Leopard predation and primate evolution

Klaus Zuberbühler
School of Psychology,
University of St Andrews,
Scotland and Centre Suisse de
Recherches Scientifiques,
Abidjan, Côte d'Ivoire.
E-mail: kz3@st-and.ac.uk

David Jenny
Zoologisches Institut,
Universität Bern, Switzerland
and Centre Suisse de
Recherches Scientifiques,
Abidjan, Côte d'Ivoire.
E-mail: jenny.d@compunet.ch

Received 21 February 2002
Revision received
30 May 2002
and accepted 10 September
2002

Keywords: alarm call, cognitive evolution, sociality, population dynamics, body size, group size, primate male, vigilance, prey.

Although predation is an important driving force of natural selection its effects on primate evolution are still not well understood, mainly because little is known about the hunting behaviour of the primates' various predators. Here, we present data on the hunting behaviour of the leopard (*Panthera pardus*), a major primate predator in the Taï forest of Ivory Coast and elsewhere. Radio-tracking data showed that forest leopards primarily hunt for monkeys on the ground during the day. Faecal analyses confirmed that primates accounted for a large proportion of the leopards' diet and revealed in detail the predation pressure exerted on the eight different monkey and one chimpanzee species. We related the species-specific predation rates to various morphological, behavioural and demographic traits that are usually considered adaptations to predation (body size, group size, group composition, reproductive behaviour, and use of forest strata). Leopard predation was most reliably associated with density, suggesting that leopards hunt primates according to abundance. Contrary to predictions, leopard predation rates were not negatively, but positively, related to body size, group size and the number of males per group, suggesting that predation by leopards did not drive the evolution of these traits in the predicted way. We discuss these findings in light of some recent experimental data and suggest that the principal effect of leopard predation has been on primates' cognitive evolution.

Journal of Human Evolution (2002) **43,** 873–886
doi:10.1006/jhev.2002.0605
Available online at http://www.idealibrary.com on IDEAL®

Introduction

Predation is frequently mentioned as a factor in evolution although its actual selective impact is often not well understood. In primates, predation is thought to have affected body size, group size and composition, vigilance and ecological niche, as well as vocal and reproductive behaviour (van Schaik, 1983; Cheney & Wrangham, 1987; Cords, 1990; Hill & Dunbar, 1998; Stanford, 1998; Uster & Zuberbühler, 2001). Despite their theoretical appeal, there are several reasons to remain sceptical about the generality of these relationships. First, much of the available empirical evidence is indirect, for example, because predation rates have been assessed through unexplained disappearances of study animals. Second, predation is often treated as a homogeneous evolutionary force, even though predators differ considerably in their hunting behaviour and the consequential selective pressures they impose on a primate community. Finally, even within a particular predator class there can be significant differences among individuals' prey preference and hunting behaviour (Jenny & Zuberbühler submitted).

In the Taï forest of Ivory Coast, chimpanzees (*Pan troglodytes*) are hunted by leopards (Boesch, 1991), while the eight monkey species are hunted by chimpanzees, crowned-hawk eagles (*Stephanoaetus coronatus*), and leopards. Human poachers also exert a strong hunting pressure, though this factor may have been too recent to be evolutionarily relevant. Each of these

0047–2484/02/120873+14 $35.00/0

predators employs highly specific hunting techniques, requiring elaborate defence behaviours to avoid predation. Predatory chimpanzees, for instance, locate monkey groups by acoustic cues and hunt for individuals in the high canopy (Boesch & Boesch-Achermann, 2000). Crowned-hawk eagles, in contrast, hunt by sweeping through the canopy to surprise their prey (Gautier-Hion & Tutin, 1988; Shultz, 2001). Not surprisingly, the presence of chimpanzees reliably elicits cryptic behaviour in all monkey species studied whereas the presence of crowned-hawk eagles elicits loud and conspicuous alarm calling and even mobbing behaviour by some monkeys (Zuberbühler *et al.*, 1997, 1999*a*).

In this paper, we focus on the hunting behaviour of the African leopard, a key predator of primates in the tropical rainforest habitat and therefore a probable important selective factor in the evolutionary history of primates. To investigate the potential impact of leopard predation on primate evolution we first describe in some detail the hunting behaviour of Taï leopards. We present radio-tracking data of two wild leopards as well as analyses of faeces to assess the hunting pressure exerted by this predator on the different primate species. We relate these data to behavioural, demographic, physiological and morphological traits that are commonly viewed as anti-predation adaptations in primates: body size, group size, group composition, female reproductive rate, and use of forest strata. We used the faecal data to assess the predation rate exerted on the nine simian primates living in Taï forest: the red colobus, *Colobus badius*, the black-and-white colobus, *C. polykomos*, the olive colobus, *Procolobus verus*, the Diana monkey, *Cercopithecus diana*, the Campbell's monkey, *C. campbelli*, the lesser spot-nosed monkey, *C. petaurista*, the putty-nosed monkey, *C. nictitans*, the sooty mangabey, *Cercocebus torquatus*, and the chimpanzees (Table 1).

The general prediction was that if a trait had evolved as an adaptation to leopard predation, there would be a negative relationship between the expression of the trait and an individual's vulnerability to leopard predation. For instance, it has been suggested that large body size is an adaptation to predation (e.g., Isbell, 1994). If this were the case, then the larger Taï primates should be underrepresented in the leopards' prey spectrum. Similarly, it has been suggested that individuals living in a large group are less susceptible to predation than individuals living in a small group (e.g., van Schaik, 1983). This is because individuals may benefit from the presence of conspecific group members, due to safety-in-number effects or improved predator detection. Thus, Taï primates that live in larger groups should be less susceptible to predation and therefore under-represented in the leopard's prey spectrum. It has also been argued that the formation of groups containing several adult males is an adaptation to predation pressure, specifically in species where males engage in cooperative defence against predators (Stanford, 1998). Although no systematic studies have been conducted in the Taï primates, cooperative defence behaviour has been observed in red colobus and olive colobus males in the presence of crowned-hawk eagles (Korstjens, 2001; Beerlage unpublished data). According to this hypothesis, Taï primates living in multi-male groups should be better protected against predation and therefore under-represented in the leopard's prey spectrum relative to single-male groups. Another hypothesis states that natural selection can lead females to accept higher levels of predation, if their potential reproductive rate is high enough to compensate for the losses incurred from predation (Hill & Dunbar, 1998). In that case, rather than evolving predator-specific defence mechanisms, natural selection favours females, who shorten their interbirth intervals to increase

