

Diana monkey long-distance calls: messages for conspecifics and predators

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Abstract. Primate long-distance calls have typically been interpreted as communication signals between conspecific groups (the 'resource defence hypothesis'), but their potential role as anti-predator alarm calls has received comparably little attention. Male diana monkeys, *Cercopithecus diana diana*, in the Taï forest of Côte d'Ivoire often utter long-distance calls, either spontaneously or in reaction to a variety of stimuli, including predators and non-predators. The present study focuses only on predation contexts and provides evidence for communication to both predators and conspecifics. Males called only in response to predators whose hunting success depends on unprepared prey, that is, leopards and crowned hawk eagles, but not in response to pursuit hunters, such as chimpanzees and humans, which can pursue the caller in the canopy. Calling was regularly combined with approaching the predator. Both observations suggest that male long-distance calls are used to signal detection to the predator ('perception advertisement hypothesis'). Analysis of male long-distance calls given to leopards and eagles showed that they differed according to a number of acoustic parameters. The two call variants were played to different diana monkey groups; conspecifics responded to them as though the original predator were present. We conclude that, in addition to their function in perception advertisement, diana monkey long-distance calls function as within-group semantic signals that denote different types of predators.

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A number of forest dwelling primates, including the diana monkey, *Cercopithecus diana diana*, have strikingly loud vocalizations known as loud calls or long-distance calls (Gautier & Gautier 1977; Snowdon 1986). The long-distance calls can be heard over distances that are typically greater than the diameter of the home range (Tenaza & Tilson 1977; Whitehead 1989). Spectral energy is concentrated at frequencies between 100 and 1000 Hz (Whitehead 1987). Attenuation in the upper forest strata is low in this frequency range, leading some to hypothesize that calls within this range are particularly well suited for long-distance communication (Wiley & Richards 1978; Richards & Wiley 1980; Waser & Brown 1984). Thus far, most functional explanations of primate long-distance calls have focused on their role in intraspecific communication (Byrne 1982; Kinzey & Robinson 1981; Sekulic 1982; Snowdon

1986; Tenaza 1989; Gautier & Gautier 1977; Waser 1978). For example, long-distance calls mediate spacing, increase group cohesion and alter the movement of groups in the grey-cheeked mangabey, *Cercocebus albigena* (Waser 1975), the eastern black-and-white colobus, *Colobus guereza*, the blue or Sykes' monkey, *Cercopithecus mitis* (Waser 1977), the yellow-handed titi, *Callicebus torquatus* (Kinzey et al. 1977), the dusky titi, *C. moloch* (Robinson 1979; 1981), and the cotton-top tamarins, *Saguinus oedipus* (Snowdon et al. 1983).

Functional Hypotheses

Table I lists possible functions of primate long-distance calls. In the one-male groups of diana monkeys, only the adult male produces long-distance calls (Hill 1994). Females, in turn, utter other call types that are not used by the male. During the pilot phase of the study (January–September 1991), diana monkey males produced long-distance calls in different contexts, such as

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Table I. Functional hypotheses for diana monkey long-distance calls

Function	Context	Recipient	Predictions
Resource defence signals	Non-predation	Conspecific	Males defend range or cluster of females; males call when acoustic attenuation is low
Detection signals	Predation	Predator	Calls given to stalker-type predators only; approaches to stalker-type predators only
Warning signals	Predation	Conspecific	Calls appear in structural variations; variations correlate with different predators; conspecifics are sensitive to the variations

Table II. Predators of monkeys in the Taï National Park

Predator	Main hunting techniques	Expected behaviour of the male
Crowned hawk eagle, <i>Stephanoaetus coronatus</i>	Surprise attacks Sit-and-wait Hunting in pairs	Detection signalling and attacking; warning mates and kin
Leopard, <i>Panthera pardus</i>	Sit-and-wait Stalking, ambush, stealth	Detection signalling; warning mates and kin
Chimpanzee, <i>Pan troglodytes</i>	Cooperative hunting Pursuit in tree crowns	Temporarily cryptic behaviour; warning if predators are far from group
Human, <i>Homo sapiens</i>	Long distance weapons Monkeys reached at all heights	Temporarily cryptic behaviour; warning if predators are far from group

after a long-distance call of a neighbouring male, after a tree fall, in reaction to the presence of a crowned hawk eagle or without any apparent stimulus.

Long-distance calls as resource defence signals

Primate long-distance calls have repeatedly been interpreted as sexually selected signals used in male contests ('resource defence hypothesis': Sekulic 1982; Tenaza 1989; Mitani 1990; see Andersson 1994 for the application of this hypothesis to bird song). We assume that the 'resource defence hypothesis' can also explain a substantial proportion of the long-distance calls given by male diana monkeys. Here we focus on a less acknowledged function of long-distance calls in the avoidance of predation.

Long-distance calls as detection signals to predators

Taï primates are faced with four confirmed predators that differ in hunting technique (Table II). Long-distance calls could serve as part of an anti-predation strategy to alert predators that they have been detected ('perception advertisement hypothesis': Flasscamp 1994). This hypothesis

predicts that males should give long-distance calls only to those predators that rely on stealth and ambush, such as leopards, *Panthera pardus* (Hoppe-Dominik 1984) or crowned hawk eagles, *Stephanoaetus coronatus* (Klump & Shalter 1984 and references therein), and not to predators that can successfully pursue their prey even after they have been detected, such as chimpanzees, *Pan troglodytes* (Boesch & Boesch 1989) and humans (Martin 1989).

Long-distance calls often occur spontaneously or after non-predatory stimuli, however, such as the fall of a tree or a large branch. The simple occurrence of a call may thus be too ambiguous to signal detection to a predator. Additional evidence is necessary to demonstrate that calls served a perception advertisement function. For example, if males combined their acoustic signals with signals in another modality, ambiguity in communicating to predators would be greatly reduced. Primate males often approach or even attack eagles as part of their defence tactics (Gautier-Hion & Tutin 1988). For a predator, a calling and approaching male would provide a clear signal that the prey is aware of the predator's presence and that it might even attack.

Chimpanzees and human poachers, the two other very frequent predators for the Tai monkeys, both search for prey by acoustic cues (Boesch & Boesch 1989; Martin 1989). Once they have located a group, both are able to reach prey in the canopy, either by cooperative hunting or by using weapons. For diana monkeys, the only effective strategy against these predators is to remain temporarily cryptic. Thus, we predicted that males would remain cryptic when perceiving cues of the presence of one of these predators and would start calling and approaching when perceiving cues of eagles or leopards.

Long-distance calls as semantic signals to conspecifics

Seyfarth et al. (1980) showed that alarm calls in one primate species, the vervet monkey, *Cercopithecus aethiops*, inform conspecifics about the presence of particular predators. They have therefore been described as semantic signals (Seyfarth & Cheney 1992). For diana monkey long-distance calls to qualify as semantic signals, (1) the calls must show clear structural acoustic variation that correlates with the presence of specific predators or predator classes, and (2) conspecifics must be sensitive to these structural variations. Operationally, this can be demonstrated if conspecifics react to a specific long-distance call just as they would to the predator that normally elicits that call. For example, we predicted that female diana monkeys would show the same response to playbacks of leopard vocalizations and to playbacks of a male long-distance call originally given to a leopard.

