



Causal knowledge of predators' behaviour in wild Diana monkeys

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Wild Diana monkeys, *Cercopithecus diana*, of Tai forest, Ivory Coast, are preyed upon by leopards, *Panthera pardus*, and chimpanzees, *Pan troglodytes*. These two predators differ in their main hunting tactic and Diana monkeys attempt to avoid predation with two distinct antipredator strategies: conspicuous alarm-calling behaviour to leopards and silent, cryptic behaviour to chimpanzees. However, the Diana monkeys' choice of the appropriate antipredator strategy is complicated by the fact that chimpanzees themselves also fall prey to leopards. Chimpanzees give loud and conspicuous alarm screams when they detect a leopard. When these chimpanzees' leopard alarm calls were played back to different groups of Diana monkeys, in about half of the cases recipients switched from a chimp-specific cryptic response to a leopard-specific conspicuous response, suggesting that some individuals assumed the presence of a leopard. Groups whose home range was in the core area of the resident chimpanzee community were more likely to respond this way than more peripheral groups, indicating between-group differences in semantic knowledge. In a follow-up experiment, the monkeys' understanding of the chimpanzee alarm calls was further assessed with a prime-probe technique. Monkeys were primed with chimpanzee alarm calls and then, 5 min later, tested with leopard growls to see whether they were able to anticipate the presence of a leopard. Results were consistent with the hypothesis that monkeys responding cryptically to chimpanzee alarm calls did so because they were not able to understand the calls' meaning. Data are discussed with respect to three possible cognitive mechanisms, associative learning, specialized learning programmes, and causal reasoning, that could have led to causal knowledge in some individuals but not others.

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In several studies, nonhuman primates have shown a surprising inability to understand even basic causal problems of impulse mechanics (Visalberghi & Tomasello 1998). In a colony of captive longtailed macaques, *Macaca fascicularis*, for example, individuals failed to develop a very simple tool use technique invented by one colony member, raking in a fruit from outside the enclosure with a stick, even though subjects were highly motivated, had ample exposure to the problem, and were given plenty of opportunities to practise the technique themselves (Kummer 1995; Zuberbühler et al. 1996). Because most nonhuman primates do not normally use tools in the wild, one hypothesis is that the neural resources necessary for an understanding of causality in the physical domain are simply not present (but see Hauser et al. 1999).

However, causal understanding might be advanced in contexts involving social interactions, such that monkeys

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perform better when problems involve animate beings rather than inanimate objects (Humphrey 1976). Cheney et al. (1995), for example, have shown that free-ranging chacma baboons, *Papio cynocephalus ursinus*, may perceive or even recognize cause-effect relations in the context of social interactions. In this species, dominance relationships are partially mediated by two kinds of vocalizations: the 'grunts' given by a female to lower-ranking group members and the 'fear barks' given to higher-ranking ones. Through the use of a playback experiment, it was possible to show that causally inconsistent call sequences, a higher-ranking animal responding with fear barks to a lower-ranking animal's grunts, elicited stronger responses in recipients than control sequences that were made causally consistent.

In the wild, there is selective pressure for monkeys to predict not only the behaviour of other group members but also that of neighbouring groups, heterospecific competitors and predators. Here I describe experiments designed to investigate monkeys' understanding of cause-effect relations involving predators. The

experiments examined whether wild Diana monkeys, *Cercopithecus diana*, living in the Tai forest, Ivory Coast, recognize the causal factors that govern vocal behaviour in two of their predators, the chimpanzee, *Pan troglodytes*, and the leopard, *Panthera pardus*.

Causal knowledge in animals has been portrayed as either weak or strong, depending on the amount of exposure necessary for a particular causal relation to become established in memory (Kummer 1995). Within this theoretical framework, weak causal knowledge is viewed as the result of an associative learning mechanism (e.g. Pavlov 1927), while strong causal knowledge results from either (1) a specialized learning programme, a prominent example being taste aversion learning in rats, *Rattus norvegicus* (Garcia et al. 1966) or (2) causal reasoning, a human-like understanding of how events relate causally to each other.

Diana monkeys live in small groups of one adult male and several adult females with their offspring. They use two different antipredator strategies to defend themselves against predators. After detecting a leopard, both male and female Diana monkeys respond by giving loud conspicuous alarm calls that appear to function both to warn others and to signal to the predator that it has been detected (Zuberbühler et al. 1997). Leopards tend to give up their hiding position and leave the area once they have been discovered (Zuberbühler et al. 1999b). In contrast, upon detecting a chimpanzee, female Diana monkeys give only a few quiet alarm calls and flee quickly to hide in the canopy, while the adult male of the group does not vocalize at all (Boesch 1994; Zuberbühler et al. 1997). Tai chimpanzees have sophisticated climbing skills that allow them to hunt for monkeys, mainly red colobus monkeys, *Colobus badius*, even in the high strata of the forest canopy (Boesch & Boesch 1989; Boesch 1994). Diana monkeys are captured less frequently by chimpanzees but are nevertheless exposed to chimpanzee hunting behaviour because of their high association rates with red colobus monkeys (Wachter et al. 1997).

Previous research has shown that Diana monkeys respond to the social screams and pant hoots given by chimpanzees by adopting cryptic positions in the canopies of trees and remaining silent (Zuberbühler et al. 1999b). However, their choice of an appropriate antipredator strategy to chimpanzees is complicated by the fact that chimpanzees themselves also fall prey to leopards (Hoppe-Dominik 1984; Boesch 1991). When encountering a leopard, chimpanzees give loud and conspicuous alarm calls (Marler & Tenaza 1977, page 993; Boesch 1991) described as 'SOS alarm screams' and 'waa barks' by Goodall (1986, page 135). To escape successfully from leopards and chimpanzees, therefore, Diana monkeys must distinguish between, and respond differently to, chimpanzee alarm calls and chimpanzee vocalizations given in nonpredatory contexts. In most cases, a chimpanzee vocalization simply signals the presence of one or several chimpanzees and therefore should evoke silent flight. Chimpanzees' alarm screams and waa barks, in contrast, additionally signal the presence of a leopard and should elicit loud, conspicuous alarm calls (see below).