Table 1 Data on population density, group size, body weight, strata use, number of males per group, birth rate, and usage of the lower forest strata for the Taï primates

Species	Density	Body size	Group size	*n* Males	Reproduction	Habitat
Cercopithecus diana	48·2	3·9	20·2	1·0	0·62	6·1
C. campbelli	24·4	2·7	10·8	1·0	0·63	36·8
C. petaurista	29·3	2·9	17·5	1·0	0·52	9·9
C. nictitans	2·1	4·2	10·5	1·0	0·50	0·7
Colobus badius	123·8	8·2	52·9	10·1	0·42	0·4
Colobus polykomos	35·5	8·3	15·4	1·4	0·59	1·3
Procolobus verus	17·3	4·2	6·7	1·4	0·61	13·2
Cercocebus torquatus	11·9	6·2	69·7	9·0	0·40	88·9
Pan troglodytes	2·6	47·5	61·1	6·7	0·23	85·0

Density: Estimated number of individuals per square kilometre; *Body size*: adult female body weight in kg (from Oates *et al.*, 1990); *Group size*: average number of individuals per group; *n males*: average number of adult males per group; *Reproductive rate*: average number of infants per adult female per year; *Habitat*: percent time observed in lower forest strata (data from McGraw, 1998, 2000; Eckardt 2001). *C. diana*: *Density*: Holenweg *et al.* (1996): 3·5 groups/km^2=68·3; Höner *et al.* (1997): 2·1 groups/km^2=52·5; Galat & Galat-Luong (1985)=17·5; Korstjens (2001: 120): 39–70=54·5; ESTIMATE: 48·2. *Group size*: Uster (2001): 29; Höner *et al.* (1997): 25; Galat & Galat-Luong (1985): 11, 17; Korstjens (2001: 120): 14–25=19·5; ESTIMATE: 20·2. *Males*: Galat & Galat-Luong (1985): 1, 1; Uster (2001): 1; Höner *et al.* (1997): 1; ESTIMATE: 1·0. *Reproduction*: Uster (2001): 0·40; Galat & Galat-Luong (1985): 0·66; 0·8; ESTIMATE: 0·62. *C. campbelli*: *Density*: Galat & Galat-Luong (1985): 15·0; Wolters (2001) 33·8; ESTIMATE: 24·4. *Group size*: Wolters (2001): 13·5; Galat & Galat-Luong (1985): 9, 7; ESTIMATE: 10·8. *Males*: Galat & Galat-Luong (1985): 1, 1; Wolters (2001): 1; ESTIMATE: 1·0. *Reproduction*: Wolters (unpublished data): 0·40; Galat & Galat-Luong (1985): 0·5, 1·0; ESTIMATE: 0·63. *C. petaurista*: *Density*: Galat & Galat-Luong (1985): 29·3; ESTIMATE: 29·3. *Group size*: Galat & Galat-Luong (1985): 24, 11; ESTIMATE: 17·5. *Males*: Galat & Galat-Luong (1985): 1, 1; ESTIMATE: 1·0. *Reproduction*: Galat & Galat-Luong (1985): 0·71; 0·33; ESTIMATE: 0·52. *C. nictitans*: *Density*: Eckardt & Zuberbühler (in prep.): 8 groups/40 km^2=2·1; ESTIMATE: 2·1. *Group size*: Eckardt (2001): 14; 7; ESTIMATE: 10·5. *Males*: Eckardt (2001): 1·0; ESTIMATE: 1·0. *Reproduction*: Eckardt (2001): 0·5; 0·5; ESTIMATE: 0·50. *Colobus badius*: *Density*: Holenweg *et al.* (1996): 2·4 groups/km^2=174; Höner *et al.* (1997): 2·0 groups/km^2=145; Galat & Galat-Luong (1985): 66; Korstjens (2001: 88): 110; ESTIMATE: 123·8. *Group size*: Höner *et al.* (1997): 72·5. Galat & Galat-Luong (1985): 32, 37; Korstjens (2001: 127): 41; 64; 60; 44; ESTIMATE: 52·9. *Males*: Höner *et al.* (1997): 17; Galat & Galat-Luong (1985): 3; 9; Korstjens (2001: 127): 6; 15; 12; 9; ESTIMATE: 10·1. *Reproduction*: Galat & Galat-Luong (1985): 0·23; 0·3; Korstjens (2001: 127): 0·57; 0·57; 0·36; 0·47; ESTIMATE: 0·42. *Colobus polykomos*: *Density*: Galat & Galat-Luong (1985): 23·5; Korstjens (2001: 120): 47; ESTIMATE: 35·5. *Group size*: Galat & Galat-Luong (1985): 12; 11; Korstjens (2001: 88): 16; 15; 16; 17; 15; 19; 18; 16; 15; 17; 14; ESTIMATE: 15·4. *Males*: Galat & Galat-Luong (1985): 2; 3; Korstjens (2001: 127): 1; 1; 1; 1; 2; 1; 2; 1; 1; 1; ESTIMATE: 1·42. *Reproduction*: Galat & Galat-Luong (1985): 1·0; 0·0; Korstjens (2001: 127): 0·6; 0·25; 0·67; 0·6; 0·8; 0·8; 0·25; 1·0; 0·6; 0·5; ESTIMATE: 0·59. *Colobus verus*: *Density*: Galat & Galat-Luong (1985): 21·0; Korstjens (2001: 88): 13·6; ESTIMATE: 17·3. *Group size*: Galat & Galat-Luong (1985): 6; 7; Korstjens (2001: 127): 6; 4; 4; 8; 12; ESTIMATE: 6·7. *Males*: Galat & Galat-Luong (1985): 1; 1; Korstjens (2001: 127): 1; 1; 2; 2; 2; ESTIMATE: 1·43. *Reproduction*: Galat & Galat-Luong (1985): 0·5; 0·5; Korstjens (2001: 127): 0·67; 1·0; 1·0; 0·33; 0·33; ESTIMATE: 0·61. *Cercocebus torquatus*: *Density*: Galat & Galat-Loung (1985): 10·0; Bergmüller (1998): 13·7; ESTIMATE: 11·9; *Group size*: Range (1998: 25): 96; Bergmüller (1998: 68): 69; Galat & Galat-Loung (1985): 45; ESTIMATE: 69·7. *Males*: Range (1998: 53): 10; Bergmüller (1998: 68): 11; Galat & Galat-Loung (1985): 6; ESTIMATE: 9·0. *Reproduction*: Range (1998: 25): 0·85; Range (unpublished data): 0·29; 0·82; Bergmüller (1998: 68): 0·32; Galat & Galat-Loung (1985): 0·14; ESTIMATE: 0·40. *Pan troglodytes*: *Body weight*: 32–37 kg (Goodall 1986); ESTIMATE: 34·5; *Density*: 61·1 ind./per group; 23·7 km^2 territory size (Boesch & Achermann-Boesch 2000: 107); ESTIMATE: 2·6; *Group size*: 61·1 (Boesch & Boesch-Achermann 2000: 21) *Adult Males*: 6·7 (Boesch & Boesch-Achermann 2000: 21). *Reproduction*: 75 births in 15 years; average number adult females=21·5; ESTIMATE: 0·23; *Habitat*: ESTIMATE: 85%.

