

## The Predator Deterrence Function of Primate Alarm Calls

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### Abstract

It is generally assumed that alarm calls function in intraspecific communication, for example to warn close relatives about the presence of a predator. However, an alternative hypothesis suggests that, in some cases, signallers may also gain fitness benefits in directly communicating to the predator, for example by advertising perception and unprofitability to predators that depend on unprepared prey. In this study, we show that six monkey species in Taï forest, Ivory Coast, produce significantly more alarm calls to leopards than to chimpanzees, although both are notorious monkey predators. The conspicuously high vocalization rates to leopards had adaptive consequences for the monkeys. By following a radio-collared leopard, we found that after detection and high alarm call rates the leopard gave up its hiding location and left the group significantly faster than would be expected by chance. We discuss these data with respect to the various functional hypothesis of alarm call behaviour and conclude that the high alarm call rates to leopards are part of an anti-predator strategy in primates that may have evolved to deter predators that depend on surprise.

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### Introduction

In Taï forest, Côte d'Ivoire, both chimpanzees *Pan troglodytes* and leopards *Panthera pardus* regularly hunt monkeys. The two predators differ considerably in both hunting technique and prey spectrum. Chimpanzees hunt cooperatively, pursue their prey in the trees, use acoustic cues to locate monkey groups, and predominantly capture colobine monkeys (Boesch & Boesch 1989). In contrast, leopards hunt solitarily, surprise their prey, and do not show any clear preferences for certain monkey species (Hoppe-Dominik 1984; Jenny 1996, unpubl. data).

Primates, like many other bird and mammalian species respond to predator presence by producing specific vocalizations, usually termed ‘alarm’ calls (Hauser 1996). These calls may function as semantic labels for predator categories. In diana monkeys, for example, both the single adult male and the adult females produce acoustically different vocalizations to crowned eagles *Stephanoaetus coronatus* and to leopards. Playback experiments have shown that when females hear the alarm calls of their male, they respond with their own, acoustically distinct calls as if they had detected the predator themselves (Zuberbühler et al. 1997). Moreover, females do not simply respond to the acoustic features of the male’s calls but seem to understand the semantic content of the calls, i.e. the predator type they denote (Zuberbühler et al. 1999). These and other studies (e.g. Seyfarth et al. 1980) suggest that intraspecific communication is the main function of primate alarm calls.

From a theoretical viewpoint, such altruistic behaviour in the presence of a predator is paradoxical because it is likely to be costly for the signaller. Three different mechanisms have been proposed to explain the evolution of alarm calls as intraspecific social signals. Alarm calls may benefit the signaller: 1. directly by causing anti-predator behaviour in others, such as synchronization of flight (Charnov & Krebs 1975); 2. indirectly by enhancing the survival chances of close kin (Maynard-Smith 1965); or 3. indirectly by facilitating social transmission of predator knowledge in inexperienced offspring (Curio et al. 1978). All three explanations provide a rationale for why it is adaptive to vocalize in the presence of a predator rather than to remain silent. However, they do not make any predictions about how many vocalizations an individual should produce. To a first approximation, signallers should give as few calls as possible to ensure that conspecifics detect the signal while avoid being localized by the predator (Marler 1955).

Observations on diana monkeys suggest, however, that additional rules govern the monkeys’ vocal behaviour to predators. Although both chimpanzees and humans hunt diana monkeys, these predators typically elicit only very few alarm calls. Eagles and leopards, in contrast, cause a much stronger and highly conspicuous vocal response, specifically after the monkeys have spotted a leopard (Zuberbühler et al. 1997).

### **Conspicuous Behaviour and Communication to the Predator**

Conspicuous behaviour to predators has been described in various species. The eastern swamp hen *Porphyrio porphyrio*, for example, conspicuously flicks its tail when threatened by a predator (Woodland et al. 1980). Similarly, skylarks *Alauda arvensis* start singing when chased by predatory merlins *Falco columbarius*. Non-singing or poorly singing individuals were chased for longer periods and were more likely to be caught than individuals that sang well (Cresswell 1994). These, and other studies (Smythe 1970; Bildstein 1983; Caro 1995) have shown that conspicuous signals are often produced in the absence of conspecific recipients, suggesting that they have evolved as a specifically designed behaviour to communicate directly to the predator. However, empirical evidence that a predator is actually deterred by these signals is still widely lacking.

