



ARTICLES

Referential labelling in Diana monkeys

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Animal semantic communication has received considerable theoretical and empirical attention because of its relevance to human language. Advances have been made by studies of alarm-call behaviour in nonhumans. In monkeys, for example, there is evidence that recipients have a fairly sophisticated understanding of a call's meaning; that is, the predator type usually associated with a certain alarm call. Little is known, however, about the mental mechanisms that drive call production in nonhuman primates. In some nonprimate species, it has been found that signallers do not respond to a predator's physical features but instead seem to respond to its relative threat or direction of attack. In these species, therefore, alarm calls do not denote different predator categories but simply reflect different types or levels of danger. Because different predator categories typically impose different types and degrees of threat it is entirely possible that nonhuman primates also respond to threat rather than a predator's category. This study examined how wild Diana monkeys, *Cercopithecus diana*, of the Tai forest, Ivory Coast, label predation events. By altering playback stimuli and the position of a concealed speaker, I investigated whether Diana monkeys respond with acoustically different alarm calls depending on a predator's (1) distance (close versus far), (2) elevation (above versus below), or (3) category (eagle versus leopard). Analysis of male and female alarm-call behaviour showed that Diana monkeys consistently responded to predator category regardless of immediate threat or direction of attack. Data further suggested that, in addition to predator category, monkeys' alarm calls might also convey information about the predator's distance.

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Some animal vocalizations have been described as functionally referential, or semantic, because individuals respond to them as if these calls designate an external object or event (reviewed by [Macedonia & Evans 1993](#); [Hauser 1996](#)). Functional semanticity was first demonstrated in East African vervet monkeys, *Cercopithecus aethiops*, which produce several acoustically distinct alarm calls in response to different predators and recipients respond to these calls as if the corresponding predator were present ([Struhsaker 1967](#); [Seyfarth et al. 1980](#)). These and other studies have challenged the traditional notion of animal vocalizations as purely motivational displays (e.g. [Lancaster 1975](#), page 64) and suggest parallels between animal vocalizations and human language ([Seyfarth & Cheney 1992](#)).

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Recent experiments on Diana monkeys, *C. diana*, have confirmed these findings and suggest that functional semanticity might be relatively common in primate communication. Diana monkeys live in small groups with one adult male and several adult females with their offspring. Adult males and females produce acoustically distinct alarm calls to leopards, *Panthera pardus*, and crowned hawk-eagles, *Stephanoaetus coronatus*, and there is a marked sexual dimorphism in call structure between the male and female alarm calls to these two predators ([Zuberbühler et al. 1997](#)). Playback experiments have shown that females respond to the alarm calls of the male by giving their own acoustically distinct alarm calls as if the corresponding predator were present ([Zuberbühler et al. 1997](#)). Habituation–dishabituation experiments have further demonstrated that the individuals attend to the calls' associated meaning rather than to their acoustic structure alone ([Zuberbühler et al. 1999a](#)). As call recipients, therefore, Diana monkeys do not simply respond to

Table 1. Three types of functional semanticity

Hypothesis	Relevant information	
	For signaller	For recipient
Ground squirrel semantics* (response urgency hypothesis)	Predator distance	Escape urgency
Domestic chicken semantics† (escape strategy hypothesis)	Predator elevation	Escape response
Conceptual semantics‡ (referential labelling hypothesis)	Predator category	Predator category

*Owings & Hennessy (1984).

†Gyger et al. (1987).

‡Pereira & Macedonia (1991).

the physical features of the calls but behave as if they process the associated semantic features. That is, they behave as if they have some sort of a mental representation of the predator category that typically causes the alarm calls (Zuberbühler 2000).

Far less is known, however, about the mental mechanisms that underlie call production in nonhuman primates. It is possible that callers simply respond to very general features of a predator attack, such as a predator's distance and immediate threat or its probable direction of attack, regardless of the predator's biological category. For example, an individual could give one type of alarm call when startled by a close predator and give another one when detecting the same predator at a safe distance. Because most predators use characteristic hunting techniques (e.g. eagles attack suddenly through the canopy, while leopards approach slowly on ground), predator category and attack mode will typically be tightly linked together and therefore potentially confounded in observational and even some playback studies. Because of this, communication about predators in monkeys may be based on a profound 'misunderstanding' between signalers and recipients. Whereas signalers might simply label the spatiotemporal features of a predator attack, recipients could still use these calls as labels to access stored mental representations of the different predator categories.

The vocal behaviour of a number of nonprimate species suggests that noncategorical labelling of predators may be widespread in animal communication. California ground squirrels, *Spermophilus beecheyi*, for example, give 'whistles' to raptors and 'chatter-chat' alarms to terrestrial predators (Owings & Virginia 1978; Owings & Leger 1980), but these calls are not labels for raptors and terrestrial predators. Instead, the squirrels give whistles whenever a predator arrives suddenly and there is little time for escape. Most sudden attacks come from raptors, but occasionally a mammalian carnivore will surprise a squirrel. When this occurs, the mammalian carnivore elicits whistles. Similarly, chatter-chat alarms are given to predators that have been spotted at a distance. Typically, such 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). Although it seems generally true that adult squirrels are capable of producing acoustically distinctive alarm calls to aerial and terrestrial predators, the degree to which such calls are predator specific seems to differ across species. Belding's

ground squirrels, *Spermophilus beldingi*, for example, seem to be even less specific than California ground squirrels: adults give 'trills' to any slow-moving predator that does not pose an immediate threat. Fast-moving predators that impose an immediate threat, however, elicit whistles, again regardless of the predator type (e.g. Mateo 1996).