I examined Diana monkeys' responses to chimpanzee vocalizations in two different types of playback experiments. In the first, I played tape recordings of either chimpanzees' social screams or alarm calls and noted the monkeys' responses. In this experiment, the monkeys were presented with a problem whose solution required some knowledge of the relationship between chimpanzee vocalizations and the presence of a leopard, a cause-effect relation in the biological domain. Subjects perceived only the second part of the causal chain, the chimpanzees' alarm calls, and had to identify the cause, the leopard, in order to respond properly. In comparable situations, humans use causal reasoning to determine the reason of a surprising event.

In a second set of experiments, I played leopard growls to monkeys shortly after having exposed them to the playbacks of either chimpanzees' alarm calls or social screams. If Diana monkeys recognized and responded to the causal mechanisms underlying chimpanzee vocalizations, I predicted that they should show little response to leopard growls after hearing chimpanzees' alarm calls (because the presence of a leopard could be anticipated), but show a strong response to leopard growls after hearing chimpanzee social screams (because the presence of a leopard could not be anticipated).

GENERAL METHODS

Study Site and Subjects

Data were collected in the Tai National Park, Ivory Coast, between July 1994 and February 1999 in a study area of ca. 50 km² of primary rain forest surrounding the Institute d'Ecologie Tropicale (5°50'N, 7°21'W). I conducted playback experiments between July and August 1994 and 1995, between June 1996 and May 1997, and during December 1998. None of the groups examined in this study was habituated to human observers and the majority were exposed to human poaching. The average home range size of a Diana monkey group is ca. 0.5 km² (Höner et al. 1997), with the females defending the group's range against neighbours (Hill 1994). Based on these data, I estimated the Diana monkey population in the study area to be ca. 60–70 different groups. To avoid dependencies in the data, I never tested a particular group more than once with a particular playback stimulus unless trials were separated by at least 1 year. This level of independence was obtained by testing a group only if it was at least 1 km (i.e. two home range diameters) away from any previously conducted trial of the same series. Leopards in the Tai forest are solitary with a population density of 7–11/100 km², covering home ranges between 22 and 86 km² (Jenny 1996). A chimpanzee community of 80 individuals covers a range of ca. 27 km² (Boesch & Boesch 1989).

Experimental Protocol

In conducting playback experiments, I systematically searched the study area until I found a Diana monkey

Table 1. Independent variables potentially related to the monkeys' perceived vulnerability to chimpanzee predation

Variable	Definition
Distance	Horizontal distance between the speaker and the group: close: <25 m; intermediate: 25–50 m; far: >50 m
Stratum	Position of the group in the canopy; low: >5 m; intermediate: 5–23 m; high: 24–40 m; emergent: >40 m (see McGraw 1998)
Vegetation	Description of the local vegetation: dense: thick undergrowth, upper canopy not visible; moderate: moderate undergrowth, some tree crowns visible; open: little undergrowth, several tree crowns visible
Illumination	Description of the general illumination: dark: no shadows on ground, sky heavily overcast or twilight; moderate: no shadows on ground, sky moderately overcast; light: shadows visible, sky little overcast or direct sunlight
Progression	General movement behaviour of the group: move: group travels through trees at time of playback; rest: group does not move or moves within the same tree*
Red colobus	Red colobus group is (not) within 100 m of the focal Diana monkey group

*As assessed by their vocalizations.

group, typically by hearing their vocalizations. I then determined whether the group was progressing, its approximate distance and elevation from the ground, the density of the surrounding vegetation, the general illumination, and whether they were associated with red colobus monkeys (Table 1). Owing to the high rates of poaching in the Tai forest, nonhabituated Diana monkeys show a strong antipredator response after detecting a human observer. Their response to a human is similar to that when detecting a chimpanzee: while the male stays silent the females typically give a few alert calls and then rapidly move away to hide silently in the vegetation of the upper canopy. Therefore, to ensure that my presence did not distort the monkeys' behaviour, I monitored each group's vocal behaviour for about 15 min prior to each experiment, while avoiding visual contact completely. If no predation event occurred during that period and no monkey had detected me or part of the equipment, I initiated a playback trial. The speaker was positioned ca. 2 m above the ground and 25–75 m from the group, that is, outside the group's visual range. Recordings of the subjects' vocal behaviour began 5 min before the first playback stimulus and lasted for 15 min. In all cases, sample sizes indicate the number of individual groups tested. Since Diana monkey groups consist of several adult females but only one adult male, the number of males is equal to the number of groups tested.

Playback Stimuli

I used the following recordings as playback stimuli: (1) growls of an African leopard; (2) chimpanzee screams and grunts produced in a social context; or (3) chimpanzee alarm calls (SOS screams and waa barks) to a leopard model. Figure 1 shows spectrographic representations of the chimpanzee vocalizations used. Spectrograms of leopard growls have been published elsewhere (e.g. Zuberbühler et al. 1997). Calls were digitized at 16 bits, 44 kHz and displayed with an analysis resolution of

170.97 Hz/1024 points, 2.902 ms, 87.5% and a grid resolution of 10.77 Hz/4096 points using a Hanning window function. All stimuli were presented as natural series lasting ca. 15 s. Leopard growls were purchased from the National Sound Archive, London, U.K. All other vocalizations were recorded in the study area. Chimpanzee leopard alarm calls were recorded when a bypassing chimpanzee accidentally detected a hidden leopard model, a torso of ca. 40 × 120 cm in imitation leopard fur.