In this study, we first examined whether other Taï monkey species show the same vocal pattern to leopards and chimpanzees like the diana monkey, i.e. high call rates to leopards and low call rates to chimpanzees. Such a pattern across many monkey species would be difficult to explain with differences in predation pressure, i.e. perceived risk, or differential demands in warning. It is more likely that the high calling rates to leopards function as a deterrent signal to a surprise hunter, while the low calling rates to chimpanzees reflect a trade-off between conspecific warning and avoiding being detected by a pursuing hunter.

Second, to investigate whether high call rates have adaptive consequences for the monkeys, we studied the hunting behaviour of a wild leopard. From previous research we knew that Taï chimpanzees are not deterred by monkey vocalizations but may even use them to localize their prey (Boesch & Boesch 1989; Boesch 1994). If high call rates function to deter leopards, however, then their occurrence should terminate a leopard's hiding and cause it to leave the monkey group. To test this prediction, we captured, radio-tagged, and followed an adult leopard and examined the effect of monkey alarm calls on its hunting behaviour.

## Methods

### Study Site

The data were collected in the Taï National Park between August 1993 and June 1997. The study area consisted of approximately 100 km<sup>2</sup> of primary rain forest surrounding the station of the Centre de Recherche en Ecologie (CRE, formerly Institut d'Ecologie Tropicale, 5°50'N, 7°21'W) about 25 km south-east of the township Taï Côte d'Ivoire.

### Part I. Prey Behaviour

#### *Subjects*

The following monkey species were sample in this study: the western red colobus *Colobus badius*, the western black-and-white colobus *C. polykomos*, the diana monkey, the lesser white-nosed monkey *Cercopithecus petaurista*, the Campbell's guenon *C. campbelli*, and the sooty mangabey *Cercocebus atys*.

#### *Materials and experimental design*

We simulated predator presence by playing back typical vocalizations, i.e. leopard growls and chimpanzee pant hoots in the vicinity of a monkey group (see Zuberbühler et al. 1997 for a sonographic representation of the stimuli). Previous work has shown that primates recognize predators by their vocalizations (Hauser & Wrangham 1990; Zuberbühler et al. 1997; Noë & Bshary 1988), suggesting that acoustic models are appropriate to simulate predator presence. Observations during real predator encounters indicated that the monkeys' vocal response after detection of real chimpanzees or a real leopard was identical to their vocal response after playbacks of these predators' vocalizations (K. Zuberbühler, unpubl. data).

To avoid pseudo-replication, we prepared a selection of at least eight different playback tapes for each predator from the available master material. For the leopard, we used two master recordings consisting of growls and breathing from zoo animals (purchased from the National Sound Archive, London, UK). For the chimpanzees, we used several pant-hoots and intragroup vocalizations recorded in the study area. All vocalizations were given in a predation-free, social context (Mitani & Nishida 1993). Each playback tape contained the vocalizations of one individual. The playbacks were broadcast with a Sony WMD6C connected to a Nagra DSM speaker-amplifier to mimic the natural intensity of the sounds (range 85–105 dB SPL as measured with a Radio Shack 33-2050 sound level metre, C-weighting at 1 m distance from a Nagra DSM speaker). The vocal response of each monkey group was documented as a continuous recording starting at least 1 min before the 15 s playback. All sounds were tape-recorded with the Sony recorders WMD6C or TCM 5000EV and a Sennheiser directional microphone.

#### *Data collection*

We searched for monkey groups throughout the study area. Once a group was located, usually by hearing their vocalizations, we marked its geographical location on a map and hid the speaker about 50 m away. A playback trial was conducted if no monkey had detected the observer or part of the equipment and no predator alarm calls had occurred for at least 30 min. To maintain statistical independence between trials, we only sampled groups that were located  $>1$  km (*C. atys*,  $>2$  km), i.e. more than one home range diameter (R. Noë, unpubl. data), from the site of a previously conducted trial. This distance criterion greatly minimized the risk that a particular group had previous experience with a playback stimulus, because playback stimuli could not be heard for more than about 100 m.

We recorded the focal group's vocal response on audio tapes and determined whether or not it approached the speaker after a playback trial. Approach was defined as a horizontal movement of at least 5 m that brought the individuals closer to the speaker. In practice, the presence or absence of an approach was clear; groups progressed through the trees from distances of up to 50 m to look for the disturbance, often until they found the observer or the speaker.