A second example is the domestic chicken, *Gallus gallus domesticus*. The males possess two acoustically distinct alarm calls, one for aerial and one for ground predators (Gyger et al. 1987). Following playback of aerial alarm calls, hens are more likely to crouch or run towards an area of cover than after ground alarm calls, which usually cause them to adopt an erect 'vigilant' posture (Evans et al. 1993). Cockerels, however, give ground alarm calls to many objects moving on the substrate and aerial alarm calls to many objects moving above in free space, regardless of whether they are predators (Gyger et al. 1987). For example, when video scenes of real predators are shown such that a racoon, a typical ground predator, is either flying overhead or moving on the ground, signalers produce aerial alarm calls in the first case and ground predator alarm calls in the second (Evans & Marler 1995), suggesting that chickens do not respond to the predator category but instead to the spatial characteristics of the threat.

These examples cast doubt on the assumption that monkeys denote the 'categorical' features of a predator when giving alarm calls. Perhaps monkeys simply respond to the 'proxemic' features of an attack, that is, the predator's distance, regardless of its category, as if to indicate response urgency (e.g. Owings & Leger 1980). Alternatively, monkeys may respond to the 'vectorial' features of an attack, as if to indicate an escape tactic (e.g. Smith 1977, page 181). In the present study, I investigated whether Diana monkeys respond to the proxemic, vectorial, or categorical features of a predator (Table 1; the simplistic framework used in this Table 1 serves only to model three paradigmatic types of alarm call systems and is by no means intended to propose taxonomic differences in calling systems between, for example, squirrels and primates). Apart from the Diana and vervet monkeys, referential alarm calling has only been documented in one prosimian species (e.g. Macedonia & Evans 1993), while evidence is still lacking for any other primate species, including the great apes (Hauser 1996, page 520). At the same time, there is much variation in the alarm-calling behaviour of ground-dwelling squirrels,

with some species appearing to use a response–urgency continuum whereas others appear to use calls more referentially (e.g. Slobodchikoff et al. 1986, 1991).

To distinguish between the above three hypotheses, I experimentally simulated the presence of a predator and manipulated (1) its distance from the subjects in the horizontal plane to vary immediate threat, (2) its elevation in the vertical plane to vary direction of attack, and (3) its category to vary the biological class and associated conceptual features. I then studied the effect of these manipulations on the acoustic structure and overall alarm-calling behaviour of wild Diana monkeys. Prior work on Diana monkeys (Zuberbühler et al. 1997) and other monkey species in the Taï forest (Zuberbühler et al. 1999b) has shown that the presentation of acoustic predator models provides a reliable way of simulating predator presence.

I performed acoustic analyses on the alarm calls of wild Diana monkeys to investigate what information the individuals encode (i.e. which of the three independent variables affect the acoustic structure of their alarm calls). Previous studies have shown that females respond to playback of male alarm calls with their own acoustically distinct alarm calls, as if the corresponding predator were present. However, given the previous theoretical considerations, the females' response could be the result of a misunderstanding. For example, if males do not encode predator category but do encode the direction of attack, females could still take the male's calls to a leopard as 'leopard' alarm calls because leopards are typically encountered on the ground. In this paper I investigate what information Diana monkeys encode in their alarm calls when they encounter a predator.

METHODS

Study Site and Subjects

Data were collected in the Taï National Park, Ivory Coast, between June 1994 and June 1997 in an approximately 40-km² study area of primary rain forest surrounding the Institut d'Ecologie Tropicale research station (5°50'N, 7°21'W). Diana monkey groups forage and travel as cohesive units typically spread over an area less than 70 m in diameter (R. Noë, unpublished data). A previous study estimated the density of Diana monkey groups to about two per km² (Höner et al. 1997), suggesting that the study area may have contained at least 60 different groups. None of the groups investigated in this study was habituated to human presence.

In conducting playback experiments, an assistant and I systematically searched the study area for Diana monkey groups. Once a group was located, typically by hearing their vocalizations, I determined their location and monitored their vocal behaviour for at least 30 min. I tested only groups that were unaware of our presence. If no predation event occurred during that time period and no monkey had detected us, or part of the equipment, a playback trial was initiated. We then silently positioned the speaker in the vicinity of the group in the following way: (1) the relative distance of the speaker to the group

was either 'close' (about 25 m) or 'far' (about 75 m); (2) the relative elevation of the speaker to the group was either 'below' (0–2 m) or 'above' the group (20–35 m); and (3) the predator category represented by playback of predator vocalizations was either a 'leopard' (15-s recording of leopard growls) or an 'eagle' (15-s recording of crowned hawk-eagle shrieks).

The most obvious disadvantage of acoustic models, compared to visual models or natural predator encounters, is that predators are unlikely to vocalize while hunting (e.g. Boesch & Boesch 1989). However, acoustic models have a number of advantages in studies of primate antipredator behaviour. First, they represent a more natural simulation of predator presence than, for example, motionless predator models. Second, they allow the experimenter to control a number of relevant variables, such as the time and distance of detection, the stimulus intensity, and the duration of exposure. Third, they ensure that all individuals obtain information about the presence of a predator simultaneously. A number of recent studies have shown that nonhuman primates respond to acoustic predator models as if the real predator were present (e.g. Hauser & Wrangham 1990; Noë & Bshary 1997; Zuberbühler et al. 1997). This seems adaptive because a vocalizing predator might soon start hunting if its prey consistently failed to show antipredator behaviour simply because it was vocalizing. Thus, I expected the monkeys to show a predator-specific response regardless of whether they learned about the predator's presence visually or acoustically. I purchased recordings of close-up growls of leopards from the National Sound Archive, London, U.K. (Wildlife Section, number 18445, cut 1, recorded by Richard Ranft). I recorded vocalizations of an adult crowned hawk-eagle in the study area at a distance of about 20 m with a Sennheiser ME88 directional microphone and a Sony WMD6C recorder. Figure 1 depicts the two playback stimuli as spectrograms. Crowned hawk-eagle vocalizations can be heard frequently, often several times per day. Leopard vocalizations are rare during the day and seem to be more common at night.