their lifetime reproductive success. Species with short interbirth intervals, thus, should be over-represented in the leopard's prey spectrum. Finally, Taï primates show species-specific preferences for particular forest strata (McGraw, 1998, 2000), presumably as a result of interspecies competition. A tacit assumption here is that species living in the lower forest strata are more exposed to ground predators (Dunbar, 1988; Plavcan & van Schaik, 1992) and therefore should be over-represented in the leopard's prey spectrum. In addition to these specific variables it needs to be pointed out that the different primate species in the Taï forest vary drastically in their population density. Some species, such as the red colobus and the Diana monkeys, occur at extremely high rates of 1–2 groups per square kilometre while others, such as the putty-nosed monkeys are exceedingly rare (Eckardt & Zuberbühler, submitted). Previous work has shown that leopards may prey on a large array of different species, suggesting that population density may be an important variable in explaining variation in leopard hunting success.

Methods

Study site

Data collection on leopard behaviour was conducted by DJ between June 1992 and August 1994 in the Taï National Park, Ivory Coast, in a study area of about 100 km^2 in the western part of the park, about 25 km east of the Liberian border (5°50′N, 7°20′W). The Taï Forest is classified as a tropical moist forest, with a protected area of roughly 4000 km^2 of largely undisturbed forest, the largest remaining block of primary forest in West Africa (Martin, 1991).

Focal animal sampling

Leopards are found in a wide variety of habitats, ranging from open savannah to dense rainforests (Kitchener, 1991). To date, most information on leopard ecology and behaviour comes from the East and South African savannah (e.g., Bailey, 1993) and very little is known about forest leopards. Nevertheless, as the largest forest predator, leopards are a key component in this ecosystem and it is likely that they play an important role in the evolution of primates and other groups of animals. Since direct focal sampling of leopards is not possible in the forest, four study animals, two adult males ("Cosmos" and "Arthur") and two adult females ("Adele" and "Cora") were equipped with radio transmitters. The methodology is discussed elsewhere in detail (Dind, 1995; Jenny, 1996). Repeated localizations of these animals revealed that home ranges of individuals of the same sex did overlap very little while the overlap between one adult male and one adult female was almost complete (Dind *et al.* 1996), suggesting that leopards defend their home ranges against members of the same sex.

In this paper, we report on the hunting behaviour of two individuals, the adult male "Cosmos" and the adult female "Adele", because these two were followed on a regular basis. Ranging data were collected in two ways. First, simultaneous monitoring by two observers from platforms installed in the high canopy allowed locating the focal animal by triangulation (accuracy ± 0·01 km^2). Distance was determined by the strength of the signal using a reference table. Once a leopard was located, one observer rushed to the presumed area and then followed the animal at a close distance ranging from 30 to 150 metres. The two focal individuals were radio-tracked between February 1993 and August 1994 (15 and 11 months, respectively). Second, platform monitoring was used to determine the activity patterns of the individuals as a function of daytime, month, and amount of rain. Readings were taken every 15 minutes during both the day and the night.

Faecal analysis

Between June 1992 and June 1994, a total of 200 faecal scat samples were collected systematically along trails and throughout the 100 km^2 study area. At least four resident leopards occupied home ranges in this area (Dind *et al.*, 1996), but the setting of an infrared triggered photo-trap revealed that at least seven different individuals contributed to the total sample (Jenny, 1996). A day's search rarely led to the recovery of more than one faecal sample, indicating that faecal samples were the results of independent predation events. Samples were collected regularly throughout the study period. All samples were inspected for the presence of hairs, bones, teeth, nails, and other remains. Hairs were identified using a reference collection compiled by Hoppe-Dominik (1984) and reference photographs made by Bodendorfer (1994).

Primate evolution

To assess how the various primate traits affected leopard hunting success, we compiled a data set for the Taï primate species, using several sources of information from studies conducted in the study area (Table 1). These data were natural log transformed [$y = \text{LN}\ (x+1)$] to ensure normality before performing linear regression analyses, analogous to Hill & Dunbar (1998).

Results

Activity patterns of Taï leopards

Platform monitoring revealed that both radio-tracked individuals were more active during the day than during the night. The male was monitored for a total of 54 hours, the female for a total of 223 hours. We calculated the relative activity rate every 15 minutes, yielding a total of 96 intervals per 24 hours for each animal. The relative activity was significantly higher during daytime intervals (06:00–19:00 GMT) than during nighttime intervals (19:15–05:45 GMT) for both individuals (Adele: $\text{mean}_{\text{day}} = 46{\cdot}9\%$, $n = 53$, $\text{mean}_{\text{night}} = 26{\cdot}3\%$, $n = 43$, $z = 6{\cdot}34$, $P < 0{\cdot}001$; Cosmos: $\text{mean}_{\text{day}} = 49{\cdot}3\%$; $n = 53$, $\text{mean}_{\text{night}} = 30{\cdot}3\%$, $n = 43$, $z = 4{\cdot}384$, $P < 0{\cdot}001$, Mann–Whitney U-tests, two-tailed).

Prey spectrum of Taï leopards

Table 2 illustrates the wide variety of prey species found in leopard faeces, most of them (79·0%) stemming from mammals weighing less than 10 kg. The large proportions of monkeys and duikers were particularly remarkable. Remains of chimpanzees were found only once. Adele was followed most extensively, allowing us to assess her hunting behaviour qualitatively. During her daily trips, she often hid in dense thickets or in dense undergrowth, particularly when close to a monkey group. In one of 91 observed hidings Adele successfully attacked and killed a *C. torquatus*. At the same time, she avoided nearby chimpanzee parties. In 40·0% of cases ($n = 15$) when chimpanzees were drumming or screaming in the vicinity she began moving away, or changed her travelling direction to distance herself from the chimpanzee group, and she never approached a chimpanzee party.