#### *Data analysis*

Taï monkeys produce a number of call types in response to predators that differ both within and between species and sexes (Zuberbühler et al. 1997; K. Zuberbühler, unpubl. data). Since our hypothesis is concerned with call usage and not with call structure, we compared the call rates (i.e. the total number of calls given in the first minute after the beginning of either playback stimulus) for each species. We analysed only the first minute because approaching groups tended to detect the speaker or the experimenter after this time interval. In trials where call rates were too high to score by ear, we digitized the entire recording using the software CANARY 1.2. (Charif et al. 1995) and determined the exact call rate from the sonograms.

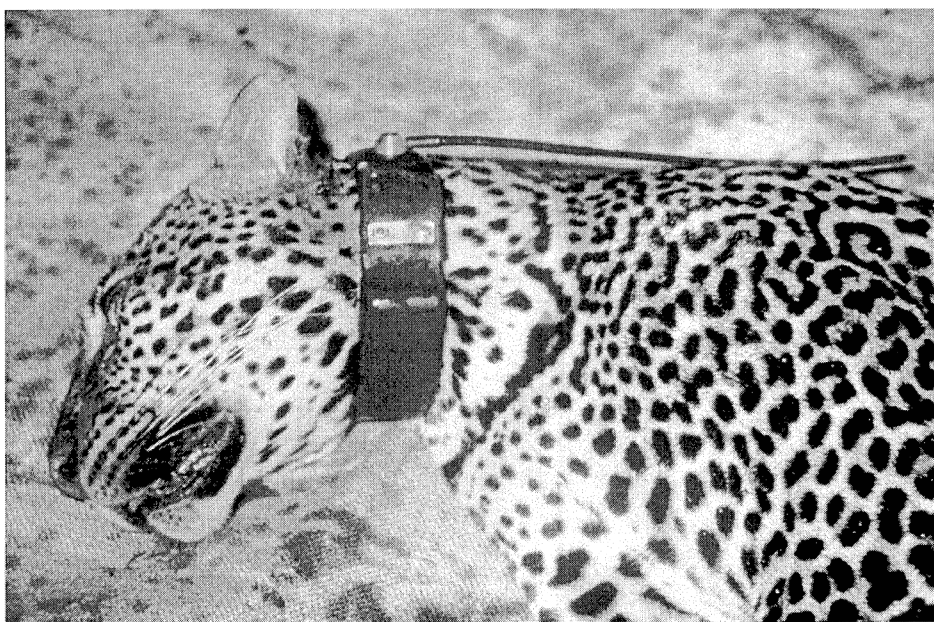
## Part II. Predator Behaviour

### *Subject*

Leopards in the Tai forest live solitary in a population density of 7–11/100 km<sup>2</sup>, covering home ranges between 22 and 86 km<sup>2</sup> (Jenny 1996). On Aug. 16, 1993 an adult female (bodyweight: 34 kg, Fig. 1) was captured with a cable snare, sedated with a mixture of Domitor (0.03 mg/kg body weight; Farnos, Turku, Finland) and ketamine (6 mg/kg body weight), fitted with a radio-collar (Wagener, Cologne, Germany), and anti-sedated with Antisedan (0.04 mg/kg body weight). All drugs were administered with syringes fired from a carbon-dioxide powered gun (Gut50, Telinject, Romerburg, Germany). Jenny (1996) provides a more detailed description of the procedures.

### *Data collection*

Between August 1993 and June 1994 the leopard was followed using tracking equipment on 27 days (310 h) at a distance of 30–150 m, i.e. outside the visual range. We scored the following behavioural classes based on changes in the strength and constancy of the received signal. An 'encounter' between the leopard and a group of monkeys started when the leopard came to rest within about 50 m of a monkey group. Then the observer (D. Jenny) identified the monkey species present according to their vocalizations and concealed himself at a distance of 50–100 m



