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Diana monkeys, *Cercopithecus diana*, adjust their anti-predator response behaviour to human hunting strategies

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Abstract In Ta National Park, Ivory Coast, humans with guns hunt monkeys for their meat. The poachers imitate animal calls to feign the presence of eagles or leopards, two predators to which monkeys react with high calling rates and approach. In the presence of humans, monkeys become silent and move off. A small area of the park is now avoided by poachers, due to the establishment of a field project on chimpanzees in 1979. This offered the opportunity to investigate whether sudden changes in predation pressure lead to a rapid alteration in prey behaviour. Playback experiments, using groups of Diana monkeys, *Cercopithecus diana*, as subjects, revealed that the poachers' strategy works well in the home range of the habituated chimpanzee group. However, monkeys which are frequently exposed to poachers are rarely fooled by the imitations. Adaptive discrimination abilities can thus be acquired or lost within the lifespan of individual monkeys.

Keywords Diana monkey · Poaching · Predation · Learning · Arms race

Introduction

For arms races between predator and prey to be stable, adaptations to changes in strategies of one side have to be countered rapidly by counteradaptations of the other side. However, few empirical studies have addressed this issue under natural conditions. Reznick et al. (1990) provided the first experimental field evidence that guppies (*Poecilia reticulata*) alter important life history traits in response to translocation, which altered predation pressure on different age classes. Adaptations were linked to anatomy and physiology and were achieved within 30–60 generations.

Boesch (1994) and Bshary and Noë (1997), using red colobus, *Procolobus badius*, as prey and chimpanzees, *Pan troglodytes*, as predators, provide an example that both predator and prey can use behavioural strategies which are adapted to those of their opponent. Behavioural traits can be changed much more rapidly than can anatomy in response to changes in an opponent's strategies, but how fast adaptations at the behavioural level might take place remains unresolved.

In this study, I tested for short-term alterations in the behaviour of Diana monkeys, *Cercopithecus diana*, in response to recent changes in human predation pressure in Ta National Park, Ivory Coast. Monkeys are killed by local people for their meat. While searching for monkeys, poachers stop about every 200 m and either imitate the territorial call of a crowned hawk eagle, *Stephanoaetus coronatus*, or the distress call of a duiker, *Cephalophus* sp., which is given when the duiker is caught by a leopard, *Panthera pardus* (personal communication with local villagers). Both eagles and leopards prey on monkeys (Hoppe-Dominik 1984; Skorupa 1989). The monkeys react to their presence with high vocalisation rates and approach (Zuberbühler et al. 1997), probably to mob or to deter pursuit (Caro 1995) to these typical 'ambush' predators whose hunting success is thought to be low if they are detected before the final strike (Hoppe-Dominik 1984; Klump and Shalter 1984; Zuberbühler et al. 1999). Zuberbühler et al. (1999) demonstrated that a radio-tracked leopard left monkey groups in response to the monkeys' behaviour, allowing the monkeys to continue with their normal daily activities. In contrast, poachers in Ta are pursuit predators: they hunt the monkeys with guns and look for individuals close enough to shoot, and mobbing or perception advertisement would therefore have negative fitness consequences. Instead, monkeys become silent and retreat from approaching humans

(Zuberbühler et al. 1997). Thus poachers, by successfully imitating the presence of either an eagle or a leopard, may increase the probability of detecting monkey groups, inducing the monkeys to come closer, and consequently improving their hunting success.

Poaching is ubiquitous in the National Park, the few exceptions being mainly research areas, because poachers avoid contact with researchers and local field assistants. In 1979, a chimpanzee field project was established (Boesch 1994) and has since provided monkey groups within the home range of the chimpanzee group (27 km^2) protection against poaching, while monkey groups adjacent to the chimpanzee home range are still hunted by poachers.