Pseudoreplication

Pseudoreplication is a potential problem in studies using playback stimuli (e.g. McGregor et al. 1992; Poole 1999). I obtained statistical independence by testing a large number of different Diana monkey groups, such that each group heard a particular stimulus or stimulus pair only once. To maximize the external validity of the results one would ideally play different exemplars of each stimulus class in every trial. The number of available master recordings, however, prevented me from doing so; playback tapes of leopard growls ($N=5$) were each made from two different master recordings. Playback tapes with chimpanzee social screams and grunts ($N=2$), also made from two different master recordings, contained three grunts and 16 social screams and 17 grunts and six social screams, respectively, both times conserving the natural call sequence. Playback tapes of chimpanzee alarm calls to a leopard ($N=5$) were made from one master recording containing a series of several alarm calls. Playback tapes contained either 15 alarm screams and eight waa barks, 16 alarm screams and eight waa barks, seven alarm screams and five waa barks, four alarm screams and four waa barks, or five alarm screams and no waa barks. Earlier studies had shown that real predators elicited the same vocal behaviour, both quantitatively and qualitatively, in Diana monkeys as did playbacks of recordings of their vocalizations (e.g. Zuberbühler et al. 1999b), indicating that a small number of good

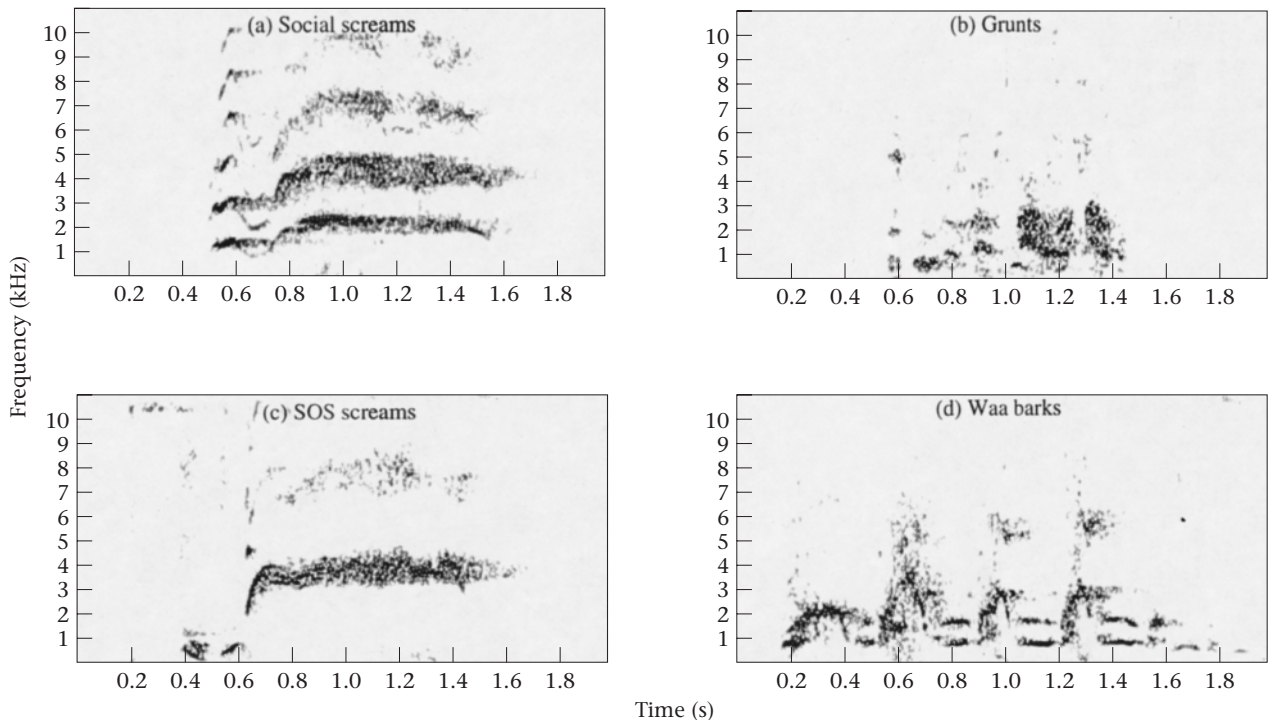


Figure 1. Sonographic representations of the chimpanzee vocalizations used as playback stimuli. (a) Social screams, (b) grunts: both are given to conspecifics in a nonpredatory situation. (c) SOS screams, (d) waa barks: both are alarm calls given to a leopard.

recordings can usefully represent the different predation situations.

Equipment

The playback stimuli were broadcast with a Sony WMD6C Professional Walkman connected to a Nagra DSM speaker-amplifier. The vocal responses of the monkeys to the playback stimuli were tape-recorded with the Sony WMD6C or TCM5000EV recorders in combination with a Sennheiser ME80 directional microphone. Using Canary 1.2. (Charif et al. 1995) the monkeys' alarm call responses to playbacks were digitized and displayed as sonagrams on a Macintosh computer.

Diana Monkey Vocal Behaviour

Male alarm calls consist of very loud and low-pitched blocks of syllables. Spectrally, the calls are best described as consisting of a number of syllables of a very low fundamental frequency and two bands of acoustic energy, the first around 1 kHz, the second around 1.5 kHz. Males produce two acoustically distinct call types to crowned eagles, *Stephanoaetus coronatus*, and to leopards. Calls to leopards consist of syllables whose formants show distinct frequency transitions while calls to eagles do not show such transitions (Zuberbühler, *in press*). Females also produce structurally distinct alarm calls to leopards and crowned eagles that can be distinguished by ear. Spectrographic representations of Diana monkey vocalizations have been published elsewhere (Zuberbühler et al. 1997).

EXPERIMENT 1: RESPONSE TO CHIMPANZEES AND LEOPARDS

Methods

Rationale and hypotheses

To investigate whether Diana monkeys possess knowledge about the relationship between chimpanzees' alarm calls and the presence of a leopard, I played back tape recordings of either (1) chimpanzees' alarm calls, (2) chimpanzees' social screams, or (3) leopard growls and noted the monkeys' responses. If monkeys were able to respond to the causal information conveyed in the chimpanzee vocalizations, then I expected them to respond with cryptic behaviour to chimpanzee social screams and with their own leopard alarm calls to chimpanzee alarm calls and leopard growls. This is based on the assumption that it is more adaptive for Diana monkeys to adopt a conspicuous leopard-type response than a cryptic chimpanzee-type response because failing to give an alarm call in response to a leopard is likely to be more costly to Diana monkeys than revealing one's location to a chimpanzee. Although both chimpanzees and leopards hunt Diana monkeys, the relative predation risk is greater from leopards (Hoppe-Dominik 1984; Boesch & Boesch 1989). Moreover, chimpanzees are unlikely to persist in hunting monkeys when confronted with a leopard. Diana monkeys can benefit from alarm calling to leopards because their calls can warn close relatives (Maynard Smith 1965), transmit the caller's knowledge about predators to inexperienced close relatives (Curio

Table 2. Diana monkeys' vocal behaviour in response to playback of predators

Playback stimulus	Number of groups giving alarm calls		
	Yes	No	Rate (%)
Males			
Chimpanzee social screams	0	15	0.0
Chimpanzee alarm calls	20	14	58.8
Leopard growls	13	0	100.0
Females			
Chimpanzee social screams	1	14	6.7
Chimpanzee alarm calls	15	19	44.1
Leopard growls	11	2	84.6

et al. 1978) and cause the leopard to leave the area (Zuberbühler et al. 1999b).

