1
Predation and Primate Cognitive Evolution

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Introduction

Predation is a major cause of mortality in non-human primates (Cheney et al., 2004), but its impact as a selective force on primate evolution is not well understood. Predation has long been thought to affect traits such as body size, group size, group composition, and ecological niche, as well as the traits of vigilance and vocal and reproductive behaviour (Anderson, 1986). The general assumption is that if a trait has evolved as an adaptation to predation, then there should be a negative relationship between the expression of the trait and the individual's vulnerability to predation. First, if large body size is an adaptation to predation (Isbell, 1994), then larger primates should be underrepresented in a predator's prey spectrum compared to smaller ones. Second, if individuals living in large groups are less susceptible to a certain kind of predation, leopard predation, for example, due to enhanced levels of predator vigilance, then individuals of larger groups should be underrepresented in the prey spectrum (van Schaik, 1983; Cords, 1990). Third, if multi-male groups are an adaptation to predation, for example due to the possibility of cooperative defence (Stanford, 1998), then species living in multi-male groups should be underrepresented in a predator's prey spectrum compared to single-male groups. Fourth, if females shorten their inter-birth intervals to increase their lifetime reproductive success to compensate for higher levels of predation (Hill & Dunbar, 1998), then individuals with short inter-birth intervals should be over-represented in the prey spectrum. Finally, if living in higher forest strata is an adaptive response to predation (Enstam & Isbell, 2004), then individuals that are generally more exposed to the ground should be over-represented in the prey spectrum of ground predators.

Although intuitively convincing, strong empirical data for these ideas are often lacking. Another problem is that in most primate habitats the predator fauna is severely understudied, often rendering statements about possible selective pressures a matter of speculation. Moreover, there are theoretical reasons to remain cautious about some of the proposed relationships. Predation is not a homogeneous evolutionary force, and predators differ considerably in their hunting behaviour and the selective pressure they exert on a primate population (Struhsaker, 1969; Treves, 1999). It is also the case that the current selection pressure exerted by a predator may not be representative for those of the evolutionary past. Finally, individual predators may be forced into particular ecological niches due to competition with other non-predatory species, and many of the traits mentioned above could be the direct product to these habitat-related factors.

The predator-prey system in the Taï Forest, Ivory Coast, is an ideal system for addressing some of these questions. A body of recent work conducted on the hunting behaviour of the four main predators on the Taï monkeys has enabled direct assessments of their impact as a force of natural selection. This chapter reviews some of the major findings, and it makes two basic claims. First, a number of behavioural and morphological traits that are classically interpreted as adaptations to predation fail to explain the differences in vulnerability in the Taï monkeys. At the same time, experimental studies have shown that the predation context reliably triggers sophisticated and flexible vocal behaviour in monkeys in a previously undescribed way. This has lead to the hypothesis that the main legacy of predation was not upon the morphology and social behaviour of these monkeys, but upon the evolution of communicative and cognitive abilities necessary to avoid predation. The most important impact of predation on primate evolution, therefore, may have been a cognitive one.

Methods

Habitat

The Taï forest is one of the largest blocks of intact tropical forest in West Africa, originally stretching from Ghana to Sierra Leone. The Taï National Park consists of a protected area of 330,000 ha covered with dense evergreen ombrophilous forest vegetation, habitat to 47 species of large mammals and a largely intact predator fauna. UNESCO declared the Taï Forest a World Heritage Site in 1982 (http://whc.unesco.org). The land is state property located in the southwest Ivory Coast between the Cavally and Sassandra rivers. Rainfall ranges from 1,700 mm to 2,200 mm, reaching peaks in June and September/October, which are followed by a marked dry season from December to February. Humidity is constantly 85% or higher, and temperatures range from 24 to 27°C.

The following eight monkey species can regularly be observed in the park: Diana monkeys (*Cercopithecus diana*), Campbell's monkeys (*C. campbelli*), lesser spot-nosed monkeys (*C. petaurista*), putty-nosed monkeys (*C. nictitans*, northern parts of the forest only), red colobus monkeys (*Procolobus badius*), black-and-white (or King) colobus monkeys (*Colobus polykomos*), olive colobus monkeys (*Procolobus verus*), and sooty mangabeys (*Cercocebus atys*). Table 1.1 provides an overview of some of the most important species differences.