*Fig. 1:* The adult female leopard 'Adele' after being sedated and fitted with a radio-collar (Photograph by D. Jenny)

from leopard and monkeys in order not to interfere with their interaction. As long as a constant signal was received, the leopard was scored to be resting, presumably ‘hiding’ from the monkeys; a changing signal indicated ‘movement’, which could be anything from body movements to changing the hiding location. Movement that increased the distance from the monkey group beyond the 50-m radius was scored as ‘departure’, which ended an encounter. During each encounter, the observer monitored the vocal behaviour of the monkey group. As soon as the monkeys started to give loud and conspicuous vocalizations at high rates, it was assumed that the group had noticed the leopard and ‘detection’ was scored. It is important to note that visual contact with the animals was avoided because neither the leopard nor the monkey groups were habituated to human presence. Hence, the data could contain some cases where the leopard was resting close to a monkey group without the intention to hunt. At that same time, monkeys could have alarm called for other reasons. Note, however, that our method is still conservative because such false positives would simply make it more difficult to reject the null hypothesis, i.e. that detection has no effect on the leopard’s hunting behaviour.

#### *Data analysis*

To assess whether detection affected the leopard’s hunting behaviour, we performed two kinds of analyses. First, we determined whether detection had an effect on the predator’s hiding behaviour by comparing the duration of hiding before and after detection. Second, we determined whether detection reliably resulted in departure. For this purpose, we calculated the duration of all resting bouts when no monkey group was present. This value was used to calculate the expected probability of departure. Using a binomial test, we then compared expected and observed departure probability after monkey alarm calls had been given.

## **Results**

### **Field Experiments**

All six monkey species gave significantly higher rates of alarm calls to playback of leopard growls than to playbacks of chimpanzee pant-hoots (Mann–Whitney U-tests, two-tailed: *Colobus badius*,  $z = 3.37$ ,  $p < 0.001$ ; *C. polykomos*,  $z = 2.68$ ,  $p < 0.01$ ; *Cerocebus atys*,  $z = 1.99$ ,  $p < 0.05$ ; *Cercopithecus diana*,  $z = 3.816$ ,  $p < 0.001$ ; *C. campbelli*,  $z = 2.45$ ,  $p < 0.02$ ; *C. petaurista*,  $z = 2.92$ ,  $p < 0.005$ ; Fig. 2).

Groups occasionally approached the speaker after hearing playback stimuli, but only after playback of leopard growls (*Colobus badius*, zero out of eight trials; *C. polykomos*, zero out of nine trials; *Cerocebus atys*, two out of six trials; *Cercopithecus diana*, two out of 12 trials; *C. petaurista*, two out of nine trials; *C. campbelli*, two out of 13 trials) and never after playback of chimpanzee vocalizations. Chance observations suggested that chimpanzee pant hoots generally

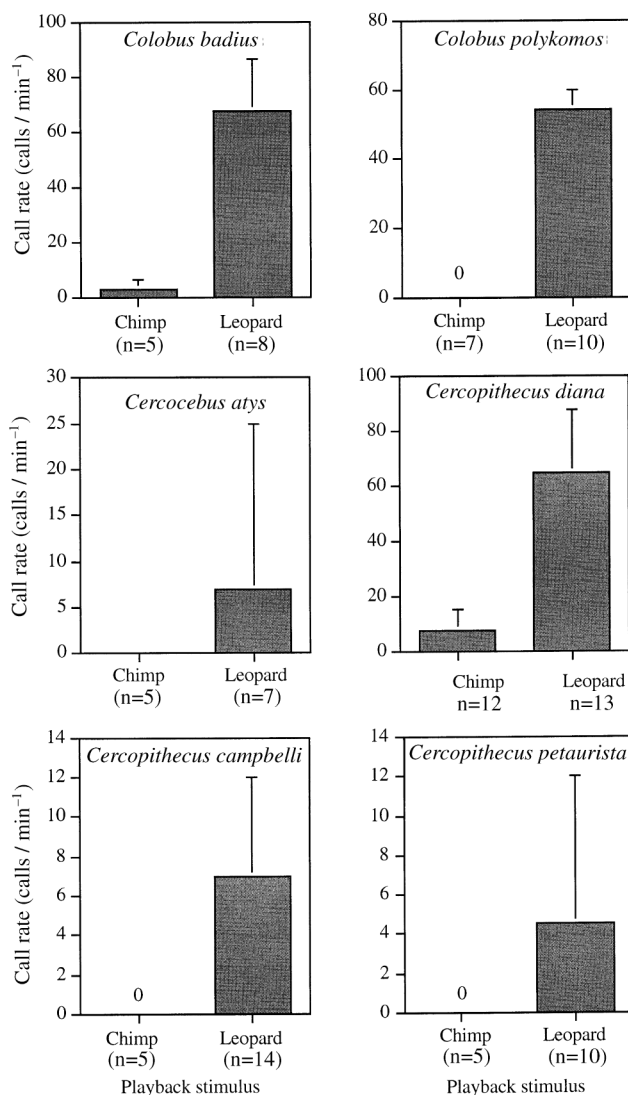


Fig. 2: Call rates of six different monkey species after detection of a chimpanzee or a leopard (median + quartile)