Leopard predation and natural selection

Univariate analyses of the six different variables using data of the eight monkey species showed that predation rate was significantly related to population density ($r^2 = 0{\cdot}583$, $F_{1,6} = 8{\cdot}383$; $P = 0{\cdot}028$) and body size ($r^2 = 0{\cdot}572$, $F_{1,6} = 8{\cdot}011$, $P = 0{\cdot}030$) (Figure 1). Contrary to predictions, however, body size and predation rates were positively related, because the larger monkey species were preyed upon more often than smaller ones. The relationships between predation rate and group size and the number of adult males per group were also positive (group size: $r^2 = 0{\cdot}390$, $F_{1,6} = 3{\cdot}836$, $P = 0{\cdot}098$; number of males: $r^2 = 0{\cdot}353$, $F_{1,6} = 3{\cdot}277$, $P = 0{\cdot}120$), although they did not reach statistical significance. Predation rates were unrelated to the reproductive rate of adult females ($r^2 = 0{\cdot}054$, $F_{1,6} = 0{\cdot}340$, $P = 0{\cdot}581$) and to a species' use of the lower forest strata ($r^2 = 0{\cdot}030$, $F_{1,6} = 0{\cdot}188$, $P = 0{\cdot}680$). A stepwise multiple regression analysis using

Table 2 Prey spectrum of Taï leopards

Prey species Scientific name	Common name	*n* predation events This study (n=200 faeces)	 Hoppe-Domínik, 1984 (n=215 faeces)
Ungulates			
Cephalophus maxwelli	Maxwell's duiker	47	31
Cephalophus ogilby/dorsalis	Bay/Ogilby's duiker	16	10
Cephalophus jentinki	Jentink's duiker	1	0
Cephalophus niger	Black duiker	1	28
Cephalophus (undet.)	Unknown duikers	17	13
Total		82	82
Primates			
Colobus badius	Red colobus	21	8
Colobus polykomos	Black-white colobus	16	5
Procolobus verus	Olive colobus	1	0
Cercopithecus diana	Diana monkey	5	17
Cercopithecus petaurista	White-nosed monkey	1	5
Cercopithecus campbelli	Campbell's monkey	3	4
Cercopithecus nictitans	Putty-nosed monkey	0	0
Cercocebus torquatus	Sooty Mangabey	6	9
Cercopithecidae	Unknown monkeys	10	3
Pan troglodytes	Chimpanzee	1	0
Perodicticus potto	Potto	0	1
Total		64	61
Other mammals			
Manis tetradactyla/triscuspis	Pangolin	43	10
Atherurus africanus	Brush-tailed porcupine	10	15
Panthera pardus	Leopard	6*	6
Epixerus ebii	Giant squirrel	1	2
Sciuridae (undet.)	Unknown squirrels	7	7
Potamocherus porcus	Bush pig	2	2
Genetta pardina	Genet	2	1
Viverridae (undet.)	Unknown mongooses	1	4
Nandinia binotata	Palm civet	1	0
Tryonomis swinderianus	Cane rat	2	0
Other mammals	Other mammals	0	40
Mammalia (undet.)	Unknown mammals	6	26
Total		81	113
Aves (undet.)		2	2

*66·7% hair of unknown origin.

all six variables indicated that population density and body size combined accounted for a significant proportion of the overall variance of the leopard predation rate ($F_{2,5}$=18·347; P=0·006).

Adding chimpanzees to the dataset did not affect the overall pattern, except for the variable body size (density: r^2=0·588, $F_{1,7}$=9·988, P=0·016; body size: r^2=0·012, $F_{1,7}$=0·087, P=0·777; group size: r^2=0·163, $F_{1,7}$=1·366, P=0·281; number of males: r^2=0·176, $F_{1,7}$=1·497, P=0·261; female reproduction: r^2=0·007, $F_{1,7}$=0·048, P=0·832; use of lower forest strata: r^2=0·078, $F_{1,7}$=0·595, P=0·466). A stepwise multiple regression analysis using all six variables indicated that density and body size continued to account for a significant proportion of the overall variance ($F_{2,6}$=8·783; P=0·017).

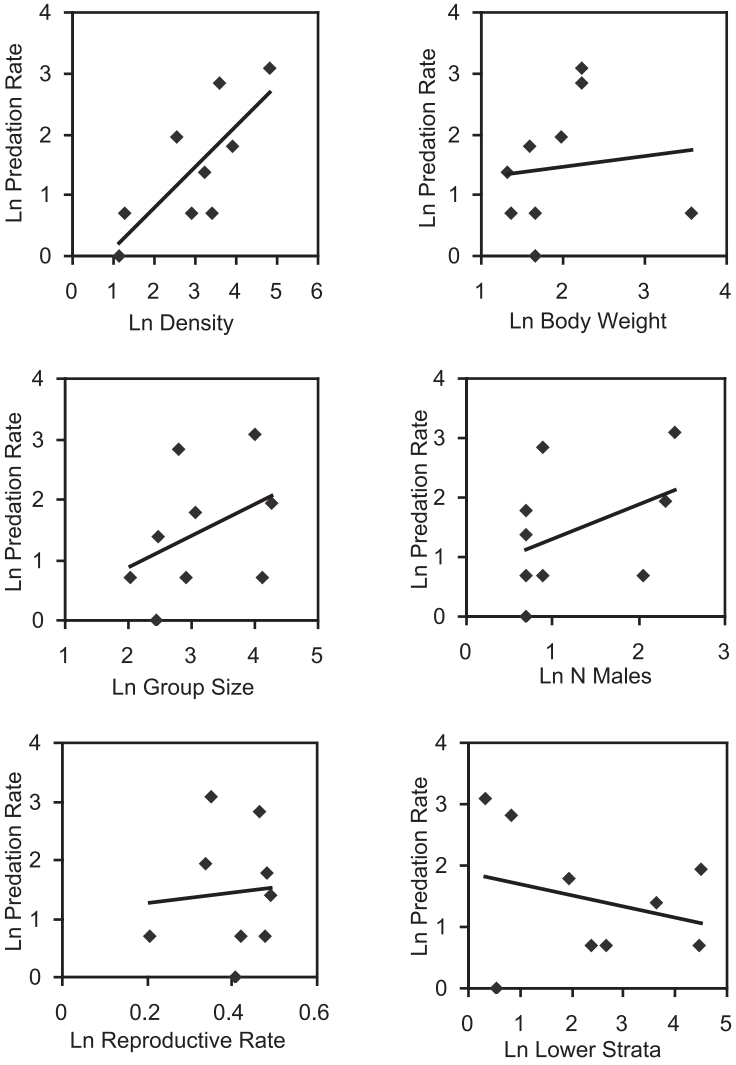

Figure 1. The relationship between the predation rate by leopards, population density and five variables commonly considered as antipredator adaptations in primates. Predation rate has been estimated by using the natural logarithm of the number of faeces that contained remains of a particular species in a sample of 200 leopard faeces collected over a period of two years from a 100 km^2 study area (Table 1).