Taï forest is characterized by a very dense vegetation with visual ranges rarely exceeding 20 m. Although this makes direct observations difficult, it also allowed us to set up the equipment at relatively short distances without the target groups noticing our presence. Due to high poaching activity in the Taï National Park, wild Diana monkeys show a strong antipredator response to humans. Typically, one individual gives a few alarm calls and the group then progresses rapidly through the canopy and hides silently in the upper forest strata. When this occurred, the trial was aborted and the group was not used for further testing. In four of 17 cases (24%) the trial had to be aborted because an individual detected us when we lifted the speaker into the trees. Recordings of the subjects' vocal behaviour began at least 1 min before a playback stimulus. To ensure that tests were independent, I tested each group only once. To guarantee that subjects had never been tested before, I tested a group only if I found it at least 1 km (i.e. two home range diameters) away from the location of the

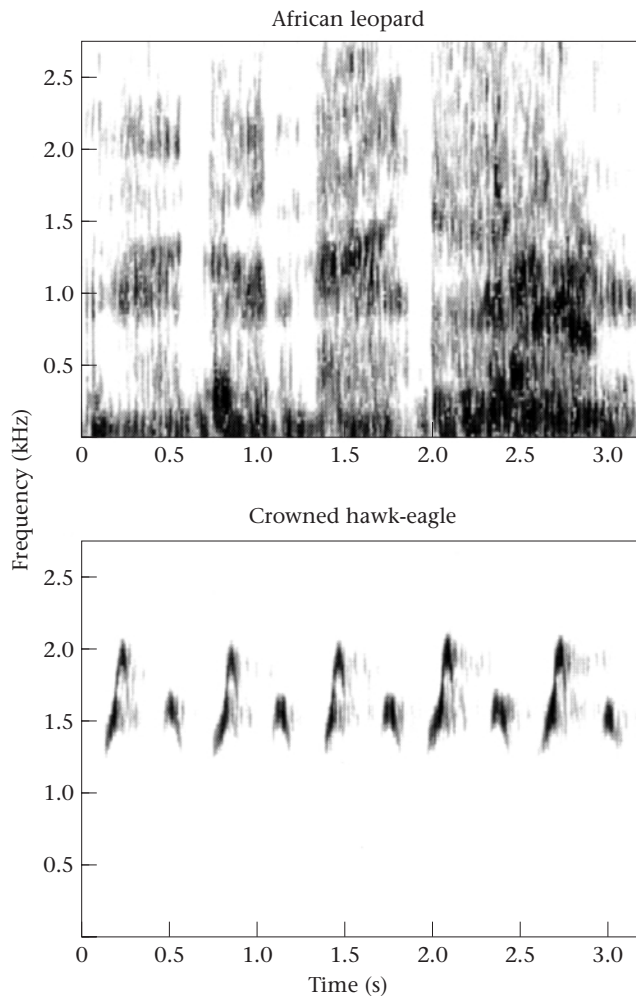


Figure 1. Spectrographic representation of the predator calls used as playback stimuli.

nearest previously conducted trial. Predator vocalizations were played to 23 different monkey groups; 11 groups heard 'eagle' shrieks and 12 groups heard 'leopard' growls. The predator (i.e. speaker) was 'close' in 12 trials and 'far' in 11 trials. Finally, the predator was 'below' the group in 10 trials and 'above' the group in 13 trials.

Although testing the same individuals in all the different conditions would have the advantage of controlling for interindividual differences in call characteristics, it would also have some serious drawbacks. Because I only worked with wild groups whose exact home range was unknown, I would have had to follow a particular group continuously and test it repeatedly. Such an experimental design seems problematic because it is likely to cause unwanted habituation to the playback stimuli and other dependencies in the data set. For this reason, I decided to test only naïve groups for each trial. Note that such a design is conservative because individual and between-group differences only increase the variation between trials and make the null hypothesis (different conditions do not cause acoustic differences) more difficult to reject.

In the Taï forest, Diana monkeys spend most of their time 5–20 m above the ground (McGraw 1998). Although leopards are probably mainly encountered on the ground (e.g. Jenny 1996), they have also been sighted in the main canopy at around 25 m (e.g. Bshary & Noë 1998). Similarly, although crowned hawk-eagles are typically found perched in the high canopy, they can be encountered on the ground; for example, when feeding on a carcass (personal observation). Although no reliable frequency estimates can be given, these observations show that monkeys must have had such encounters in the past, suggesting that the experimental conditions were not anomalous.

Materials

Playback stimuli were broadcast using a Sony WMD6C Professional Walkman connected to a Nagra DSM amplifier and a Bose 151 external speaker connected with a 14-gauge speaker cable. When required by the experiment, the speaker was hoisted into the canopy with the help of an assistant in the following way. A 50-g oval piece of lead was attached to a fishing line and shot over a suitable branch in the upper canopy with a Trumark sling shot. When the lead descended, we attached a green nylon cord (4 mm × 100 m) to it and pulled the cord back over the branch. This cord was then used to lift the speaker into its final position in the upper canopy.