caused flight away from the speaker, often to points higher in the canopy (see also Bshary & Noë 1998). Approach after leopard growls was not linked with high vocalization rates, as monkeys were not more likely to score above their median species-specific call rates to leopards when they approached than when they did not (Fisher test,  $n = 39$ , ns).

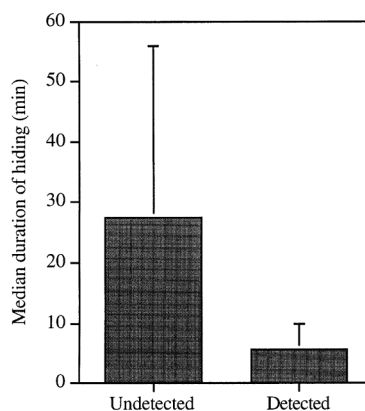


Fig. 3: Hiding behaviour close to monkey groups before and after detection (median + quartile,  $n = 18$  encounters)

### Natural Encounters with the Leopard

#### *Detection affects hunting behaviour*

We witnessed 24 different encounters between the leopard and a mono- or poly-specific monkey group. In 18 cases, we were able to determine the exact duration (median 61 min, range 7–285 min). In all cases, the monkeys detected the leopard at some point and subsequently vocalized at high rates. This affected the hunting behaviour of the leopard. The leopard's time spent hiding underneath a monkey group was significantly shorter after detection than before (Fig. 3, Wilcoxon-test, one-tailed:  $z = 2.112$ ,  $n = 18$ ,  $p < 0.02$ ).

A qualitative analysis of the data suggested that the relationship between monkey alarm calls and the leopard's departure was causal because the leopard's stay after detection was short regardless of the time already spent hiding (Fig. 4). In three cases, however, the leopard did not move after detection, suggesting that it was not hunting at those times.

#### *Detection causes departure*

The leopard not only gave up the hiding location after detection but also was more likely to move on and leave the group. We compared the number of observed departures after detection with the expected number of departures (calculated from the leopard's departure probability when no monkeys were present). We found that during the first two 5-min intervals after the detection the leopard was significantly more likely to leave the group than what would be expected based on her overall departure probability during a resting period, suggesting that detection caused the leopard to depart (Table 1).

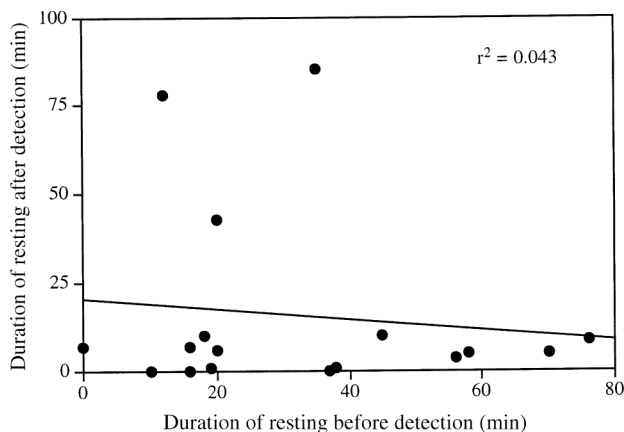


Fig. 4: Relationship between the leopard's resting behaviour close to a monkey group before and after detection (n = 18 encounters)

## Discussion

### Predator–prey Interactions

All six monkey species produced significantly higher alarm call rates to leopards than to chimpanzees, despite the fact that both predators frequently prey on monkeys. Some species approached the speaker after playback of leopard growls but not after playback of chimpanzee calls. At the same time, the monkeys' high alarm call rates had a significant impact on the hunting behaviour of the leopard because it typically left shortly thereafter.