In light of the robust effects of density and body size in both datasets we investigated whether the remaining variables explained any variation once the effects of these two variables had been controlled for. Thus, in the following analysis we used a relative estimate of predation rates (i.e., the absolute predation rate divided by density and body size). Using the monkey dataset, none of the variables explained a significant amount of variation (group size: $r^2=0{\cdot}275$, $F_{1,6}=2{\cdot}271$, $P=0{\cdot}182$; number of male; $r^2=0{\cdot}192$, $F_{1,6}=1{\cdot}422$, $P=0{\cdot}278$; female reproduction: $r^2=0{\cdot}038$, $F_{1,6}=0{\cdot}239$, $P=0{\cdot}642$; use of lower forest strata: $r^2=0{\cdot}346$, $F_{1,6}=3{\cdot}171$, $P=0{\cdot}125$). A stepwise multiple

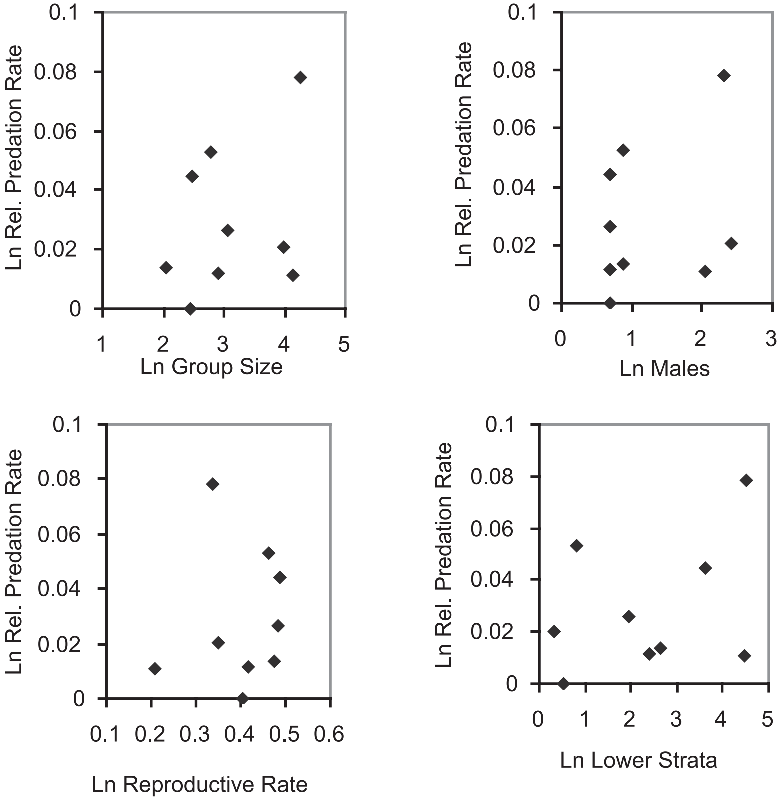

Figure 2. Relationship between relative predation rate leopards and four different variables commonly considered antipredator adaptations in primates. The relative predation rate has been estimated by using the natural logarithm of the number of faeces that contained remains of a particular species divided by its density and body size (Tables 1 and 2).

regression analysis using all four variables as well as their first interaction terms indicated that the interaction between a species' use of the lower strata and the number of males per group accounted for a significant proportion of the overall variance (r^2=0·561, $F_{1,6}$=7·671, P=0·032).

Using the dataset including the chimpanzees, none of the variables explained a significant amount of variation (Figure 2; group size: r^2=0·105, $F_{1,7}$=0·820, P=0·395; number of male; r^2=0·081, $F_{1,7}$=0·621, P=0·457; female reproduction: r^2=0·009, $F_{1,7}$=0·065, P=0·806; use of lower forest strata: r^2=0·134, $F_{1,7}$=1·080, P=0·333). A stepwise multiple regression analysis using all four variables plus their first interaction terms indicated that none of these variables or any of the first order interaction terms accounted for a significant proportion of the overall variance.

Closer inspection of Figure 2 revealed that red colobus monkeys and chimpanzees provided something of an exception to the overall pattern. Both species suffered from less predation pressure than expected, based on their group size and on the number of males per group, suggesting that forming large multi-male groups is beneficial given the species' population densities and body sizes. If the data were reanalysed without these two species, then the relationship between the two variables and relative predation rate became much stronger and reached statistical significance (group size: $r^2=0{\cdot}525$; $F_{1,5}=5{\cdot}533$; $P=0{\cdot}065$; number of males: $r^2=0{\cdot}574$; $F_{1,5}=6{\cdot}738$; $P=0{\cdot}048$), yet again in the wrong direction.

Discussion

Leopard hunting behaviour

The leopards in Taï forest showed a predominant diurnal activity pattern. Both radio-tracked individuals were significantly more active during the day than at night with relative peaks at dawn and dusk (see Jenny & Zuberbühler, submitted). Individual follows further suggested that hunting leopards selectively searched for monkey groups and hid in their vicinity, which sometimes led to a successful attack (Zuberbühler *et al.*, 1999*a*). It is unlikely that this is due to a sampling bias since the large proportion of primates found in leopard faeces in this and the previous study (Hoppe-Dominik, 1984) suggested that diurnal hunting for primates was common. Comparable observations have also been made in Asian forest leopards (Karanth & Sunquist, 1995, 2000), suggesting that diurnal hunting is widespread in forest leopards. This finding contrasts with reports from the savannah, where leopards hunt and travel predominantly at night (e.g., Bailey, 1993). A number of factors could be responsible for the differences in activity patterns between the two habitat types. For example, diurnal hunting in rainforest leopards could be a consequence of forest preys' decreased detection abilities; the absence of competing diurnal predators such as the lion (*P. leo*), or it could be an adjustment to diurnal activity of the main prey, duikers and monkeys.