I addressed two points: (1) I estimated the impact of human predation on the Ta monkey population, and (2) I tested which strategies (if any) monkeys use to avoid being mislead by the human imitations. The monkeys could either remain silent while they only receive acoustic but not visual cues for an eagle or a leopard, or they may discriminate between original calls and human imitations.

I chose Diana monkeys as subjects to answer these questions because their behavioural and vocal reactions to humans, eagles and leopards are well documented (Zuberbühler et al. 1997). Both males and females react to playbacks of eagle and leopard calls with predator-specific alarms and become silent in response to playbacks of a human voice (Zuberbühler et al. 1997). I tested the reaction of monkey groups to playbacks of original calls and human imitations in both the poaching and non-poaching areas. The two areas are separated by one small road which leads to the scientific station inside the Park. Monkeys can easily cross the road (personal observation). Despite the differences between the two areas in levels of protection against poaching, all monkey groups which see or hear humans talking react with typical escape behaviour, i.e. they move away and hide, both in the protected and the unprotected areas (see Zuberbühler et al. 1997).

Methods

Study site and species

Data were collected between July and September 1996 in Ta National Park, Ivory Coast (for more detailed information, see Noë and Bshary 1997). Diana monkeys are medium sized (ca 5 kg) arboreal monkeys which live in harem groups of about 25 individuals, including 10–12 philopatric adult females.

Estimation of the human impact on the monkey population

The following information was obtained from local villagers who are closest to the study areas, at the western border of the Park, all members of the Oubi tribe: (1) the number of poachers in each village; (2) the number and duration of poaching trips per month; (3) the number of animals killed per trip; (4) the percentage of monkeys among the animals killed. The information was gathered by a project assistant who is a member of the Oubi tribe and a former poacher himself. I had no influence on how he approached the people in the village. He probably knew most poachers personally, as poachers often meet by chance in the forest at sites suitable for camping (personal communication). I hoped that the village people would be much more confident that the identities of the poachers would be kept secret if a member of the tribe rather than a foreigner asked the questions. This should have had a positive influence on the accuracy of their answers. The Oubi villages only form a fraction of all the villages around the National Park. To calculate the number of monkeys killed by humans per year per square kilometre, I therefore had to attribute an area of the park to these villages. I calculated this area by assuming that poachers from each village go no further than to the centre of the park and not further north or south than half of the distance to neighbouring (Oubi and non-Oubi) villages. Density estimates of the monkey population stem partly from published data (Holenweg et al. 1996; Höner et al. 1997) and partly from unpublished data of the Ta Monkey Project.

Study groups

In both the poaching and the non-poaching area, I used three different transects, which varied in length between 3,000 and 6,000 m. The transects were far enough apart from each other (at least 1,000 m) to ensure that the same Diana monkey group could not be encountered on more than one transect (home ranges of the Diana monkey study groups are about 800 m in diameter; Höner et al. 1997). The transects followed researchers' trails in the non-poaching area and poachers' trails in the poaching area. I monitored one transect per day, and each transect was monitored on three different occasions, with a minimum time interval of 1week between visits. As the home ranges of Diana monkey groups along the transects were not known, I avoided testing the same group with the same stimulus more than once by using a different stimulus on each visit to the same transect.

Playback experiment

I used three different recordings of the territorial call of an eagle, three recordings of the human eagle imitation and three recordings of the human imitation of a duiker distress call. I could not acquire a recording of an original duiker distress call. The recordings of the eagle calls were provided by Klaus Zuberbühler and by the National Sound Archive, London. I recorded imitations from three Africans working for the scientific station (Institut d'Ecologie Tropicale) or the Ta Monkey Project. All three had poached monkeys using imitation calls before they started to work in the park.