Observations on three other radio-tracked leopards, who were followed as part of another study, indicated that our data represent a general pattern of leopard hunting behaviour in the Tai forest (Dind 1996; D. Jenny, unpubl. data). Our data are observational only and experiments would be necessary to provide strong evidence that monkey alarm calls directly affect a leopard's hunting behaviour.

Table 1: Observed versus expected number of departures after detection

Interval (min)	Number of departures after detection (expected)		p
	Yes	No	
1–5	6 (2.2)	18 (21.8)	<0.02
6–10	9 (1.6)	9 (15.4)	<0.001
11–15	0 (0.8)	9 (8.2)	ns
16–20	0 (0.8)	9 (8.2)	ns

p = binomial probabilities.

Nevertheless, our data support the hypothesis that monkey alarm calls have a predator deterrence function because: 1. leopards but not chimpanzees elicited conspicuously high alarm call rates; 2. high alarm call rates were the only conspicuous behaviour elicited; and 3. high alarm call rates affected the leopard's hunting behaviour.

### **The Predator Deterrence Function of Primate Alarm Calls**

Monkeys consistently vocalized at high rates to leopards but not to chimpanzees. Such conspicuous vocal behaviour is costly both energetically and because it attracts other predators, for example, crowned eagles or human poachers (K. Zuberbühler & R. Bshary, unpubl. data). What are the potential benefits then that would favour the evolution of high alarm call rates to one predator class?

First, differences in predation pressure (and hence perceived risk) between the two predators could have selected for different predator specific alarm call rates. This hypothesis is difficult to reconcile with the fact that all six species — including the two Colobine species who suffer very high mortality rates from chimpanzee predation — alarm-called at much higher rates to leopards than to chimpanzees.

Second, the demands for conspecific warning might be greater in one predator class relative to the other. Again, this seems unlikely because, in monkeys, a small number of alarm calls are generally sufficient to transmit predator information efficiently across individuals (Zuberbühler et al. 1997; Seyfarth et al. 1980). Perhaps, one would want to argue that it is the call rate itself that codes for different predator classes. Although we cannot rule out this possibility, we find it implausible that this is the evolved function of the consistent call rate differences because acoustically distinct alarm calls transmit semantic information much more efficiently. Moreover, in vervet monkeys *Cercopithecus aethiops* it was shown that the acoustic structure, but not the rate at which alarm calls were played back, affected the anti-predator responses in conspecifics (Seyfarth et al. 1980).

Third, high call rates could function in intraspecific transmission of predator knowledge if they focus the offspring's attention on the predator and enhance social learning of predator classes and their vocalizations (Curio et al. 1978). If high call rates function to enhance social learning of predator features, however, then it is not clear why alarm call rates to other predators, such as chimpanzees or crowned eagles, are consistently lower than those to leopards (Zuberbühler et al. 1997). Again, additional explanations appear necessary.

Fourth, high call rates could function to communicate directly to the predator, for example that it has been detected. Communication occurs, according to Wilson (1975, p. 111), 'when the action of, or cue given by, one organism is perceived by and thus alters the probability pattern of behaviour in another organism in a fashion adaptive to either one or both of the participants'. The fact that all monkey species vocalized at high rates in the presence of a leopard, combined with the fact that this caused the leopard to leave the area, suggests that communication between predator and prey occurs and that the high call rates function as a communication signal to the predator. In a visually dense environment, high call rates provide a

conspicuous and unambiguous acoustic signal to the predator to indicate detection and the futility of a further hunting attempt. Moreover, this could be adaptive for both participants. The signallers successfully drive away a predator to continue with their daily maintenance activity while the recipient does not waste any time hunting on aware prey.

It must be pointed out that the general behaviour pattern described here is less pronounced for *Cercopithecus campbelli* and *C. petaurista* (Fig. 2). Both species live a rather cryptic life and spend a lot of time on the ground (McGraw 1998; R. Noë, unpubl. data). It is possible, therefore, that the alarm calling behaviour of these species has not been favoured by a predator deterrence effect and can be explained sufficiently with intraspecific warning only.

### Mechanisms of Predator-deterrence

Our data provide some evidence suggestive of the nature of the information transferred from monkey to leopard. Monkey vocalizations probably do not serve to startle or confuse the leopard, although this might play some role at close distances. In the playback experiments, individuals called at uniformly high rates, even though the predator (i.e. speaker) was positioned at a considerable distance from the group. The high call rates more likely served as reliable predictors of low hunting success for the leopard. These high call rates appear to be essential to provide an unambiguous signal of detection to the leopard where visual signals are not effective.