Results

Vocal behaviour of males

Male Diana monkeys showed consistent differences in their vocal responses to leopards and chimpanzees. They remained silent after hearing chimpanzee social screams but gave loud and conspicuous alarm calls after hearing leopard growls and chimpanzee alarm calls (Table 2). They were significantly more likely to respond with alarm calls to a playback with chimpanzee alarm calls than to chimpanzee social screams (Fisher's test: $N=49$, $P<0.001$). They were also significantly more likely to respond with alarm calls to a playback of leopard growls than to chimpanzee alarm calls (Fisher's test: $N=47$, $P<0.005$). Since the chimpanzee alarm call data were used twice the significance level was set at $\alpha''=a/k=0.025$, using the Bonferroni method (Sokal & Rohlf 1995, page 240).

Vocal behaviour of females

Like males, the Diana monkey females showed consistent differences in their vocal responses to leopards and chimpanzees. They did not usually give leopard alarm calls after hearing chimpanzee social screams but frequently produced them after hearing leopard growls and chimpanzees' alarm calls to leopards (Table 2). They were significantly more likely to respond with leopard alarm calls to playbacks of chimpanzees' alarm calls than to playbacks of chimpanzees' social screams (Fisher's test: $N=49$ groups, $P<0.01$). They were also significantly more likely to respond with alarm calls to a playback of leopard growls than to chimpanzee alarm calls (Fisher's test: $N=47$ groups, $P<0.02$). Again, a significance level of $\alpha''=a/k=0.025$ was chosen for the above-mentioned reason.

EXPERIMENT 2: RECOGNITION OF CALLS

Methods

Rationale and hypotheses

In many groups in experiment 1, Diana monkeys responded to chimpanzees' alarm calls as if the apparent

predator was a leopard rather than a chimpanzee. In some groups, however, the male and the females adopted a cryptic response after hearing chimpanzees' alarm calls, behaving as if the apparent predator were a chimpanzee (Table 2). There are at least two explanations for the cryptic response to chimpanzees' alarm calls in some monkey groups.

The 'safety' hypothesis. The monkeys may have recognized that chimpanzees' alarm calls might signal the presence of a leopard, but remained cryptic because they sensed that there was still some risk of a chimpanzee attack (the 'safety' hypothesis). Table 1 explains how Diana monkeys might be more at risk of an attack when they are (1) close to a chimpanzee group, (2) low in the canopy, (3) in open vegetation, (4) in well-illuminated surroundings, (5) progressing through the forest, and (6) associated with a group of red colobus monkeys, the chimpanzees' main target. To test this hypothesis, I investigated whether these six safety-related variables were related to the monkeys' alarm-calling behaviour.

The 'knowledge' hypothesis. Some Diana monkey groups in this population may never have witnessed an encounter between a leopard and chimpanzees and remained quiet because they simply did not recognize that chimpanzees' alarm calls can signal the presence of a leopard. To test this hypothesis, I analysed two kinds of data.

First, I determined whether there was a relationship between the probability a Diana monkey group would respond with leopard alarm calls to chimpanzees' alarm calls and the group's location within the territory of the resident chimpanzee community. I predicted that Diana groups living in the periphery of a chimpanzee territory would be less likely to respond with alarm calls than groups living in the core area. Whether a group was found in the core area was determined following Herbing (1998), in which the territory use of three different chimpanzee communities in the study area was investigated to distinguish between core area (75% of all sightings) and two levels of periphery (20 and 5% of all sightings).

Second, I designed a playback experiment in which I used a priming technique to determine whether Diana monkey groups differed in their tendency to associate chimpanzees' alarm calls with the presence of a leopard. The experiment included three types of trials: a baseline, a test and a control condition. In each trial, a Diana monkey group heard two playback stimuli, a prime and a probe, separated by 5 min of silence. For example, groups first heard chimpanzees' alarm calls and then, after 5 min of silence, the growls of a leopard. Across conditions, prime and probe stimuli varied with respect to their acoustic and referential (or semantic) resemblance. Table 3 summarizes the experimental design. A more detailed discussion of the prime-probe paradigm is given in Zuberbühler et al. (1999a). Because the vocal behaviour of the females is the combined result of several individuals calling (e.g. Table 2), differences in knowledge between

Table 3. Design of the prime–probe playback experiment

Condition	Playback stimuli		Resemblance between prime and probe	
	Prime	Probe	Acoustic	Semantic
Baseline	Leopard growls	Leopard growls	High	High
Control	Chimpanzee social screams	Leopard growls	Low	Low
Test	Chimpanzee alarm calls	Leopard growls	Low	Low/high*

*Depending on the monkey's familiarity with chimpanzees' alarm calls.

females may confound two different underlying behavioural patterns. In this experiment, therefore, I concentrated only on the calls produced by each group's single male.

In the baseline series of trials, both the acoustic and semantic features remained the same across prime and probe stimulus (leopard growls→leopard growls). Individual monkey groups first heard as a prime stimulus playback of leopard growls, indicating the presence of a leopard. After 5 min of silence, the group heard as a probe stimulus playback of leopard growls, indicating the presence of a leopard again. Based on previous results (Zuberbühler et al. 1999a), I predicted that in this condition males would respond strongly to the prime stimulus (by giving many alarm calls) but weakly to the probe stimulus. Because monkeys heard the same stimulus both as a prime and a probe, the probe was acoustically and semantically redundant. These playbacks are replications of previous experiments (Zuberbühler et al. 1999a).