Following the recommendations of the NATO ARW Thornbridge Hall Consensus (McGregor 1992), the following methodological features were applied. Recordings of human imitations were tape-recorded with a Sony Professional Walkman WMD6C and Sennheiser 70-mm microphone (K3U+ME88). The playbacks were broadcast with a Sony Professional Walkman WMD6C connected to an NAGRA DSM speaker amplifier. The source level, measured with a Radio Shack Sound Level Meter 33-2050, C-weighting at 1 m distance from the speaker, ranged from 96 to 104 dB in eagle call playbacks, from 99 to 107 dB in eagle imitation call playbacks and from 100 to 105 dB in duiker imitation call playbacks. When I encountered a group, I stayed out of sight, at a distance of about 50 m to the nearest individual of that group, for 30 min, during the last 5 min of which, I recorded the total number of vocalisations per minute. Then came the playback. The speaker was placed on a fallen tree trunk, at a distance of approximately 50 m to the nearest individual. I recorded the vocalisation rates until 5 min after the playback as well as the movement of the estimated group centres (the area with the highest activity, monitored through branch movements and vocalisations) relative to the speaker. Movements of the adult male were monitored separately as he is the group member most likely to approach an eagle or leopard (Zuberbühler et al. 1997). I distinguished whether the group or the male increased or decreased the distance to the speaker. Playbacks did not take place during rain. No natural encounter with predators was observed during the 30-min observations prior to the playbacks.

Statistics

Fisher's test, Spearman rank correlation and the Mann-Whitney *U*-test were calculated according to Siegel and Castellan (1988). The Bonferroni technique (Rice 1989) was used to adjust the α-level ($\alpha'=\alpha/c$, where c is the number of tests) if several calculations were made on the basis of one data set. Each monkey group-recording pair is treated as independent from other monkey group-recording pairs and used as the unit of analysis.

Results

Predation pressure by humans

Poachers in the six villages from Gouleako to Sacre acknowledged killing 910–1,270 animals per month (Table 1). Monkeys form 50–70% of the prey items captured by poachers. This implies that 455–869 monkeys are killed per month by poachers of these villages, yielding 5,460–10,428 monkeys killed per year. The area attributed to the six villages is 477 km^2. Poachers are thus estimated to kill 11.2–21.9 monkeys/km^2 per year, or 3.7–7.3% of the monkey population (estimated 300 monkeys/km^2) per year (Table 1). All monkey species are shot, red colobus most often, followed by Diana monkeys and black-and-white colobus, an order which corresponds to the densities of the different monkey species populations. Poachers are unselective in that they shoot any monkey that is close enough. Each monkey is sold at the same price, irrespective of its size. The success rate of each shot is about 70%. Multiple kills during one hunt are frequent: up to four monkeys might be killed during one hunt, although one or two is the norm.

Playback experiment

Calling frequencies of females in groups in the unpoached area were generally high after playbacks of all three stimuli, while females in groups in the poaching area called after playbacks of eagle calls but usually fell silent after imitation playbacks (Fig. 1). All groups gave more calls during the 5 min following the playback of eagle calls than during the 5 min prior to the playback (Table 2). Females of unpoached groups were significantly more likely to increase calling frequency after playbacks of eagle imitation calls compared to females in poached groups [8/8 against 4/10, Fisher test, $P=0.023$ ($\alpha'=0.025$); Table 2]. In response to duiker imitation playbacks also, unpoached groups were more likely than poached groups to increase calling frequency [8/8 against 1/8, Fisher-Test, $P=0.0014$ ($\alpha'=0.025$); Table 2]. The few calls in poached groups elicited in response to imitation playbacks usually occurred during the first minutes. In eight of ten groups, not a single call was elicited during the fourth and fifth minutes following the eagle imitation playbacks, and a similar result was obtained for five of the eight poached groups tested with duiker imitation calls. No unpoached group was completely silent during any of the 5 min following the playbacks.