TABLE 1.1. 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 (Data from Zuberbühler & Jenny, 2002).

Species	Density (ind/km^2)	Body Size (kg)	Group Size (ø N)	Males (ø N)	Annual Reproduction Rate	Habitat (% on ground)
Cercopithecus diana	48.2	3.9	20.2	1	0.62	6.1
C. campbelli	24.4	2.7	10.8	1	0.63	36.8
C. petaurista	29.3	2.9	17.5	1	0.52	9.9
C. nictitans	2.1	4.2	10.5	1	0.50	0.7
Procolobus badius	123.8	8.2	52.9	10.1	0.42	0.4
Colobus polykomos	35.5	8.3	15.4	1.42	0.59	1.3
Procolobus verus	17.3	4.2	6.7	1.43	0.61	13.2
Cercocebus atys	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

Polyspecific Associations

Primate mixed-species associations are common in forest habitats throughout Africa; only very few species, such as the DeBrazza monkeys (*C. neglectus*), avoid them (Gautier-Hion & Gautier, 1974; Waser, 1982). In the Taï forest, mixed-species associations tend to be individualized, that is, the same groups form these associations over many consecutive years, and groups often use similar home ranges. There is good evidence that mixed-species behaviour has evolved because of its merit as an anti-predator strategy (Wachter et al., 1997; Noë & Bshary, 1997). For example, in the presence of Diana monkeys, red colobus use lower strata more often, are less vigilant, and forage in canopy parts that are more exposed to the forest floor than when Diana monkeys are absent, suggesting that associations provide protection against ground predators (Bshary & Noë, 1997a, b). Mixed-species associations appear to be beneficial in the face of raptor predation as well. Red colobus and Diana monkeys are less vigilant and use exposed locations more often when in the presence of their partner species than when either are alone (Bshary & Noë, 1997a, b).

A number of anti-predation benefits from polyspecific associations are probably a direct consequence of the increased number of individuals, rather than of species complementing each other in their anti-predator skills. For example, individuals living in large groups run a smaller risk of being singled out by a predator than individuals living in small groups (Krebs & Davis, 1993). Moreover, it is likely that chances of detecting a stalking or approaching predator is a function of group size (Treves, 2000). Finally, the adult males of several monkey species have been observed to approach and attack eagles, suggesting that mixed-species groups consisting of various males may have a dissuasive effect on some predators (e.g., Eckardt and Zuberbühler, 2004).

Why do the different monkey species not simply increase their own conspecific group sizes? One likely explanation is that the relationship between feeding competition and group size is stronger in monospecific than in polyspecific groups. At the same time, the relationship between anti-predation benefits and group size appears to be similar in both cases. In the Taï forest, the different monkey species reveal unique food and habitat preferences, leading them to only exploit a subsegment of the available resources. Niche separation of this kind automatically decreases interspecies competition and appears to make coexistence of closely related species possible (Wachter et al., 1997; McGraw, 1998, 2000; Korstjens, 2001; Wolters & Zuberbühler, 2003). These observations may also explain the substantial primate biomass in the Taï forest, which can reach densities of more than two groups per square kilometre (Zuberbühler & Jenny, 2002).

There are some striking exceptions to this general pattern. For example, the Diana monkey–putty-nosed monkey association shows a remarkable overlap in food preferences and habitat use, yet the two species do not avoid each other but form associations throughout much of the year. However, during periods of food shortage Diana monkeys have been observed to become increasingly aggressive towards putty-nosed monkeys, and association rates consequently plummet to very low levels during these times (Eckardt and Zuberbühler, 2004). It appears that the mixed-species associations follow the logic of economy, determined by the balance of anti-predator benefits and costs of feeding competition.

Primate Predators

The Taï monkeys are hunted by chimpanzees (*Pan troglodytes*), crowned eagles (*Stephanoaetus coronatus*), leopards (*Panthera pardus*), and human poachers. Snakes and other reptiles are common throughout the forest but they seem to be irrelevant as monkey predators, except in areas along the few big forest rivers, where large pythons and crocodiles can be observed. The following section describes some key characteristics of the four main monkey predators: human poachers, chimpanzees, crown eagles, and leopards.