In the control trials, both the acoustic and semantic features were different (chimpanzee social screams→leopard growls). Monkeys first heard playback of chimpanzee social screams, indicating the presence of chimpanzees, followed by playback of leopard growls, indicating the presence of a leopard. Social screams were chosen as a control stimulus because of the acoustic similarity with the chimpanzees' alarm calls (Fig. 1) and because fearful and distressed chimpanzees also give this call, although in a nonpredatory context. I predicted that monkeys would respond with chimpanzee-specific cryptic behaviour to the prime and with leopard-specific conspicuous behaviour to the acoustically and semantically novel probe.

In the test trials, the semantic features were alike while the acoustic features were different (chimpanzee alarm calls→leopard growls). Individual monkey groups first heard playbacks of chimpanzees' alarm calls followed by playbacks of a leopard's growls after 5 min. If a monkey recognized that these alarm calls potentially indicated the presence of a leopard, they should have treated the probe stimulus as similar in its semantic content to the prime, despite their acoustic differences. In this case, therefore, they should have given many alarm calls in response to the prime stimulus but only a few alarm calls in response to the probe. Ignorant monkeys, however, should have treated these two call types as signalling entirely different

information. Such individuals should have remained silent upon hearing chimpanzees' alarm calls, but responded with alarm calls when played leopard growls 5 min later.

Results

In contrast to the predictions of the 'safety' hypothesis, there was no relationship between males' responses to chimpanzees' alarm calls and the six independent variables relating to potential vulnerability at the time of the playback (Fig. 2; ANOVA: distance: $F_{2,14}=3.012$; stratum: $F_{3,14}=0.197$; vegetation: $F_{2,14}=0.265$; illumination: $F_{2,14}=0.459$; progression: $F_{1,14}=1.918$; red colobus: $F_{1,14}=1.293$, NS; $N=26$ males, $r^2=0.382$). Similarly, the females' alarm call behaviour was also not affected by potential differences in safety from a chimpanzee attack (Fig. 2; ANOVA: distance: $F_{2,14}=3.232$; stratum: $F_{3,14}=1.446$; vegetation: $F_{2,14}=0.336$; illumination: $F_{2,14}=0.341$; progression: $F_{1,14}=2.818$; red colobus: $F_{1,14}=1.684$, NS; $N=26$ groups, $r^2=0.560$).

Two sets of data supported the 'knowledge' hypothesis, however. First, there was a relationship between a group's response to playbacks and its location within the resident chimpanzee community's territory (Table 4). Of 34 Diana monkey groups tested, 25 had their home range within one of the three chimpanzee communities' territory. Groups whose home range was within the core area of the resident chimpanzee community were significantly more likely to give leopard alarm calls than groups living in the periphery (Fisher's tests, two tailed: males: $P<0.02$; females: $P<0.03$). Second, the results of the prime–probe experiments revealed the following pattern.

In the baseline condition, males in 13 groups were played leopard growls followed by playback of the same leopard growls after 5 min. Males produced significantly fewer leopard alarm calls to the second playback of leopard growls than to the first (Wilcoxon signed-ranks test, one tailed; $Z=-3.062$, $N=13$, $P<0.003$; Fig. 3).

In the control condition, males in 15 groups heard chimpanzee social screams as a prime and then, 5 min later, leopard growls as a probe. Males produced significantly more leopard alarm calls to the probe than to the prime (Wilcoxon signed-ranks test, one tailed: $Z=-2.521$, $N=15$, $P<0.006$; Fig. 3).

In the test condition, males in 24 groups heard playback of chimpanzees' alarm calls as a prime followed by