A typical group reaction to a predator is determined not only by the number of calls given by the females but also by group movements and the behaviour of the males (Table 3). It is therefore meaningful to analyse not only quantitative differences in single components of the monkeys' reaction, but whether a group responded qualitatively to a playback as if in the presence of an eagle,

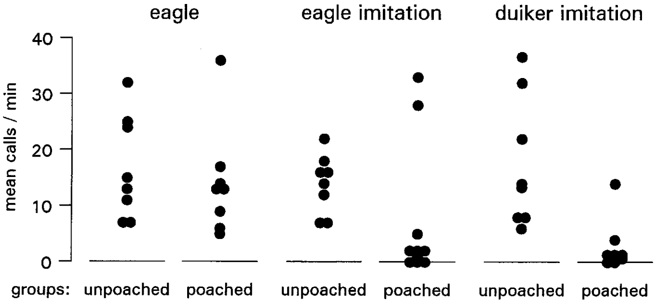

Fig. 1 Calls per minute of unpoached and poached groups in response to playbacks of eagle calls, eagle imitation calls and duiker imitation calls. Each point represents the mean call rate of one group during the first 5 min following the playback

Table 1 Quantification of illegal hunting performed in the Ta Park by people belonging to six Oubi villages. Calculations for monkey kills per month: lower value=the lower value for animals killed per trip×number of trips×0.5 (assuming that monkeys form 50% of the prey items); higher value=the higher value for animals killed per trip×number of trips×0.7 (assuming that monkeys form 70% of the prey items)

Village	Number of poacher groups	Trips per group per month	Duration of trips (days)	Animals killed per trip	Monkey kills per month
Gouleako	1	2	5–7	60–70	60–88
Poule Oula	3	2	6–7	60–75	180–305
Djara Oula	2	2	5–7	50–70	100–196
Port Gentil	1	1	6–7	50–70	25–49
Tioule Oula	2	3	1–2	10–15	30–63
Sacre	4	3	1–3	10–20	60–168
Total					455–869

Table 2 Total number of calls given by unpoached and poached groups during the 5 min before the playback of either eagle calls, eagle imitation calls or duiker imitation calls, and during the 5 min following the playback. The signs (+ or –) in *parentheses* indicate how the data point was scored for the Fisher tests

Eagle calls		Eagle imitation		Duiker imitation	
Unpoached Before/after	Poached Before/after	Unpoached Before/after	Poached Before/after	Unpoached Before/after	Poached Before/after
39/127 (+)	10/69 (+)	8/81 (+)	13/10 (–)	33/62 (+)	4/1 (–)
6/65 (+)	0/43 (+)	16/79 (+)	9/7 (–)	25/44 (+)	96/5 (–)
25/34 (+)	32/64 (+)	29/38 (+)	25/165 (+)	132/240 (+)	18/1 (–)
88/158 (+)	36/182 (+)	8/71 (+)	11/10 (–)	8/103 (+)	21/8 (–)
49/121 (+)	26/31 (+)	45/91 (+)	16/0 (–)	22/99 (+)	99/103 (+)
15/57 (+)	15/26 (+)	12/60 (+)	20/24 (+)	33/166 (+)	81/11 (–)
21/75 (+)	20/64 (+)	7/37 (+)	6/139 (+)	73/274 (+)	126/8 (–)
3/35 (+)	16/87 (+)	50/109 (+)	3/10 (+)	21/62 (+)	39/28 (–)
			9/2 (–)		
			17/0 (–)		

Table 3 Qualitative parameters for responses of unpoached and poached groups to various playback stimuli. *Typical alarm* and *Typical LC* are predator species-specific alarm calls of females and male loud calls, respectively. The numbers given represent the number of groups in which the typical alarm, flight, male LC and male approach were (*Yes*) or were not (*No*) observed