The 200 faeces analysed contained remains of at least 23 different prey species. This relatively large range reflected the high species diversity of the rainforest habitat and was comparable with a previous study, which included a large number of samples from the eastern side of the park, where disturbed secondary forest prevails and poaching pressure is much more intense (Hoppe-Dominik, 1984: Table 1). The most frequent prey species in both studies were duikers and monkeys. However, the two studies also differed in some interesting ways. In particular, *C. polykomos* and *C. badius* individuals were under-represented in the 1985 study. This was probably the result of lower population densities of these two species in the east side of the park. Colobus monkeys are particularly vulnerable to poaching, as recently documented by the extinction of a red colobus subspecies (Oates *et al.*, 2000). Unsurprisingly, recent surveys were unable to locate any red colobus or black-and-white colobus groups in the eastern side of the park (J. Refisch, personal communication), suggesting that the two primate species have become extinct locally. The different guenon species and particularly the Diana monkeys, however, are over-represented in the 1985 data, possibly due to habitat differences. The prevailing dense secondary forest on the east side of the park might have increased the leopards' hunting success by providing better hiding opportunities to stalk these more agile species. In sum, the fact that both studies found very similar results and that the main differences can be explained with density differences suggested that our assessment of the leopards' prey spectrum was reliable.

Leopard predation and primate evolution

When we related the impact of the leopards' predation pressure to various traits commonly thought to be antipredator adaptations, none was related to leopard predation in a predicted way. Instead, we found that the combination of population density and body weight was the best predictor of leopard hunting success, although in the wrong direction: the larger and more abundant species were preyed more often than the smaller and rarer species, suggesting that, if anything, leopard predation selected against large body size. Also contrary to predictions, both group size and the number of adult males per group were positively related with leopard hunting success, suggesting that these traits were also ineffective in deflecting leopard predation. These results are counterintuitive and require further explanation. Smaller primates could have a selective advantage over larger ones if they are more agile in the forest canopy and more difficult to capture. Nevertheless, large body size could still be an effective measure against other predators, notably the crowned-hawk eagle. For example, adult male guenons, which are larger than other group members, routinely attack crowned-hawk eagles (Gautier-Hion & Tutin, 1988:259; Zuberbühler *et al.*, 1997), suggesting that large body size provides reasonable protection against this predator. Second, the predation rate of individuals living in larger groups was higher than for those living in smaller groups, perhaps because larger groups were easier for the leopards to locate, thereby outweighing the benefits of increased vigilance and dilution. Alternatively, it might be that leopards preferred preying on large groups because there is a greater possibility of monkeys being on the ground. The sooty mangabeys provide an interesting example. This terrestrial species forms very large groups of up to 100 individuals but suffers substantially from leopard predation, even when controlled for the effects of their low population density and large body size. Third, the multi-male group hypothesis did not predict leopard predation either. The hypothesis states that multi-male groups have evolved because this enables males to engage in cooperative defence behaviour. Although male cooperation against predators has been observed against eagles (Korstjens, 2001) and chimpanzees (Beerlage, unpublished data), it is unlikely to be effective against leopards. Finally, in our dataset the preferred forest strata and interbirth intervals of the various species were unrelated to the predation pressure exerted by leopards. In sum, our data suggest that leopard predation was unlikely to be the cause of a variety of traits commonly thought to be adaptations to predation.

Are chimpanzees special?

Statistical analyses revealed that a number of effects became significant after the chimpanzees were removed from the dataset. Relative to their body size, chimpanzees suffered from low predation pressure; in fact, only one out of 200 faeces contained chimpanzee remains (Table 1). With their large body size, chimpanzees might have reached a critical threshold level and grown out of the main prey range of leopards, perhaps as the result of a predator–prey arms race. Studies using mitochondrial DNA sequence data indicate that modern chimpanzees emerged at least 2 m.y.a. (Adachi & Hasegawa, 1995; Horai *et al.*, 1995), while modern leopards did not emerge until about 800,000 years ago (Uphyrkina *et al.*, 2001). The fossil record suggests that the primitive condition in fossil cats was a light body structure adapted for arboreal life, similar to the living genets or palm civets (Turner & Anton, 1997:106). According to this scenario, therefore, chimpanzees have successfully avoided felid predation from early on because they entered the evolutionary arms race with a relatively large body size. Chimpanzees are much less affected by leopard predation than expected based on their group size, even if the effects of density and body size are controlled for. Forest leopards have been shown to develop prey preferences (Jenny & Zuberbühler, submitted) and the focal follows of the adult female Adele showed that forest leopards might also learn to avoid chimpanzee groups, a behaviour that differs considerably from that towards monkey groups.

Some interpretative complexities

Although our data did not support a number of popular hypotheses regarding the evolution of primate antipredator traits, the interpretation of these findings is complicated in a number of ways. Most importantly, it is difficult to infer past evolutionary processes on the basis of current patterns because the relationship between past selection pressure and extant traits are often complicated and difficult to disentangle. Second, the patterns found in this study are based on interspecies comparisons, which make evolutionary statements difficult because it is impossible to control for all the confounding variables. Natural selection acts on individuals, not on species, and so it would be more fruitful to test our hypotheses for each species separately. A proper way of dealing with this problem would be to study changes in the predation rate as a function of a purported adaptation in each species. For example, everything else being equal, how do the predation rates compare in single and multi-male groups of the same species? Third, because leopards develop prey preferences, individuals of one species are likely to compete with members of other species to avoid preference formation by leopards. For instance, although increasing group size might be an adaptive response (due to dilution effect and increased vigilance), members of large-grouped species might soon suffer higher predation rates if leopards preferably search out larger groups. Other traits might be less affected by the trade-off between intraspecies adaptation and interspecies competition. The prey spectrum in Table 1 shows that leopards are able to kill prey animals that are much heavier than they are themselves, suggesting that increasing body size alone will not be an effective anti-predation response.