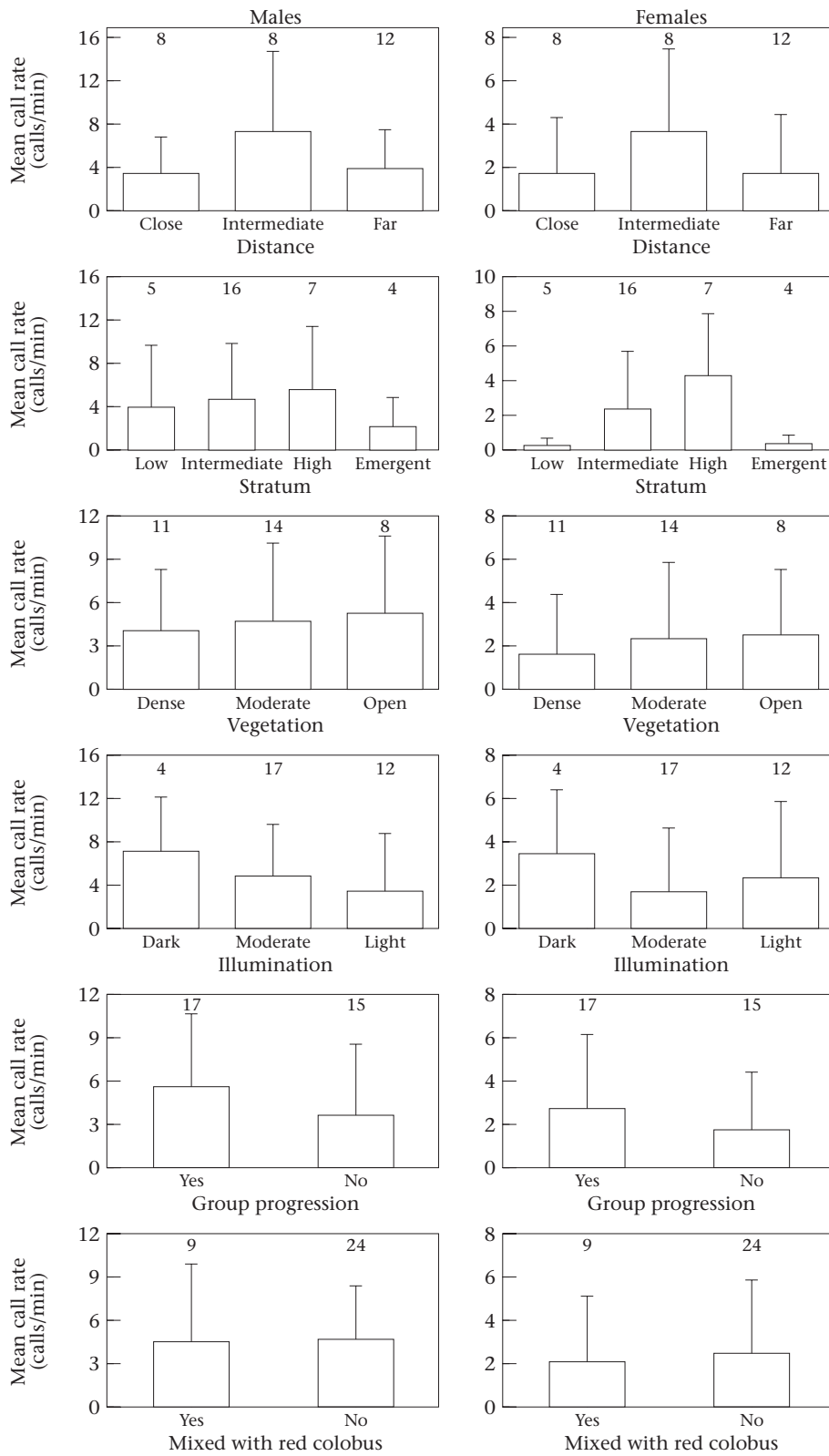


Figure 2. Diana monkey alarm call rates (\bar{X} +SD) as a function of several variables relating to the monkeys' perceived safety. Number of groups tested is given above the bars.

Table 4. Relationship between the groups' tendency to respond with leopard alarm calls to chimpanzees' leopard alarm calls and their location within the resident chimpanzees' territory

Location in chimpanzees' territory*	Trials with at least one leopard alarm call given			
	Males		Females	
	Yes	No	Yes	No
Core area (75% of encounters)	6	0	5	1
Periphery (25% of encounters)	8	11	5	14
Total	14	11	10	15

*Herbinger (1998).

playback of leopard growls as a probe after 5 min. Males in 14 of the 24 groups responded with their own alarm calls to chimpanzees' alarm calls and were termed

'conspicuous' males. Males in 10 other groups, however, did not produce any vocalizations or other kind of noticeable behaviour but hid silently in the canopy and hence were termed 'cryptic' males. The reason for this dichotomy, according to the 'knowledge' hypothesis, is that the conspicuous males gave alarm calls because they took the chimpanzees' alarm calls as evidence for the presence of chimpanzees and a leopard. The cryptic males, however, did not possess any knowledge of the meaning of chimpanzee alarm calls and consequently took them as evidence only for the presence of chimpanzees. If this is correct then the experience of chimpanzees' alarm calls should have profoundly different effects on cryptic and conspicuous males. These effects should become apparent in their response to the subsequent probe stimulus, the leopard growl. Hence, in the following, males were analysed separately according to whether they produced leopard alarm calls to the prime (conspicuous versus cryptic males).