Stimulus	Group	Typical alarm		Flight		Typical LC		Male approach	
		Yes	No	Yes	No	Yes	No	Yes	No
Eagle	Unpoached	8	0	0	8	7	1	5	3
	Poached	8	0	0	8	7	1	4	4
Eagle imitation	Unpoached	8	0	0	8	8	0	4	4
	Poached	2	8	5	5	2	8	1	9
Duiker imitation	Unpoached	8	0	0	8	8	0	2	6
	Poached	1	7	6	2	2	6	0	8

leopard or a human. This distinction is important, as some groups rested prior to the playback, reducing the likelihood that vocalisation rates could be lower after the playback than before. I scored a 'natural predator reaction' if at least three of the following five criteria were fulfilled: calling rates higher after than before the playback; typical eagle or leopard alarm calls of females; typical eagle or leopard loud calls of males (see sonograms in Zuberbuehler et al. 1997); group does not move off, and male approach. A group was scored as having shown a 'human predator reaction' if the typical calls for eagles or leopards were lacking, in combination with the calling rates being lower after the playback than before or if the groups were completely silent during the last 2 min of the observation. All groups tested could be classified according to these two definitions.

Combining all the information (Fig. 1, Tables 2, Table 3), all groups (n=16) reacted to playbacks of eagle calls with the typical response to eagles. The variation in calling frequencies (Fig. 1) can be partly explained by variation in monkey activity prior to the playbacks. High calling rates prior to the playback were correlated with high calling rates after the playback (Spearman rank correlation, r_s=0.55, n=16, P=0.03; see also Zuberbühler et al. 1997).

Most groups in the poaching area showed a typical response to humans in reaction to playbacks of human imitations (eagle imitation: 8/10; duiker imitation: 7/8) while not a single unpoached group behaved cryptically in response to these stimuli (both eagle and duiker imitation: 0/8). The reaction of poached groups to eagle imitation and duiker imitations differed significantly from their reaction to eagle calls [Fisher tests: eagle imitation-eagle calls, n=18, P=0.002 (α'=0.0071); duiker imitation-eagle calls: n=16, P=0.0002 (α'=0.0071)] and from the reactions of unpoached groups [Fisher tests: eagle imitation: n=18, P=0.002 (α'=0.0071); duiker imitation: n=16, P=0.0002 (α'=0.0071)]. No significant difference could be found between the reactions of unpoached groups to eagle calls, eagle imitation and duiker imitation. The α-level was adjusted to α'=0.0071 because seven tests were calculated with the same data set.

Discussion

The investigation in the villages suggests that humans are important predators of monkeys in the Park. For a comparison, the estimated annual offtake of monkeys by poachers (4–7%) is higher than the estimated impact of chimpanzees on the red colobus population (2.8%; Noë and Bshary 1997), though chimpanzees specialise on this monkey species (Boesch and Boesch 1989). A critical assumption in the calculation was that each village hunts in proportion to the Park area attributed to it. However, the large villages and small cities at the eastern border of the Park are likely to hunt much more than people from the Oubi tribe. Therefore, the values calculated here are probably an underestimate of the human impact on the monkey population in the entire Park. The percentage of monkeys as prey items is high compared to other areas (Colell et al. 1994). However, the poachers appear to have supplied good estimates in the questionnaire, as long-term data (1975–1983) on game found with poachers caught in the Park reveal similar percentages (58%; *n*=1,988; Hoppe-Dominik 1995). The calculations presented assume that poachers hunt all groups with equal probabilities, irrespective of the distance of the groups to the villages. This assumption is unlikely to be fulfilled, as poachers likely reduce their effort by hunting close to the villages (Hofer et al. 1996). Thus the monkey groups close to villages tested in the playback experiments probably suffered from higher than average human predation pressure (but see below). The conclusion may be drawn that there is a very high selection pressure on monkeys in poaching areas to avoid being misled and detected by human imitations.