For the leopard, low hunting success could arise because: 1. the caller has perceived the predator ('perception advertisement', e.g. Frankenberg 1981); 2. the caller's physical condition allows a safe escape ('condition advertisement', e.g. Caro 1994); 3. the caller is able to harass ('mob') the predator alone (van Schaik & van Noordwijk 1989) or as a group (Boesch 1991).

From the nature of the observed predator-prey relationship, we do not think that the high call rates advertise condition or vigour. None of the monkey species investigated has the physical power to repel a leopard, nor does the outcome of an interaction depend much on the physical condition of a monkey as it does, for example, for a Thompson's gazelle (FitzGibbon & Fanshawe 1988). Even physically weak monkeys will still enjoy an enormous locomotor advantage over the leopard in the continuous scaffolding of the rainforest canopy.

Mobbing behaviour has been said to function in predator deterrence, although the term is rarely defined. We do not think that the behavioural pattern we observed is appropriately labelled as mobbing behaviour in its original sense (Curio et al. 1978). Playback of leopard growls consistently caused high call rates but only rarely led to visual contact or close physical proximity, two defining features of mobbing behaviour.

It might be the case, however, that certain acoustic features of the monkey alarm calls are physically aversive for a leopard. For example, the leopard might have a low perceptual threshold for a particular frequency range and hence perceive sounds of high intensity within that range as noxious. We are not aware of any

studies describing the behavioural audiogram of an African leopard and hence cannot properly address this hypothesis. If the hypothesis were correct, however, then one would expect natural selection to favour calls containing the most aversive acoustic structure across all species. However, primate alarm calls to leopards differ in their acoustic structure not only between but also within species: male diana monkeys, for example, produce leopard alarm calls that are completely different from those produced by the females, yet the two call types refer to the same predator (Zuberbühler et al. 1997, 1999).

Our data and some observations on vervet monkeys suggest that the main factor determining the monkeys' vocal strategy is the predator's hunting technique. In Amboseli National Park, Kenya, leopards also hunt by stealth and vervets respond to them by giving numerous loud and conspicuous vocalizations (Cheney & Seyfarth 1990, p. 145). However, once it was observed that a leopard changed its technique and pursued a monkey through a tree. Here, the monkey remained completely silent, much like Tai monkeys when pursued by chimpanzees. In Cameroon, vervets respond with a conspicuous 'leopard-type' vocal behaviour to hunting wild dogs (e.g. *Canis aureus*). In other areas, however, where domestic dogs are often accompanied by poachers, dogs elicit a highly cryptic 'chimp-type' vocal behaviour (Kavanaugh 1980). It appears, therefore, that monkeys tend to advertise perception and futility of a hunting attempt if this deters the predator from further hunting.

### Conclusions

Differences in monkey alarm call rates appear to reflect different anti-predator strategies designed to interfere with a predator's hunting tactic. We have shown that pursuit hunters that depend on acoustic cues elicit cryptic vocal behaviour, while stalkers that depend on unprepared prey elicit conspicuous vocal behaviour in all monkey species. We suggest that this conspicuous behaviour functions to signal detection and unprofitability, as predicted by the perception advertisement hypothesis. We have argued that intraspecific communication could have driven the evolution of predator alarm calls because of kin benefits from social warning and cultural transmission of predator features. These benefits will keep individuals with close relatives from cheating, i.e. abstaining from calling in the presence of predators, but they do not explain why these animals produce so many calls in the presence of one predator, the leopard. Since our sampling units were entire groups, we can say little about individual contributions to the high call rates. Individuals without own offspring might also benefit from calling if this increases the probability that the leopard leaves the group. Continuous calling at high rates by many individuals might be necessary if the leopard does not leave unless a high threshold of conspicuousness is reached. This might specifically be the case if leopards not only hunt for monkeys but also for duikers (*Cephalophus* spp.) that often forage underneath monkey groups (D. Jenny, pers. obs.). Continuously high alarm call rates beyond average levels increase conspicuousness, provide a unique and unambiguous signal of detection, and might interfere with any of the leopard's hunting activity such that it is forced to move on and hunt elsewhere.

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