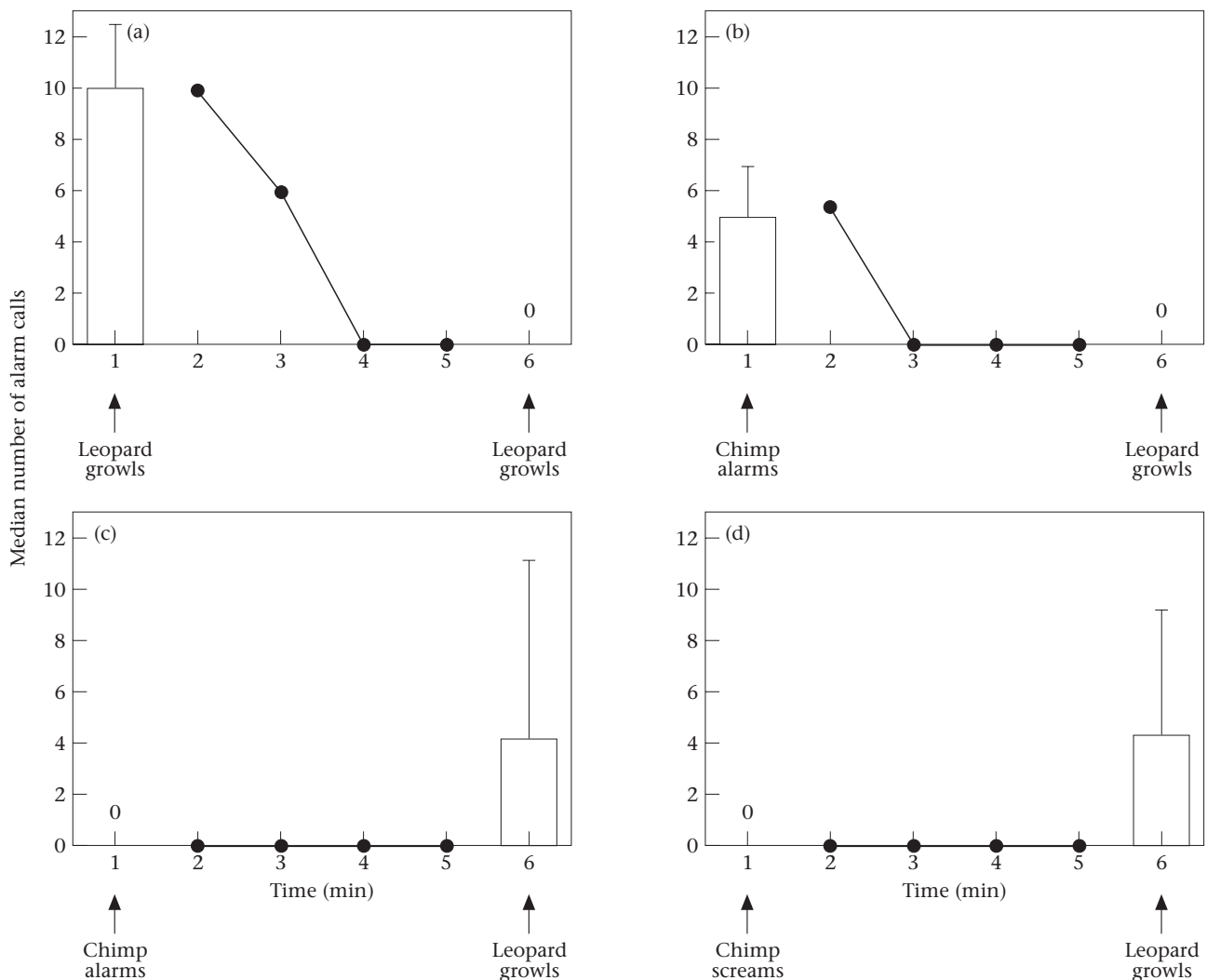


Figure 3. Median number (+third interquartile) of male alarm calls in the (a) baseline, (b, c) test and (d) control conditions. Males who responded with alarm calls to chimpanzee alarm calls were termed 'conspicuous' (b), while those who did not respond with alarm calls were termed 'cryptic' (c). See Table 3 for details of conditions. (a) Baseline: $N=13$; test: (b) conspicuous males: $N=14$; (c) cryptic males $N=10$; control: $N=15$.

(1) After having been primed with chimpanzees' alarm calls, the 14 conspicuous males were exposed to playback of leopard growls 5 min later. Only one of them (7.1%) responded with alarm calls to this probe stimulus, even though leopard growls are normally highly effective in eliciting male alarm calls (Fig. 3). As in the baseline condition, males produced significantly fewer leopard alarm calls to the probe than to the prime (Wilcoxon signed-ranks test, one tailed: $Z = -3.219$, $N=14$, $P<0.001$; Fig. 3). The number of leopard alarm calls that these 14 males gave in response to leopard growls did not differ from those given by the 13 males in the baseline condition (Mann-Whitney U test, two tailed: $Z = -0.578$, $P>0.5$; Fig. 3). These males' responses to leopard growls did differ, however, from the 15 males that had been primed with chimpanzees' social screams in the control series (Mann-Whitney U test, two tailed: $Z = -2.662$, $P<0.008$; Fig. 3). Since the data describing male responses to chimpanzee alarm calls were used twice the significance level was set at $\alpha''=a/k=0.025$, using the Bonferroni method (Sokal & Rohlf 1995, page 240).

(2) After having been primed with chimpanzees' alarm calls, the 10 cryptic males were also exposed to playback of leopard growls 5 min later. Six (60%) subsequently responded with alarm calls to playbacks of leopard growls (Fig. 3). As in the control condition, males produced significantly more leopard alarm calls to the probe than to the prime (Wilcoxon signed-ranks test, one tailed: $Z = -2.207$, $N=10$, $P<0.02$; Fig. 3). These males gave significantly more alarm calls in response to leopard growls than the 13 males who heard the baseline series (Mann-Whitney U test, two tailed: $Z = -2.407$, $P<0.02$; Fig. 3). Their behaviour did not differ, however, from that of the 15 males who were exposed to the control series. In both cases, males responded to the leopard growl probe by giving alarm calls (Mann-Whitney U test, two tailed: $Z = -0.232$, $P>0.8$; Fig. 3). Again, the data describing male responses to chimpanzee alarm calls were used twice such that the significance level was adjusted to $\alpha''=a/k=0.025$, using the Bonferroni method (Sokal & Rohlf 1995, page 240).

An alternative explanation

Chimpanzees' social screams and alarm screams differ not only in their general acoustic structure and potential to signal the presence of a leopard but also in amplitude. Although I varied amplitude for each stimulus class, it might be that amplitude differences, rather than the referential meaning of the stimuli, were responsible for the different call rates to the two stimuli (see Fig. 3). Stimuli were played back to match the natural intensity range of loud chimpanzee screams (range 94–107 dB, median 103 dB). ANOVAs did not suggest that the amplitude by which the chimpanzee vocalizations were played back affected the number of male or female leopard alarm calls produced. Semantic content, that is, whether the chimpanzee calls were given to a leopard, however, had a significant effect on both sexes (Table 5).

Table 5. ANOVA of the relationship between stimulus intensity, meaning and the number of male and female alarm calls produced

Independent variable	Sum of squares	df	F ratio	P
Male alarm calls				
Stimulus intensity	19.751	1	2.612	NS
Semantic content	133.290	1	17.628	<0.001
Error	272.207	36		
Female alarm calls				
Stimulus intensity	5.677	1	0.854	NS
Semantic content	39.577	1	5.955	<0.03
Error	239.256	36		

Male alarm calls: $N=39$ groups, $r^2=0.332$; female alarm calls: $N=39$ groups, $r^2=0.144$.

GENERAL DISCUSSION

Diana monkeys in Tai forest differed in their response to chimpanzees' alarm calls. In some groups, monkeys behaved as if they recognized that these alarm calls signalled the potential presence of a leopard: they responded to chimpanzees' leopard alarm calls by giving leopard alarm calls themselves, even though chimpanzees normally caused them to behave cryptically. Groups living in the core area of the resident chimpanzee community were more likely to do so than peripheral groups. A prime-probe experiment then indicated that for some males, chimpanzee alarm calls signalled the presence of a leopard. After being primed with chimpanzees' alarm calls, males failed to respond to the probe stimulus of leopard growls, even though this stimulus was acoustically novel and normally highly effective in eliciting a strong vocal response. These males behaved exactly like the males in the baseline condition who also gave many leopard alarm calls to the prime (playback of leopard growls) but no longer called to the probe (i.e. playback of leopard growls 5 min later). Thus, it seems that these males had some knowledge of the causal factors underlying the production of chimpanzees' alarm calls, because priming with both these alarm calls and leopard growls had similar effects on their responses to the probe. A proportion of males, however, adopted a cryptic response upon hearing chimpanzees' alarm calls. When these males were played leopard growls 5 min later, they responded by giving loud leopard alarm calls, indicating that they had not anticipated the presence of a leopard. These males did not differ in their vocal response from control males that were primed with the acoustically similar chimpanzee social screams, suggesting that these males were not able to distinguish chimpanzees' alarm calls from similar sounding social screams. These experiments suggest that some monkeys in the study population took chimpanzees' alarm calls as a sign of leopard presence, while others behaved as if they could not distinguish between the different causes underlying chimpanzee vocalizations.