METHODS

Study Site and Subjects

The data were collected in the Tai National Park, Côte d'Ivoire, between January and September 1991 (pilot observations and pilot playback experiments), and between June and August 1994 and June to July 1995 (playback experiments). All data were collected in an approximately 25-km² area of primary rain forest about 25 km southeast of the township Tai (5°52'N, 7°22'W). Seven monkey species (*Cercopithecidae*) are regularly observed in the area: three *Colobinae*: the western red colobus, *Colobus badius*, the western black-and-white colobus,

C. polykomos, and the olive colobus, *C. verus*, three *Cercopithecini*: the diana monkey, the lesser white-nosed monkey, *C. petaurista*, Campbell's monkey, *C. campbelli*, and the sooty mangabey, *Cercocebus atys*. Diana monkey groups typically consist of about 20–25 individuals with one adult male, 5–7 adult females and several subadults and infants.

The Vocal Repertoire of the Diana Monkey

Diana monkeys show age/sex dimorphism in the vocal repertoire. Adult females, subadults, and juveniles account for most of the vocal activity in a group and are responsible for the following vocalizations, which can be distinguished by ear and were scored in this study according to the following criteria:

- (1) *Contact call*, a symmetrical arched tonal signal given in a variety of contexts (Fig. 1a).
- (2) *Trill*, a sinusoid soft tonal signal given in a variety of contexts (Fig. 1b).
- (3) *Alert call*, a highly tonal call, which somewhat resembles the contact call, but is higher in intensity and lacks the low-pitched on- and offset of contact calls (Fig. 1c). This call is given after a variety of disturbances.
- (4) The alert call may have one to several repetitions (Fig. 1d). We have typically noted such repeated calls after real encounters with leopards or playbacks of vocalizations of leopards and thus termed this call-type the *leopard alarm call*.
- (5) The *eagle alarm call*, given to aerial predators, most commonly to the crowned hawk eagle, resembles the contact call but is lower in pitch and often atonal. This call can occur alone or can be followed by one or several low-pitched tonal components (Fig. 1e).
- (6) *Other call types*, such as calls given in agonistic interactions or towards neighbouring groups, were less frequent and are not discussed here.

In two habituated groups, DIA1 and DIA2, we never heard the adult males utter any of the vocalizations described above. Instead, the harem males restricted their vocal communication to long-distance calling (Fig. 2). Pilot observations suggested that female diana monkeys responded to a male's long-distance call with their own acoustically very different alarm calls.

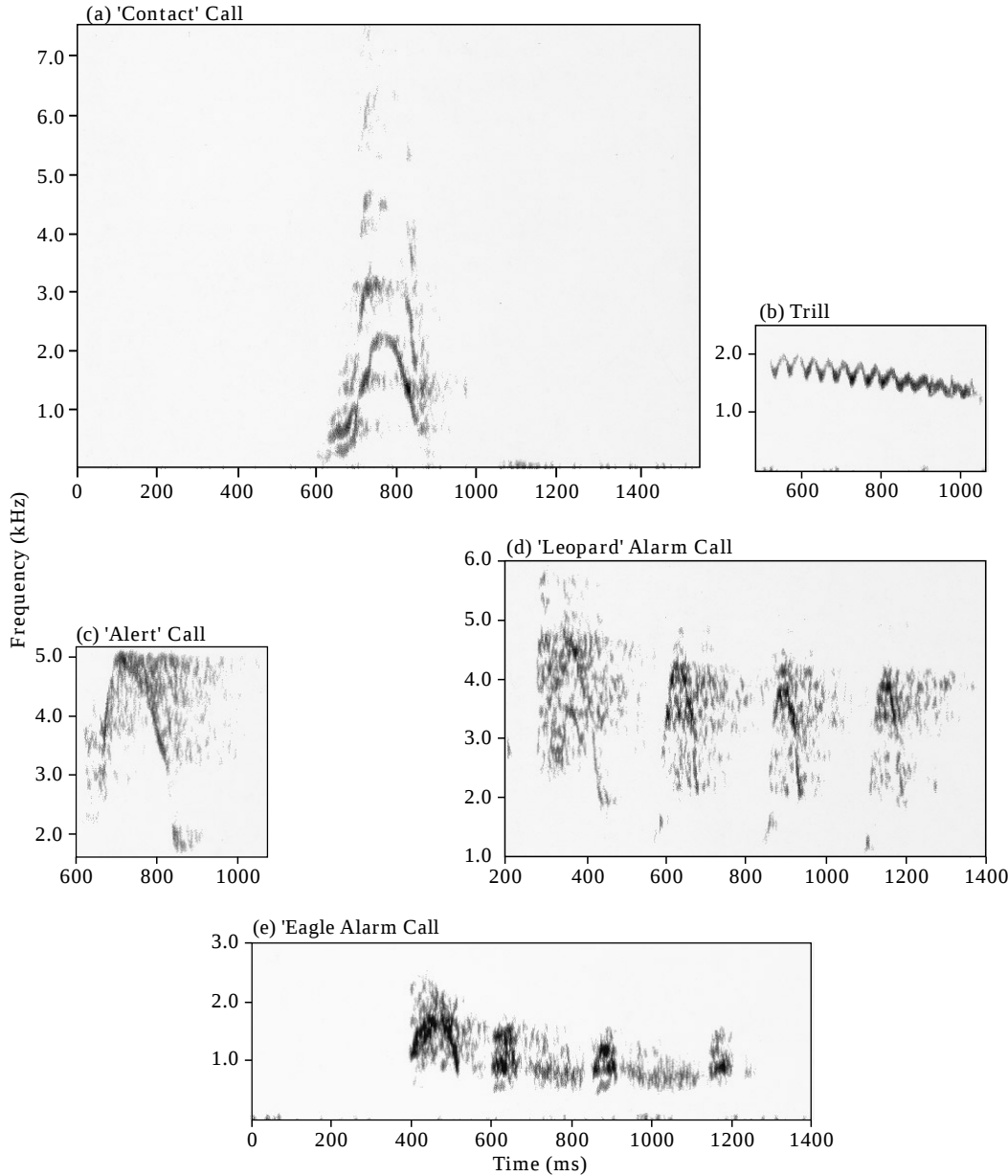


Figure 1. The five most frequent call types of female and juvenile diana monkeys. Sonograms were made with Canary 1.2. recording parameters: 22 kHz sampling frequency, 8-bit sampling. Analysis parameters: FFT, Hanning analysis window; frequency resolution: 345.12 Hz/256 points filter bandwidth; grid resolution: 0.7 ms, 93.8% overlap, 21.7 Hz, 1024 points.