Diana monkey vocalizations given in response to the playbacks were tape-recorded with a Sony TCM 5000EV recorder and a Sennheiser ME 80/K3N directional microphone. Using Canary 1.2. (Charif et al. 1995), I digitized and analysed the first five calls by the adult male of each group. Because males sometimes approach after hearing playback of leopards or eagles (Zuberbühler et al. 1997), I only analysed the first five calls of each male's calling series because the acoustic structure of later calls could have been affected when detecting the speaker in the canopy. Calls were digitized at a sampling rate of 44.1 kHz/16 bits. Quantitative analysis of calls was carried on a Macintosh Powerbook 5300, using 256-Fourier transformations (Hanning window function) that resulted in spectrograms with filter bandwidths of 684 Hz. Frequency resolution was 21.5 Hz and grid time resolution was 1.45 ms.

The Alarm-call Behaviour of Male Diana Monkeys

Male calls to eagles and leopards consist of a very loud and low-pitched series of syllables that is produced only by the single adult male in the group and the syllables are difficult to distinguish by the human ear (Fig. 2; Hill 1994; Zuberbühler et al. 1997). Spectrally, the calls are best described as a very low fundamental frequency and two bands of acoustic energy, the first one being around 1 kHz, the second one around 1.5 kHz. These two concentrations of acoustic energy appear to be resonances (i.e. harmonically unrelated to the fundamental frequency) and hence are termed formants. I used the following 10 acoustic

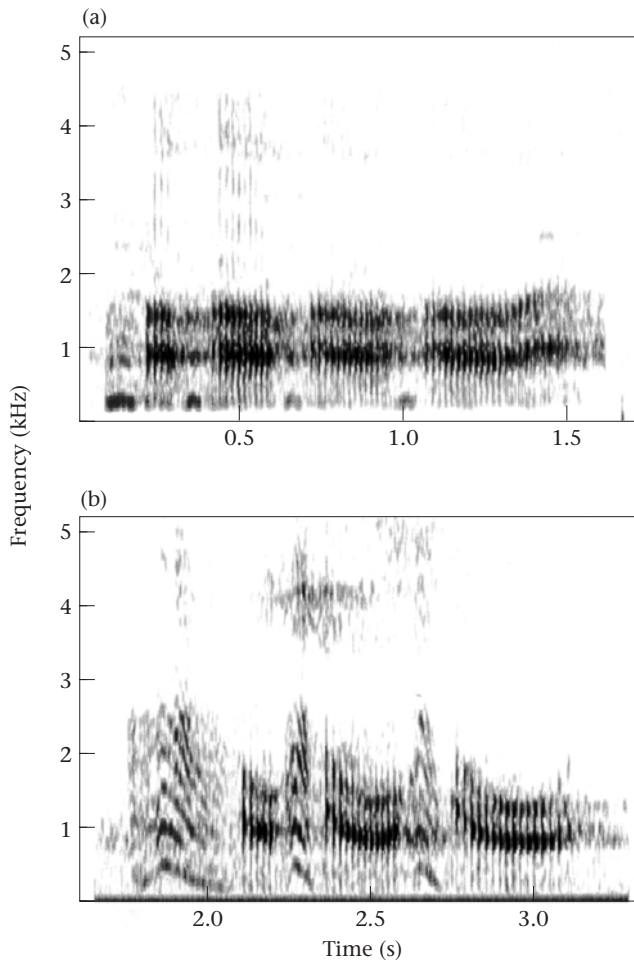


Figure 2. Alarm calls given by two male Diana monkeys to (a) a crowned hawk-eagle and (b) a leopard.

parameters, which have been used and defined in a previous study, to describe male Diana monkey vocalizations (Fig. 3; see Zuberbühler et al. 1997 for details).

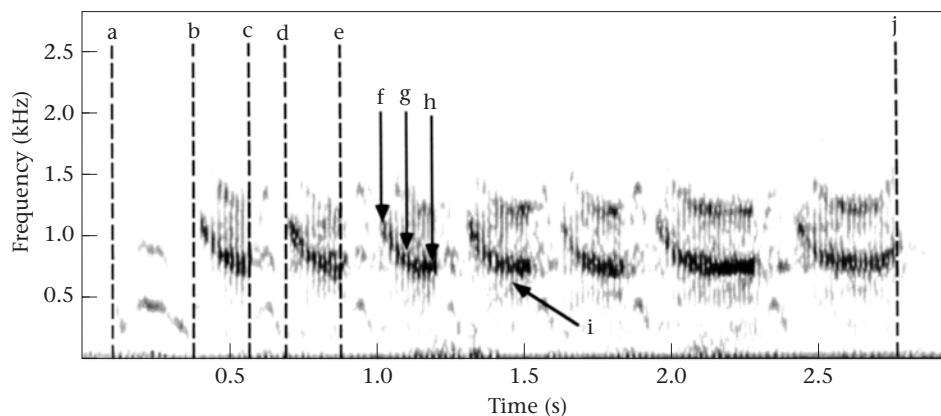


Figure 3. The acoustic parameters measured to describe male Diana monkey alarm calls. Duration (s): b–a: presyllable unit; c–b: syllable unit; d–c: intersyllable unit; j–a: call unit. Frequencies (Hz): $\Sigma i/(c-b)$: fundamental; f: formant, syllable onset; g: formant, syllable middle; h: formant, syllable end. Transitions (Δ Hz): f–g: syllable, first half; g–h: syllable, second half.

Temporal parameters

- (1) Duration of the call.
- (2) Duration of the presyllable unit (inhalation before first syllable of a call).
- (3) Duration of the syllable unit.
- (4) Duration of the intersyllable unit.

