (1965) The evolution of alarm calls. Am Nat 99:59–63

Napier JR, Napier PH (1985) The natural history of the primates, 5th edn. MIT Press, Cambridge, Mass

Owings DH, Leger DW (1980) Chatter vocalizations of California ground squirrels: predator- and social-role specificity. Z Tierpsychol 54:163–184

Owings DH, Virginia RA (1978) Alarm calls of California ground squirrels (*Spermophilus beecheyi*). Z Tierpsychol 46:58–70

Premack D (1970) A functional analysis of language. J Exp Anal Behav 14:107–125

Schaik CP van, Assink PR, Salafsky N (1992) Territorial behavior in southeast Asian langurs: resource defense or mate defense? Am J Primatol 26:233–242

Seyfarth RM, Cheney DL (1992) Meaning and mind in monkeys. Sci Am 267:122–128

Seyfarth RM, Cheney DL, Marler P (1980) Vervet monkey alarm calls: semantic communication in a free-ranging primate. Anim Behav 28:1070–1094

Struhsaker TT (1967) Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In Altmann SA (ed) Social communication among primates. University of Chicago Press, Chicago, pp 281–324

Struhsaker TT (1969) Correlates of ecology and social organisation among African cercopithecines. Folia Primatol 11:80–118

Tomasello M, Call J (1997) Primate cognition. Oxford University Press, New York

Tomasello M, Zuberbühler K (in press) Primate vocal and gestural communication. In: Collin A, Bekoff M, Burghardt GM (eds) The cognitive animal, MIT Press, Cambridge, Mass

Uster D, Zuberbühler K (in press) The functional significance of Diana monkey "clear" calls. Behaviour

Waser PM (1975) Experimental playbacks show vocal mediation of intergroup avoidance in a forest monkey. Nature 255:56–58

Wolfheim JH (1983) Primates of the world. University of Washington Press, Seattle

Zuberbühler K (2000a) Causal knowledge of predators' behaviour in wild Diana monkeys. Anim Behav 59:209–220

Zuberbühler K (2000b) Referential labelling in Diana monkeys. Anim Behav 59:917–927

Zuberbühler K (2000c) Interspecific semantic communication in two forest monkeys. Proc R Soc Lond B 267:713–718

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

Zuberbühler K, Noë R, Seyfarth RM (1997). Diana monkey long-distance calls: messages for conspecifics and predators. Anim Behav 53:589–604

Zuberbühler K, Cheney DL, Seyfarth RM (1999a). Conceptual semantics in a nonhuman primate. J Comp Psychol 113:33–42

Zuberbühler K, Jenny D, Bshary R (1999b). The predator deterrence function of primate alarm calls. Ethology 105:477–490