Human Poachers

Illegal hunting by humans is responsible for significant predation pressure on the primate population. Bush meat is widely consumed throughout West Africa; lax law enforcement and understaffing of forest police combine to make poaching a lucrative business (Martin, 1991). Poaching activity is continuous throughout the park both during day and at night. At night, animals are blinded with flashlights and subsequently killed with shotguns. Used batteries and shotgun shells litter the forest floor and poacher camps can be found regularly throughout the forest. Hunting with slings and snares is more common in the border zones of the park.

The impact of human poaching is tremendous. A recent study by Refisch & Kone (2005) estimated the annual mortality of monkeys due to human hunting in and around the Taï Forest to be at least 50,000 individuals, an estimated mass weight of 250,000 kg total. As a result primate densities in many peripheral areas of the park are already substantially reduced. Some species, such as red colobus monkeys, are already locally extinct, forcing poachers to enter the more central areas of the park. Professional hunters build and inhabit temporary camps in the park for several days and employ carriers to transport the carcasses out of the park borders to supply the various local restaurants and bush meat markets.

Archaeological evidence suggests that anthropogenic effects have been present in this area at least since the late Holocene (Mercader et al., 2003), suggesting that human predation has been present for considerable time. The human population density in the area of the Taï forest increased massively in the 20th century, suggesting that the immense hunting pressure currently exerted by humans is a recent phenomenon. Clearly, primates did not have the time to evolve efficient anti-predator behaviour to cope with this level of human predation, although research has shown that some species can employ general cognitive abilities to improve their protection from human predation and other sudden changes in the predator fauna (Bshary, 2001; Gil-da-Costa et al., 2003).

Chimpanzee Hunting

Taï chimpanzees use their home ranges in a clumped way, with small central core areas visited preferentially. There are no major shifts in home range use over consecutive months. Home range sizes of Taï chimpanzees tend to be larger than those of other African communities (Herbinger et al., 2001). Decreases in home range size is related to decreases in the number of males in the group, not overall group size or food availability (Lehmann & Boesch, 2003). The average density of the Taï chimpanzee population throughout the park was estimated at 1.84 individuals/km^2, suggesting a total population of 7,500 individuals for the Taï Forest (Marchesi et al., 1995; Herbinger et al., 2001).

Taï chimpanzees regularly hunt monkeys, which the chimpanzees probably locate by acoustic cues. They decide to hunt apparently in the absence of monkey groups, then they search for a suitable target group (Boesch & Boesch, 1989). Once a group is located, a small hunting party, usually consisting of adult males, climbs into the trees near the group to single out and capture an individual in the high canopy. In Taï, hunting is mainly focused on red or black-and-white colobus monkeys, while the other monkey species are rarely caught. However, due to the monkeys' tendency to associate in mixed-species associations all species are equally exposed to significant hunting pressure, and all take immediate evasive action in the presence of chimpanzees. There are seasonal variations in hunting activity (Boesch & Boesch, 1989). Hunts are particularly common from September through November, following a period of low food availability from June to August when chimpanzee groups are dispersed. Even though there are more than 50 different red colobus groups in an average chimpanzee home range, some monkey groups are likely to suffer attacks several times per year, especially those that live in the core area of a chimpanzee group. Thus, the hunting pressure exerted by this predator apparently varies both locally and seasonally.

In Taï, successful hunting depends on coordination with other hunters. If a hunt is successful, the meat is typically shared amongst the hunters and sometimes with other group members (Boesch, 2002). Males begin hunting at about age 10, and performance improves at a very slow rate, suggesting that hunting skills are not easily learned (Boesch, 2002). Wild chimpanzees have a life expectancy at birth of less than 15 years, which is considerably lower than that of modern human hunter-gatherers (Hill et al., 2001). It is also noteworthy that in other chimpanzee study sites across Africa, high rates of cooperative hunting for monkeys is not a particularly prominent feature (Uehara, 1997; Reynolds, 2005). It remains a distinct possibility, therefore, that the high predation pressure described for Taï is a transient cultural rather than a biological feature of chimpanzees. As with humans, it may thus be that the Taï monkeys did not have the time to evolve specialised anti-predator behaviour to cope with chimpanzee predation in an efficient way, but that they relied on their more general cognitive abilities to avoid predation. For example, the authors have never been able to identify an acoustically distinct alarm call for chimpanzees or humans in any monkey species, even though such calls exist for other predators such as leopards or crowned eagles (Zuberbühler et al., 1997).