Spectral parameters

- (1) Fundamental frequency: number of glottal pulses per second over the entire syllable. In the spectrogram these pulses are visible as dark vertical bands (Fig. 3; Zuberbühler et al. 1997).
- (2) Formant position: onset: maximum acoustic energy at the syllable onset; middle: maximum acoustic energy at the syllable middle; end: maximum acoustic energy at the syllable ending.
- (3) Formant transition: First half: energy from beginning to midpoint of the syllable; second half: energy from midpoint to end of the syllable.

It is possible that some of these variables were not independent of each other. For example, changes in the fundamental frequency tend to be correlated with changes in the position of the main acoustic energy. This concern is valid but not relevant in this context because my main question was whether any one of the independent variables (predator category, distance and elevation) has an effect on the relative acoustic structure of male calls. What exactly these effects are is of secondary concern.

To assess whether the predator's distance, elevation, or category determined the acoustic structure of male Diana alarm calls, I conducted the following analyses. First, I compared the median value of each acoustic parameter for all five calls per male (e.g. the median duration of all syllables per male to predators from below or above). To assess which of the independent variables explained the largest proportion of variance, I calculated the r^2 , that is the percentage of variance explained, for each of the 10 acoustic parameters and performed the corresponding

analyses of variance. Although the median value of the first five calls given by a male is likely to yield a reliable estimate of the male's call structure, this procedure could also conceal important information, for example, if calls change in their acoustic structure over time. Hence, I also compared the median value of all first calls given to a predator. I used discriminant function analyses to determine which of the three predator features or corresponding interactions caused significant between-group effects in the acoustic structure of male calls.

The Alarm-call Behaviour of Female Diana Monkeys

Adult females and subadults respond to the presence of crowned hawk-eagles or leopards with calls that are acoustically different from the loud roars of the adult males. Four different call types are regularly produced in the presence of these predators: (1) contact calls; (2) alert calls; (3) leopard alarm calls; and (4) eagle alarm calls. Calls not belonging to any of these categories were scored as (5) other call types. The calls can readily be distinguished by ear; spectrographic representations have been published elsewhere (Zuberbühler et al. 1997).

I analysed female calling behaviour in the following way. Using analyses of variance, I determined whether the number of calls of each type produced was independent of the different playback conditions. Using discriminant function analyses, I determined which of the experimental conditions or its interactions significantly affected the overall calling behaviour.

RESULTS

Response to Playback of Predator Vocalizations

Analyses of the first five male calls given

In all trials, the single adult male of the group responded to the playbacks of leopards and eagles with the type of vocalization shown in Figures 2a and b, respectively. I recorded the first five calls of each of these 23 males (i.e. a total of 115 calls consisting of 115 presyllables, 951 syllables and 928 intersyllable units). Of these, duration could be measured in 114 calls, consisting of 114 presyllables, 941 syllables and 828 intersyllable units. I obtained spectral measurements for the following syllables: fundamental frequency: $N=937$; formant frequency: syllable onset: $N=930$, syllable middle: $N=923$, syllable end: $N=929$. I was able to calculate formant transitions for the first and second halves of 922 syllables.

For each male, I calculated the median value for each of the 10 acoustic parameters from the first five calls given in response to a playback, leading to 23 data points per acoustic variable. When I assessed the effect of each of the three independent predator features 'category', 'elevation' and 'distance' on the different acoustic measurements, the predator's category explained the

largest amount of variation in eight out of the 10 acoustic parameters, as indicated by the r^2 values (Fig. 4).

Univariate analyses of variance revealed that seven of 10 acoustic parameters showed significant differences as a function of predator category (i.e. between playback of leopard and eagle; Table 2). In addition, the predators' distance affected the duration of the syllable, because close predators tended to elicit calls with longer-lasting syllables than distant predators. The predator's elevation affected the fundamental frequency of the calls, because predators from above elicited calls with a significantly lower fundamental frequency than predators from below.

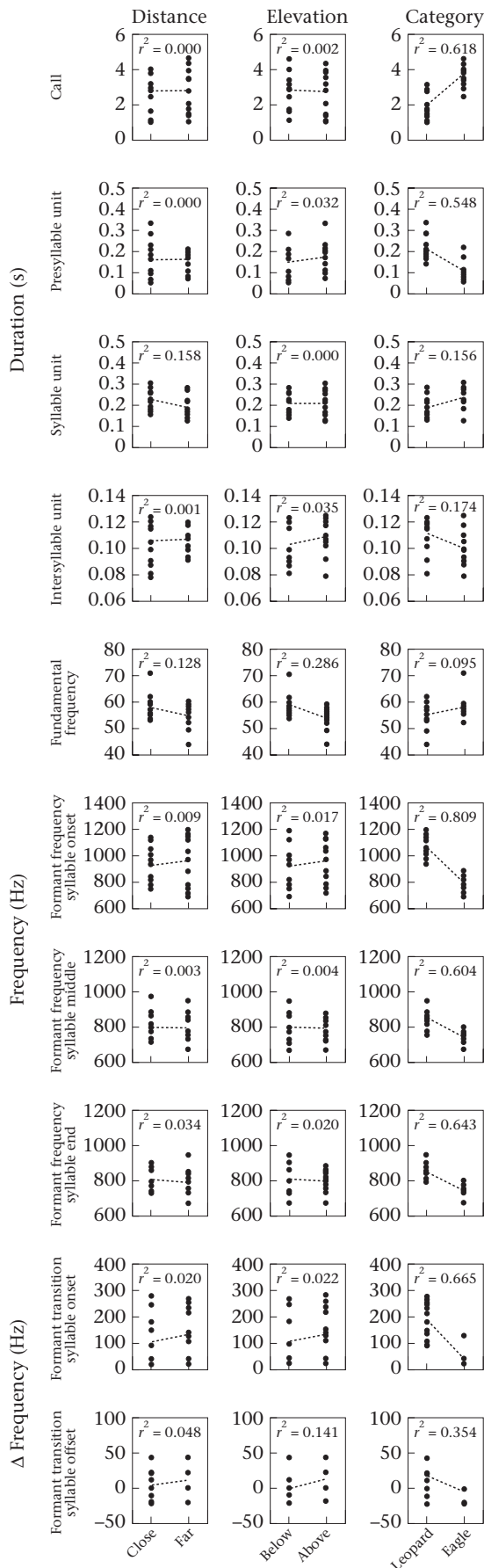
When the interaction terms between the independent variables were entered into the overall model, the effects of distance and elevation were no longer significant, while several category effects remained significant (Table 3).