Hypotheses

Long-distance calls as perception advertisement signals

To test whether long-distance calls function as perception advertisement signals against

predators, we simulated the presence of a predator by playing the following vocalizations to various groups of diana monkeys: (a) calls of a crowned hawk eagle, (b) growls ('sawing') of a leopard, (c) pant hoots of a chimpanzee and (d) speech sounds

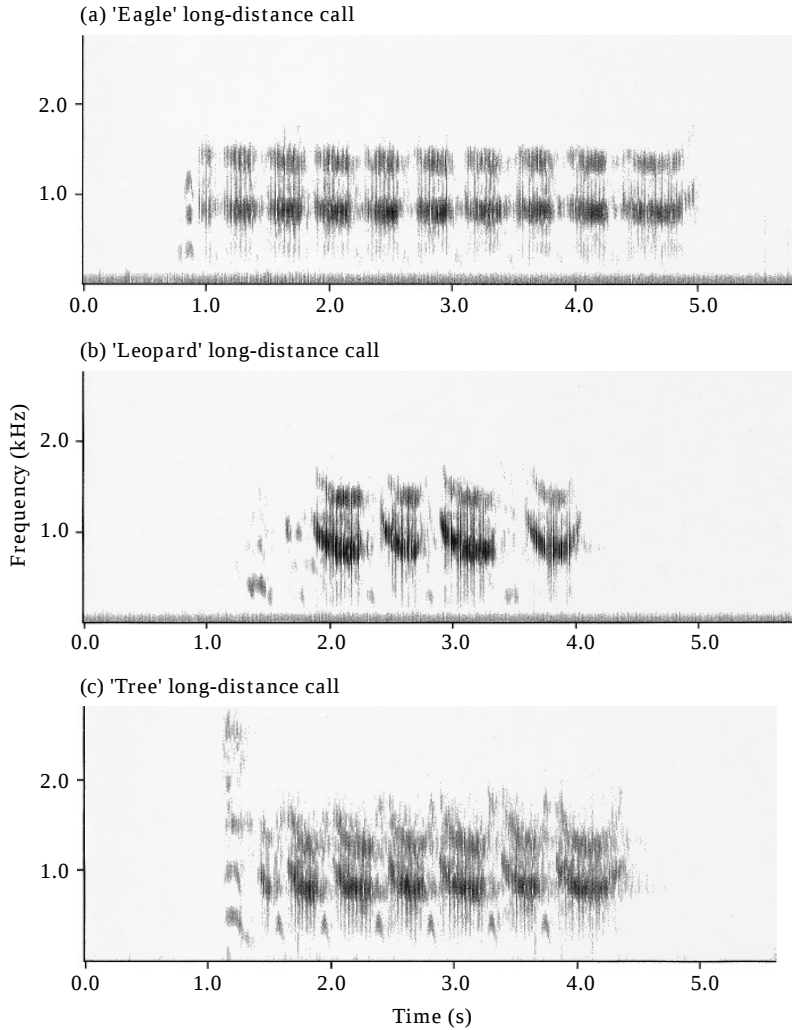
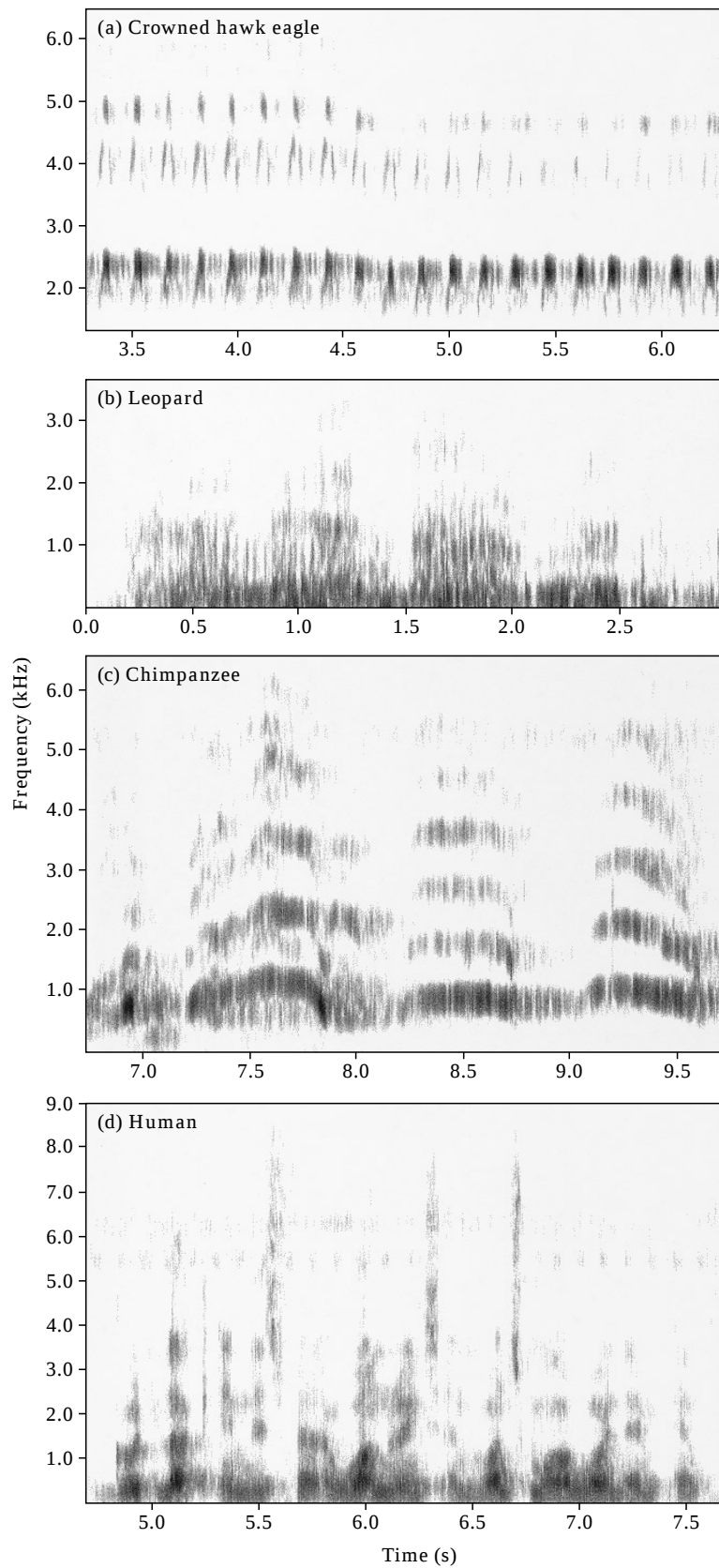


Figure 2. Three representative samples of long-distance calls by male DIA2 given to (a) a crowned hawk eagle, (b) a leopard, (c) a falling branch. The sonograms were made with Canary 1.2. recording parameters: 22 kHz sampling frequency, 8-bit sampling. Analysis parameters: FFT, Hanning analysis window; frequency resolution: 345.1 Hz/64 points filter bandwidth; grid resolution: 2.9 ms, 75% overlap, 5.4 Hz/1024 points.

of an adult human male (Fig. 3). Based on the results of Hauser & Wrangham (1990), we assumed that monkeys could recognize predators by their vocalizations.