The results from the playback experiment show that Diana monkeys in the poaching area discriminated adaptively between eagle calls and imitations: they showed mobbing or pursuit deterrence behaviour in response to playbacks of eagle calls and silently moved away from the imitations. Diana monkeys in the non-poaching area on the other hand did not discriminate between stimuli and reacted to all playbacks with mobbing or pursuit deterrence. The results demonstrate that adaptations might be achieved or lost within less than two decades – about four generations or the lifespan of an individual monkey. While humans might be regarded as atypical predators, data from Noë and Bshary (1997) and Bshary and Noë (1997) suggest that other features of the anti-predation behaviour of Ta monkeys, like the formation of mixed-species associations, are also quite flexible. Groups of Diana monkeys and red colobus adjusted association rates to perceived fluctuations in the level of predation risk. Such flexibility in anti-predator responses is being increasingly found in a variety of systems (see Lima 1998 for a review).

As yet, poachers have not adapted to the discriminatory abilities of the monkeys by changing their hunting strategies, and they continue to imitate calls (personal communication). However, most poachers have given up searching for monkeys close to the villages and instead go on longer trips (see Table 1), further into the centre of the Park. There they still find naive groups which are misled by the imitations (personal communication).

Though these data cannot identify the mechanisms by which discrimination abilities were acquired, a discussion of the potential mechanism(s) seems to be justified because it has important implications for future research questions. An extreme scenario would be that poachers selected for genetic differences in discrimination abilities by shooting those individual monkeys that were fooled by the imitations and that this process was completed in the poaching area or completely reversed in the non-poaching area within 16 years. However, it is more likely that learning was involved as well. Poached and unpoached groups belong to the same continuous Diana monkey population, with some unpoached groups separated from poached groups by one intermediate group with a home range on both sides of the road to the scientific station. This road does not function as a barrier, as different groups have been seen crossing the canopy over the road. Moreover, imitation calls were successfully used to detect unhabituated groups for playbacks on the following morning (Noë and Bshary 1997) within the study area of the Ta Monkey Project (which is adjacent to the home range of the main chimpanzee study group) as early as 1993, while scientific research started in 1990 and poachers were still encountered at the beginning (K. Zuberbühler, personal communication). One group, however, was still exposed to poaching as gun shots were regularly heard from their home range which was next to the scientific station. This group was not fooled by the imitation, while two neighbouring groups were. This indicates that discrimination abilities were acquired or lost within 4 years, or one monkey generation.

The data of the present study and those from Noë and Bshary (1997) and Zuberbühler (1999) suggest that learning might be at least partly involved in the anti-predator behaviour of Ta monkeys. While previous studies have shown that learning is involved in predator recognition (Curio et al. 1978; Seyfarth and Cheney 1986; review by Curio 1993) and estimation of predation risk in a variety of taxa (Chivers et al. 1995; Noë and Bshary 1997; Wisendon et al. 1997; for models see Bouskila and Blumstein 1992; Abrams 1994), the present data indicate that prey can even learn about predators’ strategies and consequently alter their escape behaviour. In the sense that variation in predator activity period pattern is part of a predator’s hunting strategy, Fenn and Macdonald (1995) found a similar effect in rats. The rats shifted from nocturnal to diurnal feeding in response to variation in predator activity patterns. Learning might work faster and remains more flexible than genetic adaptations, and is thus more likely to lead to real ‘arms races’ (adaptations and counteradaptations; Dawkins and Krebs 1979) between specific predator and prey species compared to changes in morphological traits, which are thought to be relatively unspecific (Abrams 1986; Futuyma 1986; Vermeij 1987; Endler 1991). Group-living animals are promising subjects for further research on this topic as they are more often attacked than solitary individuals (Turner and Pitcher 1986; Inman and Krebs 1987), and they can gather information about predator behaviour through improved early detection and even if a hunt was successful, due to the ‘dilution effect’ (Williams 1966). In addition, as predatory events are relatively rare but extremely important for individual fitness, learning by prey during predatory events might be an interesting field for research on long-term memory, which until now has focused mainly on spatial memory in food-caching birds (Balda and Kamil 1989; Krebs et al. 1990; Clayton 1995).

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