Discriminant function analysis indicated that the independent variable predator category had a significant effect on the acoustic variables considered (Wilks' lambda=0.121, $F_{10,7}=5.093$, $P=0.021$). However, no significant effects were found for predator elevation (Wilks' lambda=0.256, $F_{10,7}=2.031$, NS), or predator distance (Wilks' lambda=0.246, $F_{10,7}=2.147$, NS). Among the interaction terms, the only significant effect was found when the interaction between predator category and predator distance was tested (Wilks' lambda=0.131, $F_{10,7}=4.637$, $P=0.027$), indicating that males responded differently to leopards and eagles when these predators were either close or far. Interactions between elevation and category or elevation and distance had no significant effects (elevation*category: Wilks' lambda=0.264, $F_{10,7}=1.955$, NS; elevation*distance: Wilks' lambda=0.720, $F_{10,7}=0.272$, NS).

Analyses of the first male calls given

In the wild, female Diana monkeys often respond with their own corresponding alarm calls to the very first call in a male's calling series (Zuberbühler et al. 1997), suggesting that the crucial acoustic features are already present in the first calls. Analyses of all 23 first calls produced by the males indicated that the formant frequency at the syllable onset and its associated formant transition were the features that labelled predator category most reliably (Table 4). In the 23 first calls that were given to either leopard growls or eagle shrieks, the frequency at syllable onset ('formant position onset') and the frequency transition over the entire syllable ('formant transition') discriminated relatively well between the two call types (Fig. 5).

In addition, the predator's elevation affected the duration of the presyllable unit because alarm calls given to leopards and eagles positioned above the group contained presyllable units that were significantly longer than calls given to these predators positioned below the group (Table 4). Adding the three interaction terms into the model did not cause any novel significant effects but resulted in a number of acoustic features to become nonsignificant as a function of predator category (presyllable unit, formant middle, formant end).



The alarm-call behaviour of female Diana monkeys

Females also produced predator-specific vocal behaviour that was largely unaffected by the distance or elevation of a predator (Fig. 6). Analyses of variance revealed that the production of the five call types considered was significantly affected by predator category, but not by predator elevation or distance (Table 5). Adding the three interaction terms into the model did not cause any novel significant effects, but leopard alarm calls became nonsignificant as a function of predator category.

Discriminant analysis on a statistical model containing the three independent variables including the main interaction effects indicated that the independent variable predator category had the only significant effect on the vocal behaviour considered (Wilks' lambda=0.075, $F_{5,12}=29.811$, $P<0.001$). There were no significant effects for predator elevation (Wilks' lambda=0.911, $F_{5,12}=0.235$, NS) or predator distance (Wilks' lambda=0.538, $F_{5,12}=2.059$, NS) and no significant interaction between these terms (category*distance: Wilks' lambda=0.801, $F_{5,12}=0.598$, NS; category*elevation: Wilks' lambda=0.853, $F_{5,12}=0.413$, NS; distance*elevation: Wilks' lambda=0.587, $F_{5,12}=1.687$, NS).

DISCUSSION

In the Taï forest, monkeys are frequently preyed upon by leopards (Hoppe-Dominik 1984) and crowned hawk-eagles (Skorupa 1989; Bergmüller 1998). Male Diana monkeys respond to these two predators with loud and low-pitched alarm calls, respectively. To a human listener, these calls sound very much alike but acoustic analyses and playback experiments have revealed that consistent structural differences exist between the different conditions. The predator's category, that is, whether the predator was a leopard or an eagle, explained the largest amount of variation in eight of 10 acoustic parameters (Fig. 4, Table 2) and in the alarm-calling behaviour of the females (Fig. 6). Diana monkey alarm calls do not seem to indicate predator proximity, as do the alarm calls of Californian ground squirrels (Leger et al. 1980), nor do they seem to indicate the predator's vertical location, as do the alarm calls of the domestic chicken (Evans et al. 1993). Instead results show that Diana monkeys consistently label predator category, suggesting that alarm calls function as referential signals. Special attention was given to the very first calls given by males, because females often respond to them by giving their own acoustically different alarm calls (Zuberbühler et al. 1997), suggesting that the crucial acoustic features are already present in the very first call. When these first calls were analysed, predator category still explained most of the variation in call structure (Table 4). In particular, the calls' formant frequency at syllable onset and the

Figure 4. Results of acoustic analyses of 10 different measurements on the alarm calls of 23 different males plotted either as function of predator distance, predator elevation, or predator category. Each data point represents the median value for all measurements taken from a single male.