Acoustic predator models have both advantages and disadvantages relative to visual models or natural encounters. The most obvious disadvantage is that predators are unlikely to vocalize while they are hunting. We chose acoustic models because we thought that they represented a more natural simulation of predator presence than, for example,

stuffed and motionless predator models. Moreover, when presenting an acoustic model, the experimenter has control over a number of potentially relevant variables, such as the time and distance of detection, the stimulus intensity and the duration of exposure. Furthermore, acoustic models ensure that all individuals simultaneously obtain information about the presence of a predator; we expected the monkeys to show a predator-specific response regardless of whether they learned about the predator's presence visually or acoustically.



For each playback trial, we noted whether the harem male (1) gave long-distance calls and/or (2) approached the speaker. Approach was defined as a horizontal movement of at least 5 m that brought the male closer to the speaker. In practice, the presence or absence of an approach was clear; males came running through the trees from distances of up to 50 m to look for the disturbance and stopped calling when they found the observer or the speaker.

Long-distance calls as warning signals

If long-distance calls transmit semantic information to conspecifics, we expected conspecific listeners to give the same types and numbers of calls regardless of whether they heard a male's long-distance call for a specific predator or the predator itself. To test this hypothesis, we played recordings of the following vocalizations to different groups of diana monkeys: (a) calls of a crowned hawk eagle (Fig. 3a), (b) growls of a leopard (Fig. 3b), (c) a male diana monkey's long-distance calls given to a crowned hawk eagle (Fig. 2a), and (d) a male diana monkey's long-distance call given to a leopard (Fig. 2b). For each trial we tape-recorded the vocal response of the group 1 min before and immediately after the onset of a playback stimulus. We displayed the vocal responses as sonagrams and scored the vocalizations of females and juveniles, placing each in one of the acoustic categories described above (Fig. 1).

Playback Stimuli and Experimental Design

Sounds were tape-recorded with a Sony Professional Walkman WMD6C and Sennheiser 70 mm microphone (K3U + ME88). The sounds either originated from the study area (i.e. chimpanzee, eagle, human, diana monkey males' long-distance calls) or were purchased from the British Library Of Wildlife Sounds, London (African leopard; BBC master tape number MM

35, © South African Broadcasting Corporation). The playbacks were broadcast with a Sony Professional Walkman WMD6C connected to a NAGRA DSM speaker-amplifier. A trial consisted of a short (15 s) playback of one of the predator stimuli (Fig. 3) or of one of the recordings of diana monkey long-distance calls (Figs 2a, b), which were presented as natural series. The amplitude of the stimuli was adjusted to compensate for existing background noise at the time of the playback trial. Of the calls given by predators, leopard growls ranged from 88 to 92 dB, eagle calls ranged from 92 to 100 dB, chimpanzee pant hoots ranged from 96 to 106 dB and human speech ranged from 91 to 98 dB. Of the calls given by male diana monkeys, eagle long-distance calls ranged from 92 to 97 dB, and leopard long-distance calls ranged from 90 to 94 dB SPL. Numbers refer to the maximum sound pressure level of the stimuli as measured with a Radio Shack Sound Level Meter 33-2050, C-weighting at 1 m from the speaker.

The experimenter (K.Z.) searched for diana monkey groups at random along transects in the study area. Revisiting the same sub-area in successive days was avoided, so that a particular group was re-tested after 3 days at the earliest, if at all. Encounter rates with real predators, on the other hand, were more frequent. Attacks of crowned hawk eagles, for example, could occur several times per day (K.Z., personal observation). Eagle vocalizations can be heard almost daily, chimpanzees and human vocalizations may be heard several times a day for successive days, and leopard vocalizations are probably more frequent at night. Census data, moreover, suggest that the 25-km² area where the playbacks were conducted contains up to 40 different diana monkey groups (Galat & Galat-Luong 1985). Because of the high rate of naturally occurring predator vocalizations and the large number of target groups, we found it justified to treat each playback trial as an independent event.

Once a group was located (typically by hearing their vocalizations), the speaker was hidden near the ground 20–50 m away from the target group. To decrease attenuation by local vegetation, the speaker was positioned on elevated places, such as trunks of fallen trees or small hills. If no natural elevation was nearby, the speaker was tied to the trunk of a small tree at about 1.5 m above the ground. The playback trial was then conducted if

Figure 3. Sonagrams of the stimuli used for the playback experiments. Sonagrams were made with Canary 1.2. recording parameters: 22 kHz sampling frequency, 8-bit sampling. Analysis parameters: FFT, Hanning analysis window; frequency resolution: 690.2 Hz/128 points filter bandwidth; grid resolution: 5.8 ms, 0% overlap; and for (d) 2.9 ms, 50%; 43.5 Hz/512 points and for (d) 86.9/256.

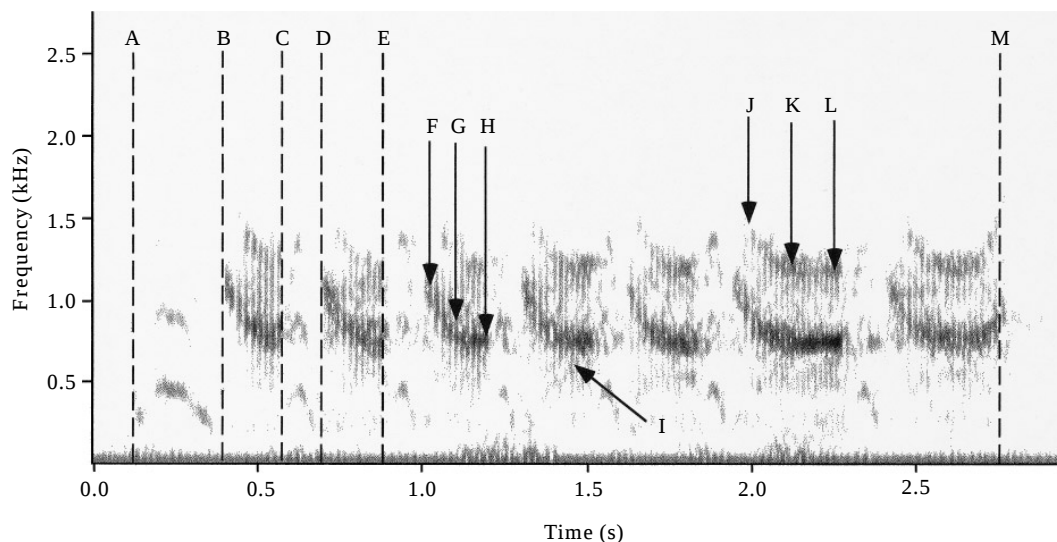


Figure 4. Parameters used in the acoustic analysis of diana monkey long-distance calls. M – A = call duration; C – B = syllable duration; D – C = inter-syllable duration; F, G, H = positions of frequency measurements of first (lower) spectral energy concentration; I = single glottal pulses; J, K, L = positions of frequency measurements of second (higher) spectral energy concentration. The sonagram was made with Canary 1.2. recording parameters: 22 kHz sampling frequency, 8-bit sampling. Analysis parameters: FFT, Hanning analysis window; frequency resolution: 172.6 Hz/128 points filter bandwidth; grid resolution: 5.8 ms, 75% overlap, 5.4 Hz/1024 points.