When a Diana monkey hears a chimpanzee giving alarm calls to a leopard, the monkey is presented with a

problem whose solution requires some knowledge of the relationship 'leopard→chimpanzee alarm call', a cause-effect relation in the biological domain. In the present study, subjects perceived only the second part of the causal chain, the chimpanzees' alarm calls, and had to infer its cause in order to give alarm calls themselves. Knowledgeable humans presented with a similar problem use causal reasoning to infer that, for example, the chimpanzees must have detected a leopard. When Diana monkeys heard chimpanzees' alarm calls, some individuals responded as if a leopard were present while others behaved as if the calls signalled only the presence of chimpanzees. Apparently, some subjects were sensitive to the causal relation between chimpanzees' alarm calls and leopards, while others were not.

These results support and contrast with experiments conducted on other primate species in a number of interesting ways. Free-ranging vervet monkeys, *Cercopithecus aethiops*, for example, seem to be unable to recognize the causal relation between pythons, *Python sebae*, and the tracks they produce or leopards and the carcasses they leave in trees (Cheney & Seyfarth 1988, 1990). Similarly, capuchin monkeys, *Cebus apella*, fail to understand the causal relations involved in a task that requires the subject to push a piece of food out of a clear plastic tube with a trap (Visalberghi & Limongelli 1994). Here, individuals appear to be unable to apply causal knowledge necessary to insert the stick from the correct side to solve the problem (Visalberghi & Tomasello 1998). It remains possible, however, that individuals did perceive the causality of the problem but nevertheless failed to transmit their knowledge into the necessary physical commands when handling the tool. Female chacma baboons, in contrast, act as if they apply causal reasoning to the interactions and relationships of others. In playback experiments, subjects appeared to recognize that an individual's submissive barks could be evoked only by interactions with dominant, but not by interactions with subordinate, group members, and they responded strongly to an interaction that violated this knowledge (Cheney et al. 1995).

It seems puzzling that in some contexts nonhuman primates fail to show evidence of causal understanding while in others individuals show rather sophisticated knowledge. There are a number of possible explanations for the apparent ability of monkeys to recognize causal relations in some contexts but not in others. First, monkeys may be better at recognizing causal associations among animate beings than inanimate objects. This hypothesis argues that natural selection has favoured cognitive abilities in the 'social' or 'biological' domain that have not been extended to other contexts (e.g. Cheney & Seyfarth 1990). It is also possible that monkeys are more sensitive to causal relations among auditory stimuli than among visual ones. Visual cues of predators, such as their tracks in the sand, are often not temporally or spatially associated with the predator that produced them, while auditory cues typically are. The high contingency in the auditory domain may make it easier for monkeys to recognize the association between different calls and specific individuals and species. Third, there

might be an important difference between perception and performance. Investigations of nonhuman primates' understanding of causal relations in the physical domain have typically asked subjects to make active and operational use of causal relations (e.g. Visalberghi & Limongelli 1994). Perhaps, nonhuman primates would perform better in this domain if only their perception were tested.

Although these experiments provide evidence for causal knowledge in Diana monkeys, they were not designed to investigate the cognitive mechanism that has led to this knowledge in some individuals but not others. Nevertheless, some discussion is possible. First, it seems important that the monkeys' chances of witnessing an encounter between chimpanzees and a leopard are very low. Boesch (1991) reported an annual rate of about six daytime interactions between chimpanzees and leopards in a study area of ca. 30 km². The true encounter rate was likely to be higher because chimpanzees were not followed every day, the presence of human observers deters leopards from approaching the study group, encounters at night remained unreported and attacks on solitary chimpanzees were underrepresented. Nevertheless, for the 30 or more Diana monkey groups living in the home range of the chimpanzee group, encounters between chimpanzees and a leopard remain rare events. This makes it unlikely that the monkeys' response to chimpanzee alarm calls were the result of weak causal knowledge (sensu Kummer 1995), because typically numerous exposures are necessary before a causal relation can be consolidated into memory. Strong causal knowledge, either the result of causal reasoning or a specialized learning programme (e.g. taste aversion learning), provides the alternative.

According to Visalberghi & Tomasello (1998), causal reasoning goes beyond causal knowledge acquired by associative learning or a specialized learning programme in two important ways. First, causal reasoning entails an explanatory attitude of the individual: a kind of hypothesis testing when challenged with a causal problem. This would be the case, for example, if Diana monkeys were considering a number of explanations for the occurrence of chimpanzees' alarm calls (for instance, the presence of a leopard as opposed to a snake or a crowned eagle) before choosing the best one among them. However, results are also consistent with the idea that individuals have learned a connection between chimpanzees' leopard alarm calls and the presence of a leopard. Second, causal reasoning involves recognition of the mediating process that connects antecedent cause and consequent effect. Again, the results are consistent with the more parsimonious explanation, mainly that individuals simply know that the stimulus 'leopard' causes chimpanzees to give 'alarm calls' but not how or why this is the case. Direct encounters with a leopard are rare and seemingly highly arousing events for Diana monkeys. When detecting a leopard the entire group approaches and follows the predator in the lower canopy while alarm calling at high rates until the leopard moves on and leaves the group (Zuberbühler et al. 1999b). Under such circumstances, perhaps, Diana monkeys are especially attentive to

contingent signals, such as alarm calls of nearby chimpanzees. Perhaps, a single experience is then sufficient for acquiring knowledge about the causal link between the presence of a leopard and chimpanzees' alarm calls. Hence, although the data are consistent with the causal reasoning hypothesis, monkeys could also have solved the problem with the help of a highly effective learning programme that becomes activated during predation contexts where adaptive behaviour is essential for each individual's survival.

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