Table 2. Statistical analyses of the different acoustic features of the first five male Diana monkey alarm calls as a function of predator category, elevation and distance

Acoustic feature	Predator feature ($F_{1,19}$)		
	Distance (close–far)	Elevation (below–above)	Category (leopard–eagle)
Call unit	—	—	***
Presyllable unit	—	—	***
Syllable unit	*	—	—
Intersyllable unit	—	—	—
Fundamental	—	*	—
Formant position			
Onset	—	—	***
Middle	—	—	***
End	—	—	***
Formant transition			
First half	—	—	***
Second half	—	—	**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$; analysis of variance for $N = 23$ data points per acoustic feature.

Table 3. Statistical analyses of the different acoustic features of the first five male Diana monkey alarm calls as a function of predator category, elevation, distance and corresponding interactions

Acoustic feature	Effects tested ($F_{1,15}$)					
	Main effects			Interaction effects		
	Distance	Elevation	Category	Distance by elevation	Distance by category	Elevation by category
Call unit	—	—	—	—	—	—
Presyllable unit	—	—	***	—	*	—
Syllable unit	—	—	—	—	—	—
Intersyllable unit	—	—	—	—	—	—
Fundamental	—	—	—	—	—	—
Formant position						
Onset	—	—	***	—	—	—
Middle	—	—	**	—	—	—
End	—	—	**	—	—	—
Formant transition						
First half	—	—	**	—	—	—
Second half	—	—	—	—	—	—

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$; analysis of variance for $N = 23$ data points per acoustic feature.

subsequent formant transition provided reliable information about the type of predator present (Fig. 4).

Acoustic analyses of Diana monkey alarm calls further indicated that males might be capable of conveying additional information about the predator's position or elevation into their calls (Tables 2–4). For example, calls given to predators from below consisted of longer presyllable units than calls given to predators from above. Although the adaptive value of labelling a predator's elevation or distance in the visually obstructive environment of a rainforest seems obvious, it will be necessary to conduct a series of playback experiments to determine whether these statistical differences are perceptually salient and functionally relevant for Diana monkeys.

Adult females and subadults do not produce any of the males' calls but use their own vocal repertoire in predation contexts. To crowned hawk-eagles, adult females tend to give specific 'eagle alarm calls'. These calls

are typically produced together with an increase in contact calls relative to baseline. To leopards, females tend to give specific 'leopard alarm calls' together with a large number of alert calls. Thus, the overall calling behaviour to these two predators differs not only qualitatively but also quantitatively. A similar finding has been reported for captive ringtailed lemurs, *Lemur catta*. A qualitative description of the calling behaviour indicated that individuals responded with some alarm calls to the presence of a dog, regardless of its distance at detection, while other calls were given to moving or stationary models of avian predators (Pereira & Macedonia 1991).

The large number of Diana monkey vocalizations given to leopards is likely to be an adaptation to this predator's hunting tactic (Fig. 6). A study of the hunting behaviour of leopards in the Tai forest showed that after detection and conspicuous alarm calling by monkey groups, leopards tend to give up their hiding location to move on

Table 4. Statistical analyses of the different acoustic features of the first male Diana monkey alarm calls as a function of predator category, elevation and distance

Acoustic feature	Predator feature ($F_{1,19}$)		
	Distance (close–far)	Elevation (below–above)	Category (leopard–eagle)
Call unit	—	—	—
Presyllable unit	—	*	**
Syllable unit	—	—	—
Intersyllable unit	—	—	—
Fundamental	—	—	—
Formant position			
Onset	—	—	***
Middle	—	—	**
End	—	—	**
Formant transition			
First half	—	—	***
Second half	—	—	**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$; analysis of variance for $N = 23$ data points per acoustic feature.

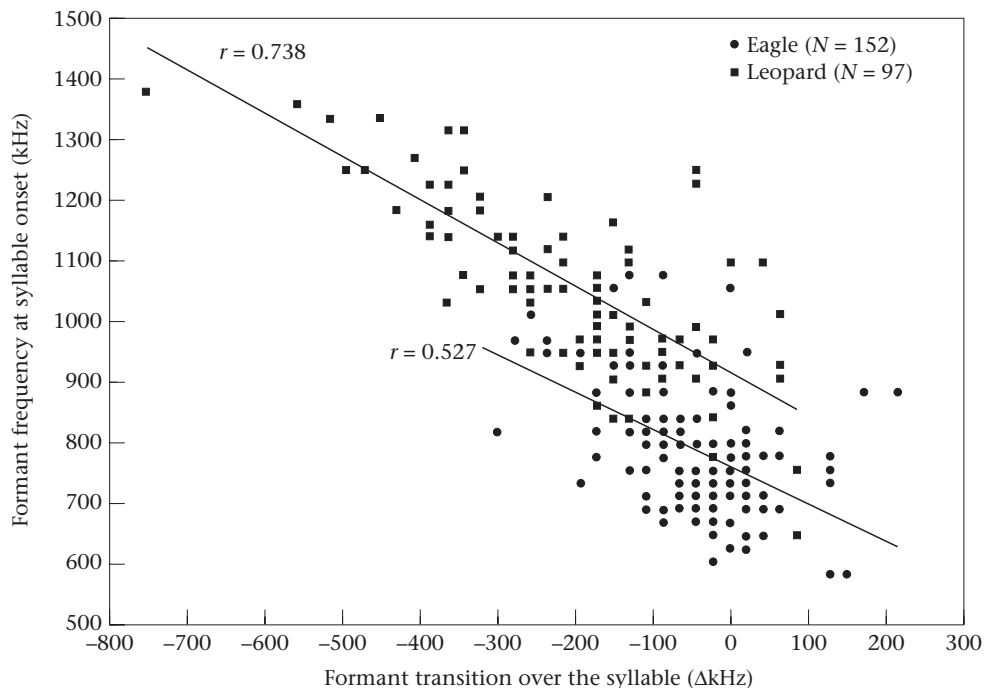


Figure 5. Relationship between the frequency of the syllable onset and the transition of the acoustic energy over the syllable for all syllables present in the first alarm calls of 23 males.

and leave the group (Zuberbühler et al. 1999b). Hence, the large number of Diana monkey vocalizations produced in response to leopards may function to signal the predator that it has been detected and that further hunting will be futile.