(1) no male long-distance calls or female alarm calls had been uttered for at least 30 min, (2) it could be safely assumed that no monkey had detected the observer or part of the equipment, and (3) no natural predation event had occurred for at least 30 min. Recordings of the subject groups' vocal behaviour began 5 min before the start of the playback trial and lasted for 15 min.

Acoustic Analysis

Sonagrams were made with Canary 1.2 software on an Apple personal computer. Acoustic analysis parameters are given in the corresponding figure legends. Acoustic analyses of diana monkey long-distance calls were carried out using XWAVES software on a Sun workstation (A/D board: 16 bit linear sampling; sampling frequency: 16 kHz; spectral analysis approach: FFT; analysis window: Hanning; frequency resolution: 20 Hz, 25 ms FFT length). We measured the following temporal and acoustic parameters of the long-distance calls: (1) the number of calls given to a particular stimulus, (2) the number of syllables in each call, (3) the fundamental frequency of each syllable (number of striations per second), (4) the

frequency of the first prominent spectral peak (a) at the beginning, (b) in the middle, (c) at the end of each syllable, (5) the frequencies of the second prominent spectral peak at, respectively, the beginning, middle, and at the end of each syllable, (6) the number of striations per syllable, (7) the duration of a call, (8) the duration of each syllable and (9) the duration of each inter-syllable interval (Fig. 4). To control for individuality in the acoustic variation of the calls, we analysed only vocalizations of the two habituated and individually known males DIA1 and DIA2 to playbacks of crowned hawk eagles and leopards. Long-distance calls of males other than DIA1 and DIA2 were analysed only with respect to the number of syllables per call and the total number of calls in response to a particular stimulus.

RESULTS

Long-distance Calls as Perception Advertisement Signals

If males use their long-distance calls to signal to predators that they have been detected, we predicted that males would be sensitive to the hunting

Table III. Male long-distance calls given in response to playbacks of the vocalizations of different predators

Stimulus	Predator type	At least one long-distance call given (N trials)		
		Yes	No	Rate (%)
Leopard	Surprise	18	0	100.0
Eagle	Surprise	16	0	100.0
Chimpanzee	Pursuit	1	12	7.7
Human	Pursuit	0	7	0.0

technique of the predator. Specifically, males should give long-distance calls to predators that rely on unprepared prey, such as leopards and crowned hawk eagles, but should remain cryptic when faced with predators that are able to pursue their prey in the canopy, such as chimpanzees or humans. Similarly, we expected males to approach the hidden speaker more often after hearing vocalizations of stalker-type predators than after hearing vocalizations of pursuit-type predators.

All males in the 34 leopard and eagle trials combined ('surprise hunters') reacted by giving long-distance calls (Table III). In contrast, in only one of 20 trials that involved a 'pursuit hunter' did a male give long-distance calls. The vocal reaction to surprise and pursuit hunter differs significantly (Fisher test, $P < 0.001$). As further predicted by the perception advertisement hypothesis, the calls of surprise-type predators were approached significantly more often than were those of pursuit-type predators (Table IV, Fisher test, $P < 0.001$).

Long-distance Calls as Warning Signals to Conspecifics

Long-distance calls function as a specific warning for conspecifics if (1) they show sufficient structural variation to allow an unambiguous labelling of different predators, and (2) conspecifics respond to these differences in an adaptive way.

Structural variations in different contexts

Figure 2 illustrates representative samples of long-distance calls by the male DIA2 given to vocalizations of a crowned hawk eagle, of a leopard and to falling wood.

Table IV. Approaches by male diana monkeys in response to playbacks of the vocalizations of different predators

Stimulus	Predator type	Approached observed (N trials)		
		Yes	No	Rate (%)
Leopard	Surprise	5	13	27.8
Eagle	Surprise	10	6	62.5
Chimpanzee	Pursuit	0	13	0.0
Human	Pursuit	0	7	0.0

Syllable number. A diana monkey long-distance call consists of a discrete number of syllables (Figs 2, 3) that varies with the eliciting stimulus. Thus, we compared the syllable number of long-distance calls to leopard and eagle playbacks and to a naturally occurring non-predation event (Fig. 5).

Long-distance calls to leopards yielded a median number of 3.0 (range 1–33) syllables per call ($N = 230$ calls, 10 different trials), whereas long-distance calls to eagles caused calls with a median of 8.0 (range 4–24) syllables per call ($N = 113$ calls, 7 different trials). Long-distance calls given to leopards had significantly fewer syllables than long-distance calls given to crowned hawk eagles (two-tailed Kolmogorov–Smirnov test $P < 0.05$). Long-distance calls given to falling trees or branches, however, had a median of 7.0 (range 1–16) syllables per call ($N = 97$ calls, 12 occasions), which was not significantly different from the eagle trials (two-tailed Kolmogorov–Smirnov test $P > 0.4$). Hence, syllable number alone did not seem to provide sufficient acoustic variation for listeners to make an accurate assessment of the particular predator involved. We therefore compared a number of additional acoustic features in long-distance calls of two known males (Fig. 6).

Temporal parameters. The duration of long-distance calls given to an eagle playback was significantly different from long-distance calls given to a leopard playback (two-tailed t -test DIA2: $t_{24} = 6.25$, $P < 0.001$, Fig. 6a). A significant difference was also found for the duration of the inter-syllable intervals (DIA1: $t_{84} = 11.45$, $P < 0.001$; DIA2: $t_{123} = 6.14$, $P < 0.001$, Fig. 6c), but not the duration of the syllables themselves (DIA1: $t_{109} = 1.31$, $P > 0.15$; DIA2: $t_{149} = 1.33$, $P > 0.15$; Fig. 6b).

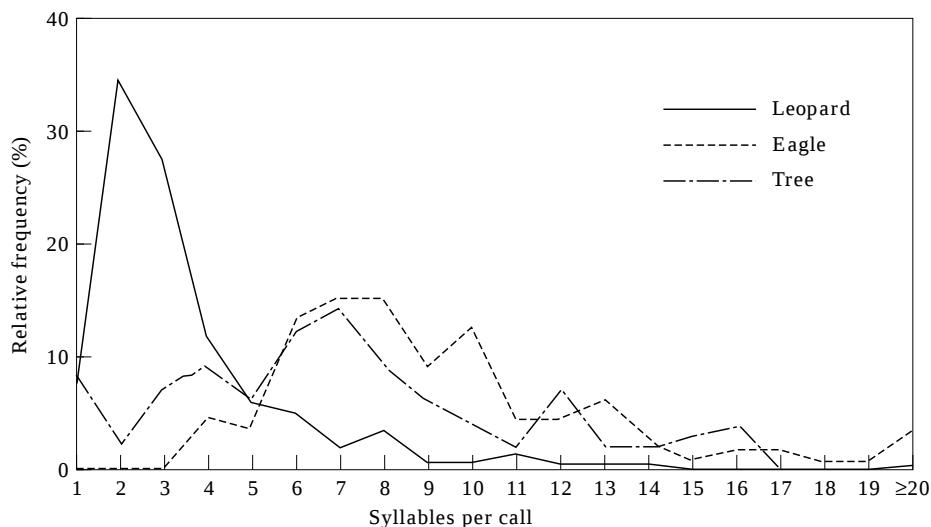


Figure 5. Relative frequency of diana monkey long-distance calls to leopard ($N=230$ calls, 10 trials), to eagle ($N=113$ calls, 7 trials), and to falling trees or large branches ($N=97$ calls, 12 occasions) as a function of the number of syllables comprising the call.