Leopard predation and cognitive evolution

Our results show that leopard predation did not have the expected effects on a number of morphological traits commonly thought to be antipredator adaptations. Hence, can predation by leopards be dismissed as a selection factor in the evolution of forest primates in general? It is a widespread tacit assumption that predation is a restrictive and simplifying force of natural selection. However, some studies have convincingly shown that the opposite can be the case. For example, in electric fish (*Gymnotiformes*) predation has selected for greater signal complexity (Stoddard, 1999). We suggest that leopard predation has increased the behavioural flexibility of primates. In particular, several guenon species have evolved acoustically distinct alarm calls to warn each other about the presence of specific predators, including leopards (Seyfarth *et al.*, 1980; Zuberbühler *et al.*, 1997; Zuberbühler, 2000*a*, 2001). It is likely that similar findings will emerge from other species, including the Colobines. Second, the suspected presence of a leopard appears to trigger complex cognitive processes (Zuberbühler *et al.*, 1999*b*; Zuberbühler, 2000*b*, 2001). For example, Diana monkeys distinguish between chimpanzee screams given in a social setting from chimpanzee screams given to a leopard (Zuberbühler, 2000*d*), suggesting that these calls are meaningful and inform the monkeys about the presence of a leopard. Diana monkey groups living in the periphery of a chimpanzee territory are less likely to understand variations in chimpanzee screams than groups living in the core area of a chimpanzee group, suggesting that monkeys need to learn the meaning of these calls. Third, call meaning is not always rigidly attached to specific acoustic structures, but it can be generated from pragmatic information (Zuberbühler, 2000*c*). This is exemplified by the Diana monkeys' response to the alarm calls of crested Guinea fowls (*Guttera* *pulcheri*). Guinea fowls forage in large groups and when chased, produce conspicuously loud alarm calls that can be heard over long distances. Guinea fowls are not hunted by chimpanzees but may be taken by leopards and human poachers. Diana monkeys respond to recordings of Guinea fowl alarm calls as if a leopard were present. Playback experiments have shown that Diana monkeys are able to take into account that Guinea fowl alarm calls can be caused by both leopards and humans, and can also determine the most likely cause of the birds' alarm calls (Zuberbühler, 2000*c*). Finally, some recent research suggested that simple syntactic elements in their vocal repertoire of some monkey species could affect the way monkeys interpret the meaning of alarm calls (Zuberbühler, 2002). In sum, it is clear that the hypothesis that leopard predation has favoured the cognitive evolution of primates will require more rigorous testing, using various empirical approaches. Nevertheless, we believe that predation has been largely underestimated as a factor in primate cognitive evolution (Grimes, 2002).

Summary

Predation has been mentioned a major driving force in the evolution of primate behaviour and morphology, but the actual effects are still not well understood. Here, we present data on the hunting behaviour of the leopard, a major primate predator in many parts of the world. Radio-tracking data showed that forest leopards primarily hunt for monkeys on the ground and during the day. Scat analyses confirmed that primates accounted for a large proportion of the leopards' diet, providing detailed information on the predation pressure exerted on the different species. Contrary to current theory, we did not find negative relationships between predation rate by forest leopards and the various traits commonly believed to be adaptations to predation, such as body size, group size or number of males per group. Instead, these relationships were all positive, which makes it difficult to maintain that these traits evolved in response to predation by leopards. Instead, we suggest that leopards have increased the cognitive flexibility in primates, as evidenced by the sophisticated ways monkeys deal with predator information.

Acknowledgements

Fieldwork in Ivory Coast was funded by the Swiss National Science Foundation, the Freiwillige Akademische Gesellschaft, the Roche Research Foundation, the Haller-Fonds, the Emilia Guggenheim-Schnurr Foundation, the Karl Mayer Foundation, and the Max-Planck-Institute for Behavioural Physiology. In Ivory Coast we thank the ministries of research and higher education, the Centre Suisse de Recherches Scientifiques, Gerard Gah, Christophe Boesch, and Ronald Noë for permission to work and support in the field Ch. Bürki who ran the study for months and F. Dind who provided additional data after August 1994. B. Hoppe-Dominik provided a detailed reference atlas of mammal hairs and T. Bodendorfer helped to analyse leopard faeces. K. Wagener provided us with the radio-tracking material and constructed the photo-trap. M. Oetliker built the cable snares. We are thankful to Dick Byrne and Jenny McClung for their comments on the manuscript.

References

Adachi, J. & Hasegawa, M. (1995). Improving dating of the human/chimpanzee separation in the mitochondrial DNA tree: heterogeneity among amino acid sites. *J. Molecular Evol.* **40,** 622–628.

Bailey, T. N. (1993). *The African Leopard.* New York: Columbia University Press.

Bergmüller, R. (1998). Feeding ecology of the sooty mangabey. Friedrich-Alexander-Universität Erlangen M.Sc. Thesis.

Bodendorfer, T. (1994). Zur Ernährungsbiologie des Leoparden *Panthera pardus*. Vienna, University of Vienna M.Sc. Thesis.

Boesch, C. (1991). The effects of leopard predation on grouping patterns inf forest chimpanzees. *Behaviour,* **117**(3–4), 220–242.

Boesch, C. & Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest. Behavioural Ecology and Evolution*. Oxford: Oxford University Press.

Cheney, D. L. & Wrangham, R. W. (1987). Predation. In (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. M. Wrangham, T. T. Struhsakes, Eds) *Primate Societies*, pp. 227–239. Chicago: University of Chicago Press.

Cords, M. (1990). Vigilance and mixed-species association of some East African forest monkeys. *Behav. Ecol. Sociobiol.* **26,** 297–300.

Dind, F. (1995). Etude d'une population cible de léopards dans le Parc National de Taï, University of Lausanne.

Dind, F., Jenny, D. & Boesch, C. (1996). Ecologie et prédation du léopard en foret de Taï (Côte d'Ivoire). In J. F. Graf, M. Zinsstag & J. Zinsstag (Eds.), *Centre Suisse de Recherches Scientifiques en Côte d'Ivoire (CSRS). Rapport d'acitivité 1992–1994* (pp. 22–26). Abidjan: Centre Suisse de Recherches Scientifiques en Cote d'Ivoire.

Dunbar, R. I. M. (1988). *Primate Social Systems*. New York: Comstock Publishing Associates.

Eckardt, W. & Zuberbühler, K. (submitted). Cooperation and competition in two forest monkeys.

Eckardt, W. (2002). *Nischenvergleich der Grossen Weissnasenmeerkatze (Cercopithecus nictitans) und der Dianameerkatze (Cercopithecus diana) im Taï Natioinalpark (Elfenbeinküste) under besonderer Berücksichtigung interspezifischer Konkurrenz. Leipzig, Leipzig.*

Galat, G. & Galat-Luong, A. (1985). La communauté de primates diurnes de la fôret de Taï, Côte d'Ivoire. *Rev. Ecol. (Terre Vie)* **40,** 3–32.

Gautier-Hion, A. & Tutin, C. E. G. (1988). Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia primatol.* **51,** 149–151.

Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior.* Cambridge: Harvard University Press.

Grimes, K. (2002). Hunted. *Sci. Am.* **2338,** 34–37.

Hill, R. A. & Dunbar, R. I. M. (1998). An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping patterns. *Behaviour* **135,** 411–430.

Holenweg, A. K. Noë, R. & Sohnbel, M. (1996). Waser's gas model applied to associations between red colobus and diana monkeys in the Taï National Park, Ivory Coast. *Folia primatol.* **67,** 125–136.

Höner, O. P., Leumann, L. & Noë, R. (1997). Dyadic associations of red colobus and diana monkey groups in the Taï National Park, Ivory Coast. *Primates* **38,** 281–291.

Hoppe-Dominik, B. (1984). Etude du spectre des proies de la panthere, *Panthera pardus*, dans le Parc National de Taï en Côte d'Ivoire. *Mammalia* **48,** 477–487.

Horai, S., Hayasaka, K., Kando, R., Tsugane, K. & Takahata, N. (1995). Recent African origin of modern humans revealed by complete sequences of hominoid mitochondrial DNAs. *PNAS* **92,** 532–536.

Isbell, L. (1994). Predation on primates: ecological patterns and evolutionary consequences. *Evol. Anthrop.* **3,** 61–71.

Jenny, D. (1996). Spatial organization of leopards (Panthera pardus) in Taï National Park, Ivory Coast: Is rain forest habitat a tropical haven? *J. Zool.* **240,** 427–440.

Jenny, D. & Zuberbühler, K. (submitted). Selective hunting in forest leopards.

Janson, C. H. (1998). Testing the predation hypothesis for vertebrate sociality: Prospects and pitfalls. *Behaviour* **135**(4), 389–410.

Karanth, K. U. & Sunquist, M. E. (1995). Prey selection by tiger, leopard, and dhole in tropical forests. *J. Anim. Ecol.* **64,** 439–450.

Karanth, K. U. & Sunquist, M. E. (2000). Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. *J. Zool.* **250,** 255–265.

Kitchener, A. (1991). *The Natural History of the World's Cats*. Ithaca: Cornell University Press.

Korstjens, A. H. (2001). The mob, the secret sorority, and the phantoms. Utrecht University, Utrecht Phd Thesis.

Martin, C. (1991). *The rainforests of West Africa: ecology, threats, conservation.* Basel: Birkhäuser.

McGraw, W. S. (1998). Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *Am. J. phys. Anthrop.* **105,** 493–510.

McGraw, W. S. (2000). Positional Behavior of Cercopithecus petaurista. *Int. J. Primatol.* **21**(1), 157–182.

Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P. G., Green, S. M., Dasilva, G. L. & Mole, S. (1990). Determinants of variation in tropical forest primate biomass–new evidence from West Africa. *Ecology* **71**(1), 328–343.

Oates, J. F. & Abedi-Lartey, M., McGraw, W. S., Struhsakes, T. T. & Whitesides, G. H. (2000). Extinction of a West African red colobus monkey. *Conservation Biol.* **14**(5), 1526–1532.

Plavcan, J. M. & van Schaik, C. P. (1992). Intrasexual competition and canine dimorphism in anthropoid primates. *Am. J. Phys. Anthrop.,* **87**(4), 461–477.

Range, F. (1998). Sozialsystem und Konkurrenztyp weiblicher Rauchgrauer Mangabe, University of Bayreuth.

Seyfarth, R. M. & Cheney, D. L. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Anim. Behav.* **28**(4), 1070–1094.

Shultz, S. (2001). Notes on interactions between monkeys and African crowned eagles in Tai National Park, Ivory Coast. *Folia primatol.* **72**(4), 248–250.

Stanford, C. B. (1998). Predation and male bonds in primate societies. *Behaviour* **135,** 513–533.

Stoddard, P. K. (1999). Predation enhances complexity in the evolution of electric fish signals. *Nature* **400,** 254–256.

Turner, A. & Anton, M. (1997). *The Big Cats and their Fossil Relatives*. New York: Columbia University Press.

Uphyrkina, O., Johnson, W. E., Quigley, H., Miquelle, D., Marker, L., Bush, M. & O'Brien, S. J. (2001). Phylogenetics, genome diversity and origin of modern leopard, Panthera pardus. *Molecular Ecology* **10**(11), 2617–2633.

Uster, D. (2001). Die funktionelle Bedeutung von Kontaktlauten bei Dianameerkatzen. Zoologisches Institut. Braunschweig, TU Braunschweig. M.Sc. Thesis.

Uster, D. & Zuberbühler, K. (2001). The functional significance of Diana monkey 'clear' calls. *Behaviour* **138,** 741–756.

Van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour* **87,** 120–144.

Wolters, S. (2001). *Einfluß der Assoziation auf das Verhalten von Campbells (Cercopithecus campbelli) und Diana (Cercopithecus diana) Meerkatzen.* Unpublished M.Sc., Westfälische Wilhelms-Universität, Münster.

Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. (1999b). Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology* **113**(1), 33–42.

Zuberbühler, K., Jenny, D. & Bshary, R. (1999a). The predator deterrence function of primate alarm calls. *Ethology* **105**(6), 477–490.

Zuberbühler, K., Noë, R. & Seyfarth, R. M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behavior* **53**(1), 589–604.

Zuberbühler, K. (2000*a*). Referential labelling in Diana monkeys. *Anim. Behav.* **59,** 917–927.

Zuberbühler, K. (2000*b*). Interspecific semantic communication in two forest monkeys. *Proc. R. Soc. Lond. B* **267,** 713–718.

Zuberbühler, K. (2000*c*). Causal cognition in a nonhuman primate: field playback experiments with Diana monkeys. *Cognition* **76,** 195–207.

Zuberbühler, K. (2000*d*). Causal knowledge of predators' behaviour in wild Diana monkeys. *Anim. Behav.* **59,** 209–220.

Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's guenons. *Behav. Ecol. Sociobiol.* **50,** 414–422.

Zuberbühler, K. (2002). A syntactic rule in forest monkey communication. *Anim. Behav.* **63**(2), 293–299.

Zuberbühler, K., Noë, R. & Seyfarth R. M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Anim. Behav.* **53,** 589–604.

Zuberbühler, K., Jenny, D., & Buhovy, R. (1999*a*). The predator deterrence function of primate alarm calls. *Ethology* **105,** 477–490.

Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. (1999*b*). Conceptual semantics in a nonhuman primate. *J. Comp. Psychol.* **113,** 33–42.