To conclude that the Diana monkey alarm call system is referential requires evidence of both production and perception specificity. The results of a recent field experiment (Zuberbühler et al. 1999a) have shown that as recipients, wild Diana monkeys do not simply respond to the acoustic features of their alarm calls but seem to attend to the underlying semantic content; that is, the

meaning associated with the alarm call. Using a prime/probe technique, it was shown that female recipients that have previously heard male alarm calls to a leopard no longer give leopard alarm calls to playback of leopard growls, even though this stimulus was acoustically novel and normally very powerful in eliciting alarm calls (Zuberbühler et al. 1999a). Recipients behaved, therefore, as if they had already anticipated the presence of the leopard. Similarly, females stopped giving eagle alarm calls to eagle shrieks, again normally a very powerful stimulus in eliciting alarm calls, if they had heard the corresponding male eagle alarm calls a few minutes

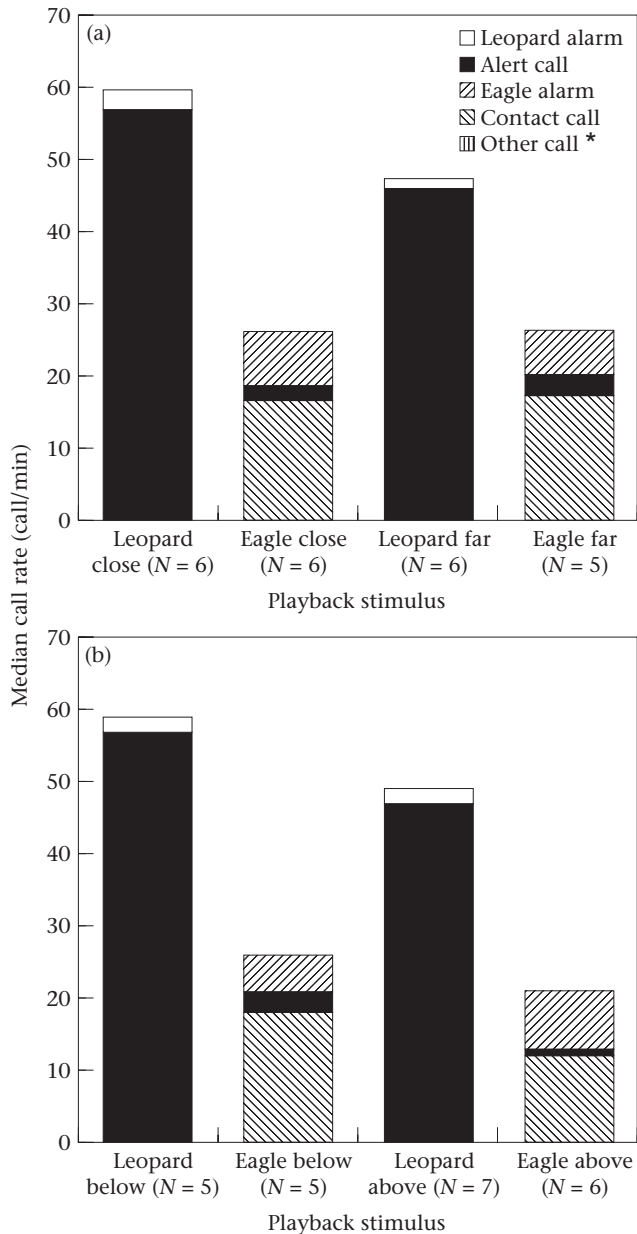


Figure 6. Female vocal behaviour in response to leopards and crowned hawk-eagles as a function of (a) predator distance and (b) elevation. Bars represent the median number of calls produced in the first minute after onset of the playback stimulus.

*The small sample size precluded calculation of the median.

earlier. Females, in other words, seemed to have gained meaningful information from the male alarm calls they heard as a prime and did not seem surprised when hearing the corresponding predator subsequently. As recipients, therefore, these nonhuman primates seem capable of mental processing that cannot be explained with simple stimulus-response arithmetic. Instead, some monkey vocalizations seem to be linked to specific mental representations of external objects or events, such as a concept of a predator, and function as their labels. The experiment described in this paper complements these previous findings by providing information on the

Table 5. Statistical analyses of the different Diana monkey vocalizations produced by adult females and subadults during the first minute in response to playback of predator calls

Vocalization	Predator feature ($F_{1,19}$)		
	Distance (close–far)	Elevation (below–above)	Category (leopard–eagle)
Leopard alarm	—	—	*
Eagle alarm	—	—	**
Alert call	—	—	***
Contact call	—	—	***
Other call types	—	—	—

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$; analysis of variance for $N = 23$ data points per vocalization type.

mechanisms driving the alarm call production of the signaller. Data show that Diana monkeys reliably label the biological categories of a predator, regardless of the relative threat imposed due to varying distances or probable directions of attack. As signallers, therefore, Diana monkeys are capable of referentially labelling the categorical features of objects, suggesting that signallers and recipient indeed communicate about the same matter, albeit in a nonlinguistic way.

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