Frequency parameters. Both males uttered syllables with a lower fundamental frequency when hearing a leopard than when hearing an eagle. This difference was statistically significant (DIA1: $t_{104}=12.70$, $P<0.001$; DIA2: $t_{129}=7.15$, $P<0.001$; Fig. 6d).

Another, structural difference concerned the frequency transitions of the lower and higher spectral energy concentrations in the calls (Figs 2a, b). When males heard a leopard, they gave calls with syllables that started above 1 kHz, but rapidly dropped below 1 kHz (Figs 2b, 6e–f), creating a frequency transition (Δ kHz front to end position of spectral energy maximum in a syllable). If males heard an eagle, the spectral energy maxima in their call syllables were below 1 kHz and did not show much subsequent change. Transitions were larger when the males heard a leopard vocalization. This difference was highly significant for both males and both spectral energy concentrations (two-tailed t -tests DIA1: $t_{104}=9.58$, $P<0.001$ (Fig. 6e); $t_{95}=8.35$, $P<0.001$ (Fig. 6f); DIA2: $t_{129}=8.21$, $P<0.001$ (Fig. 6e); $t_{113}=10.32$, $P<0.001$ (Fig. 6f)).

Reactions of conspecifics

Male diana monkeys gave acoustically different long-distance calls to different predators (Figs 2, 6). To test whether conspecifics actually perceive

these differences and respond differently to different call types, we compared the vocal reaction of different diana monkey groups to playbacks of (a) leopard vocalizations, (b) long-distance calls by a diana monkey male given to a leopard, (c) eagle vocalizations or (d) long-distance calls given by a diana monkey male to a crowned hawk eagle.

The vocal reaction of adult female and juvenile diana monkeys tended to be the same regardless of whether they heard a playback of predator vocalizations or the corresponding male diana monkey long-distance calls given to the same predator (Fig. 7). Table V shows the relative number of leopard, diana monkey long-distance calls to leopard, eagle or diana monkey long-distance calls to eagle playbacks in which at least one female uttered a given call type in the first minute after the start of a playback.

First, all four types of playbacks usually caused one or more female (or juvenile) to give alarm calls, but none of the three alarm call types appeared in any of the pre-playback periods. Second, females gave acoustically different alarm calls to different playback stimuli. Playbacks of eagles and playbacks of male diana monkey long-distance calls to an eagle usually caused one or more female to give eagle alarm calls; playbacks of leopards and playbacks of male long-distance

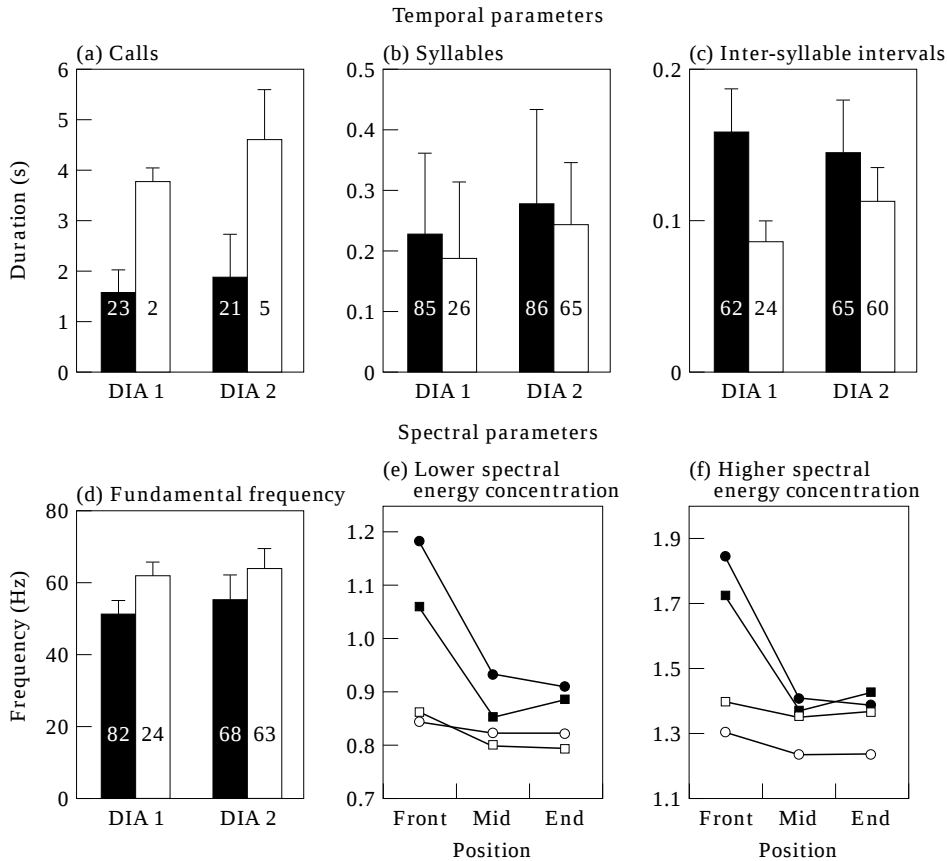


Figure 6. Mean $\pm$ SD acoustic parameters of long-distance calls given by the two males DIA1 (circles) and DIA2 (squares) to either calls of a leopard (black bars or symbols) or calls of a crowned hawk eagle (white bars or symbols). Numbers in bars indicate sample size.

calls to a leopard usually caused one or more female to give leopard alarm calls. Third, all four playback types caused one or more individuals to give alert calls. The rate of these calls was many times higher after playbacks of a leopard or long-distance calls to a leopard than they were after playbacks of an eagle or long-distance calls to an eagle (Fig. 7). Fourth, playbacks of leopards and diana monkey long-distance calls to a leopard, but not playbacks of eagles or diana monkey long-distance calls to an eagle, usually caused a cessation of contact calls and trills.

Fisher's exact probability tests were used to compare vocal responses. In these tests, we asked whether the utterance of one or more calls of a specific type was independent of the playback stimulus. This analysis is conservative, because it

treats each trial as an independent event, and makes no assumption about the extent to which individuals in any given trial responded independently of one another. Females gave significantly more leopard alarms when hearing a playback with leopard vocalizations than with eagle vocalizations ($P < 0.001$) or with male long-distance calls to an eagle ($P < 0.001$). They also gave significantly more leopard alarms when hearing a playback of male long-distance calls to a leopard than when hearing a playback of eagle vocalizations ($P < 0.001$) or a playback of male long-distance calls to an eagle ($P < 0.001$). The analogous case occurred when we analysed the occurrence of females' eagle alarm calls. Females gave significantly more eagle alarms when hearing a playback with eagle vocalizations than when hearing a

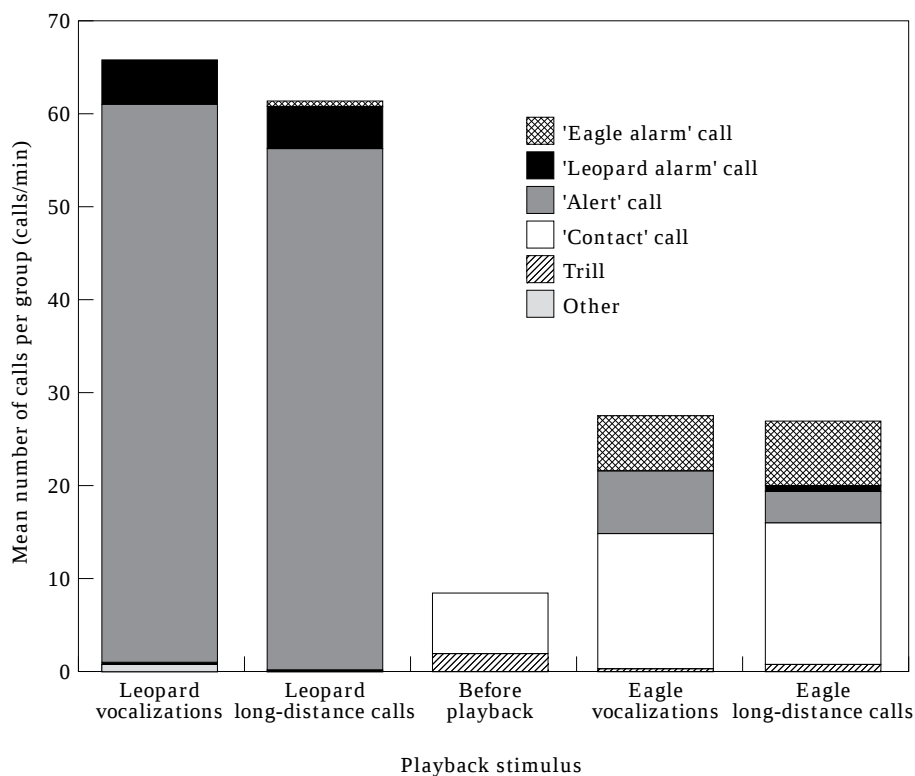


Figure 7. Vocal behaviour of diana monkey groups before and after hearing either vocalizations of a predator ('Leopard vocalizations' ($N=14$) and 'Eagle vocalizations' ($N=15$)) or diana long-distance calls to that predator ('Leopard long-distance calls' ($N=14$) and 'Eagle long-distance calls' ($N=14$)). 'Before playback' ($N=57$) represents the mean vocal behaviour of the groups prior to the playback trials.

Table V. The percentage of trials involving playback of different predator vocalizations and different long-distance call types in which at least one animal uttered a given call type in the first minute after the beginning of the playback

Playback stimulus (N)	Call type (% trials with at least one call)					
	Alarm calls			Other calls		
	Eagle	Alert	Leopard	Trill	Contact	Other
Before playback (57)	0.0	0.0	0.0	59.7	82.5	1.8
Leopard vocalizations (14)	0.0	100.0	100.0	7.1	7.1	28.6
Leopard long-distance calls (14)	7.1	100.0	78.6	0.0	7.1	14.3
Eagle vocalizations (15)	86.7	80.0	6.7	20.0	100.0	0.0
Eagle long-distance calls (14)	85.7	57.1	7.1	35.7	100.0	0.0

playback with leopard vocalizations ($P<0.001$) or a playback with male long-distance calls to a leopard ($P<0.001$). They also gave significantly more eagle alarms when hearing a playback of male long-distance calls to an eagle than when hearing a playback of leopard vocalizations

($P<0.001$) or male long-distance calls to a leopard ($P<0.001$). There was no significant difference, however, in the occurrence of female eagle alarms after hearing playbacks of eagle vocalizations or male long-distance calls to an eagle ($P>0.4$), nor was there any statistical difference in the

occurrence of female leopard alarms after hearing playbacks of leopard vocalizations or male long-distance calls to a leopard ($P > 0.24$).

DISCUSSION

Acoustic Specialization of Diana Monkey Long-distance Calls

Long-distance calls in non-human primates show remarkable acoustic specialization. Calls are given at a high amplitude and have the spectral energy concentrated below 1 kHz. Calls are structurally stereotyped and are given repetitively (Gautier & Gautier 1977). The diana monkey long-distance calls are well described by these patterns. Two further aspects of acoustic specialization in this species need to be highlighted. First, we found a marked discrepancy between the fundamental frequency of the calls (i.e. 50–70 Hz) and the frequency regions that show the greatest spectral energy (800–1200 Hz). This result suggests that males produce the calls using strong and possibly specialized supra-laryngeal filtering and/or resonance effects, probably caused by an extra-laryngeal vocal sac. Data on the vocal tract anatomy of an adult diana monkey male would help to interpret the mechanism of call production in this species. Second, males who responded to the presence of a leopard produced calls in which the individual syllables showed substantial frequency transitions (Fig. 6). Spectral energy concentrations changed from 1.1 kHz at the beginning to 0.9 Hz at the end of individual syllables. These transitions do not seem to be laryngeal in nature (i.e. they are not a mere consequence of changes in the fundamental frequency) but appear to be caused by supra-laryngeal articulatory manoeuvres (Fig. 2), a hitherto underdocumented fact in non-human primate vocal repertoires (M. Owen, personal communication).

Function of Diana Monkey Long-distance Calls

Research on primate long-distance calling has emphasized its role in inter-group spacing. Neither interspecific communication between predator and prey nor the role of long-distance calls as predator-specific alarm signals have received much attention (cf. Tenaza & Tilson 1977).

We found a variety of evidence indicating that the male diana monkey long-distance call is not a functionally homogeneous signal. First, male diana monkey long-distance calls appear in both predation and non-predation contexts. Second, the calls are given only to surprise hunters and are often delivered as a male approaches these predators. Third, calls show subtle acoustic differences that depend on the eliciting stimulus. Fourth, conspecifics respond differently to two structural variants of the male's call. Our data thus show that, besides their commonly assumed function in resource defence against conspecific males, diana monkey long-distance calls also function in defence against predation, both by communicating detection to predators and by warning conspecifics about the type of danger present.

What initially appeared to the human listener as an acoustically and functionally homogeneous long-distance call turned out to be at least three acoustically distinct call types: calls given to leopards ('leopard alarm calls', Fig. 2b), calls given to eagles ('eagle alarm calls', Fig. 2a), and calls given in non-predation contexts ('long-distance calls', Fig. 2c). These different call types appear to serve at least three different functions. General long-distance calls apparently function in resource or female defence against conspecific males. Predator-specific alarm calls warn conspecifics of the type of predator present. Finally, because alarm calls are given only to surprise hunters (eagles, leopards), alarm calls also function to communicate detection to predators.

Male Alarm Calls as Interspecific Communication Signals

In many non-primate species, prey can decrease their vulnerability by communicating directly with the predator (Hasson 1991). For example, song is an effective response of skylarks to merlin attacks: non-singing or poorly singing birds were attacked more often than others. Communication to predators has also been reported in klipspringers *Oreotragus oreotragus* (Tilson & Norton 1981), eastern swamp hens *Porphyrio porphyrio* (Woodland et al. 1980), rails *Gallinula chloropus* (Alvarez 1993) or ungulates (Caro 1994).

In rain forest habitats where visibility is generally poor, the acoustic domain provides the most efficient means by which a prey animal can communicate to a predator. In the present study, two

sorts of data support the hypothesis that male alarm calls function as perception advertisement signals to predators. First, calls are given only to surprise hunters (leopards and eagles) and not to hunters that pursue their prey (chimpanzees and humans). Second, calls given in predation contexts are regularly combined with approaching the predators both under experimental (Table III) and natural conditions. For example, males have repeatedly been observed to leave their group and rush towards an eagle if it has landed on a nearby tree after an unsuccessful attack. In all observed cases, the eagle flew away from the approaching male and the calls ceased.

Support for the perception advertisement hypothesis is not conclusive, however. One untested hypothesis is whether leopards who hear male diana monkey alarm calls give up their hunt significantly more often or sooner than others who receive a control stimulus or no stimulus at all. Preliminary data from an ongoing study in Tai forest, where leopards are followed by radiotracking, support our hypothesis. Leopards appear to hide in the vicinity of a monkey group, but tend to leave as soon as the monkeys give alarm calls (D. Jenny & F. Dinde, personal communication).

Because male diana monkeys' eagle alarm calls are so often followed by approaching the predator, alarm calls may also serve as reliable signals of an imminent attack. This hypothesis goes beyond a pure perception advertisement function because the predator is not only signalled detection but also physically threatened. Again, more rigorous testing of the predator's behaviour following calling and approach by a male is necessary.

Male Alarm Calls as Warning Signals to Conspecifics

Acoustic structure

Male alarm calls show consistent differences in acoustic and temporal structure depending on whether they are given to leopards or to eagles (Fig. 2). Our acoustic analyses show that several acoustic features of the alarm call and their combinations could be responsible for coding messages.

The most salient feature of these alarm calls to us, the number of syllables, did not seem to be sufficient for an unambiguous identification.

Although leopards tended to elicit calls with very few syllables and eagles elicited calls with more syllables (Figs 2b, 5), overlap created ambiguity between the two types of calls. Some of this ambiguity could be resolved by what is known as 'pre-boundary-lengthening' (e.g. van Santen & Olive 1990) in human speech. An English speaker, for example, marks meaningful boundaries in the sound stream (for instance when reading a telephone or social security number) by lengthening the syllable duration prior to that boundary. A similar mechanism could also act in alarm calls and might account for the high standard deviations in syllable duration (Fig. 6b). Males responding to a leopard sometimes give calls with many syllables (Fig. 5). These calls are often interspersed with longer than average syllables, however. Further experiments involving artificially composed calls (e.g. Owren 1990) might address the question of whether males systematically use pre-boundary lengthening, i.e. longer than average syllables, to effectively break down calls with many syllables into continuous streams of several short calls and whether listeners perceive this feature as semantically meaningful.

Semantic function

Because of the limited visibility in the rain forest, we could not use escape responses as dependent variables and instead measured the vocal responses. Females and juveniles responded in qualitatively and quantitatively similar ways both to the male's call to a predator and to the predator that typically caused that call. This result suggests that the females perceived the male's calls as denoting the presence of particular predators. Thus, in addition to advertising perception to the predator, the male alarm calls may serve as semantic signals to conspecifics.

It might be argued that the females' responses to different predators and to male calls represent different response intensities and do not involve semantic information about the type of predator present. Indeed, leopards do evoke a more intense response than eagles in both sexes if one considers the number of alarm calls per trial. The same might be true for the amplitude of the individual calls, since leopard alarm calls could be generally louder than eagle alarm calls. If male leopard alarm calls are played to females, this could cause a more intense response because of the amplitude

of the stimulus and not because of their semantic meaning. The data, however, do not support this interpretation. First, playbacks of eagle and leopard vocalizations did cause differences in the acoustic structure of male alarm calls (Fig. 6) but not in the intensity of calling. Second, even if there were slight differences in the amplitude of naturally occurring male calls to different predators, the experimental design of playbacks controlled for intensity. Male alarm calls to both eagles and leopards were played within the same range of amplitudes (90 to 97 dB SPL) and from the same distances. Third, females responded with their own predator specific alarm calls to both predator vocalizations and to males' alarm calls to the predators. Playbacks of leopard vocalizations and male leopard alarm calls elicited female leopard alarm calls, and playbacks of eagles and male eagle alarm calls elicited eagle alarm calls (Fig. 7).

Another line of evidence in favour of the semantic hypothesis comes from ad libitum observation on the females' locomotor behaviour. Both leopard vocalizations and male leopard alarm calls frequently caused the whole group to descend to the lower canopy and approach the speaker while vocalizing at high rates. This behaviour was never observed when eagle vocalizations or male eagle alarm calls were played. Instead, only the male rushed towards the speaker while other group members stayed behind and vocalized at elevated rates (Table IV, Gautier-Hion & Tutin 1988). The fact that (a) different predators evoked different alarm calls in males and females, (b) playbacks of male calls caused females to respond as if the predator itself was present, (c) call intensity of male calls did not matter, and (d) the playback stimuli also elicited adaptive locomotor responses all make us confident in interpreting the male alarm calls as functionally semantic signals.

What these calls mean to the monkeys, however, is debatable. Perhaps when hearing a male eagle alarm, the female listener automatically responds with her specific eagle alarm without knowing the meaning of the perceived stimulus. Alternatively, hearing the male eagle alarm call may invoke a representation of an eagle just as the sight or the vocalizations of a real eagle do. Experiments involving a habituation–dishabituation technique might get at the issue of whether diana monkeys assess the meaning of the

male alarm calls or whether they simply respond to the acoustic structure of the calls (Cheney & Seyfarth 1988).

Although playback of male diana monkey leopard and eagle alarms elicited vocal responses from females, similar experiments involving savanna-living vervet monkeys (Seyfarth et al. 1980) never elicited vocal responses from conspecifics. Experiments on diana monkeys, unlike those of vervets, thus allow us to study not only the responses to alarm calls but also the factors that influence call production. Results indicate that when a female diana monkey hears a male give a leopard alarm call, she responds by giving a vocalization that is acoustically different from the male's but none the less associated, among females, with the presence of a leopard. Such an observation raises the strong possibility that, in the mind of a female diana monkey, some sort of mental representation of a leopard serves as an intervening variable between hearing one type of call and producing another.

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