Crowned Eagles

The African crowned eagle (*Stephanoaetus coronatus*) is the primary aerial predator for primates throughout sub-Saharan forests. Breeding pairs defend the areas surrounding their nests, which they build in high emergent trees with open flight paths to facilitate transport of prey (Malan & Shultz, 2002). The eagle density in the Taï forest is estimated to be 0.4 individual per km^2, suggesting a total population of about 1,500 individuals in the park (Shultz, 2002). Breeding is seasonal, with one or two chicks fledging in March, followed by a prolonged period of provisioning of the surviving one (Brown, 1982; Shultz & Thomsett, 2007).

Crowned eagles rely on surprise to hunt successfully. Pairs of eagles sweeping through the canopy to attack monkey groups have been observed, possibly older juveniles following a parent (Gautier-Hion & Tutin, 1988; Shultz & Thomsett, 2007). In Taï, however, their preferred hunting strategy is to sit and wait in the high canopy until a sudden surprise attack on an unsuspecting prey individual becomes possible (Shultz & Thomsett, 2007). Eagles have been observed to track monkey groups and to fly around them to position themselves in front of the approaching monkey group to drop down onto unwary individuals. Interestingly, during these observations monkeys showed no signs of being aware of the eagle's presence, suggesting that vigilance behaviour is not very effective in avoiding eagles (Shultz, 2001; Shultz & Thomsett, 2007). An interesting implication is that travelling in a straight line, for example, to reach an anticipated food tree, may not be the most adaptive way of foraging for primates because it would allow sit-and-wait predators to predict group movement. A study on the sooty mangabeys at Taï has found that although the monkeys know which trees carry fruits their approach path to these trees often deviates substantially from a straight line (Janmaat et al., 2006a & b). Whether or not this is an adaptation to eagle hunting behaviour is currently not known.

Predation rates by Taï eagles are not uniformly distributed: a radio tracking study has shown that hunting activity is concentrated to the core areas of the eagles' home ranges (Shultz & Noë, 2002), suggesting that predation pressure varies not only by time of year but also with location. By and large eagles are opportunistic predators, taking prey roughly according to abundance, although there are some interesting deviations (see below).

Leopards

As the largest of carnivore predators, leopards are an important force of natural selection. Leopards traditionally have been studied in the African savannah (Bailey, 1993), but data are now also available for the forest leopards in Taï (Jenny, 1996; Jenny & Zuberbühler, 2005). For this project, four adult leopards were captured, fitted with radio collars, and subsequently monitored for about two years (Table 1.2; Fig. 1.1). Two of the study animals were monitored systematically both by triangulation from treetops and by directly following them through the forest. Results showed that both animals were more active during the day than at night, with relative peaks at dawn and dusk, a pattern that differed from those of savannah leopards (Bailey, 1993; Fig. 1.2). At night, activity patterns consisted of either complete inactivity or of travelling over large distances. Daytime activity showed a more evenly distributed pattern, and inactive periods were always less than five hours (Jenny & Zuberbühler, 2005). The adult male covered a home

TABLE 1.2. Information on the four radio-tracked leopards (Jenny, 1996).

Individual	Capture Date	Sex	Age (years)	Weight (kg)
Cosmos	5 Feb 93	Male	3–5	56
Adele	16 Aug 93	Female	3–5	34
Cora	16 Jun 94	Female	2–3	32
Arthur*	11 Oct 94	Male	3–4	49

*Dind et al. (1996)

FIGURE 1.1. Left: Adult male "Cosmos" passing a photo-trap; Right: adult female "Adele" is fitted with a radio collar (Photos: D. Jenny)

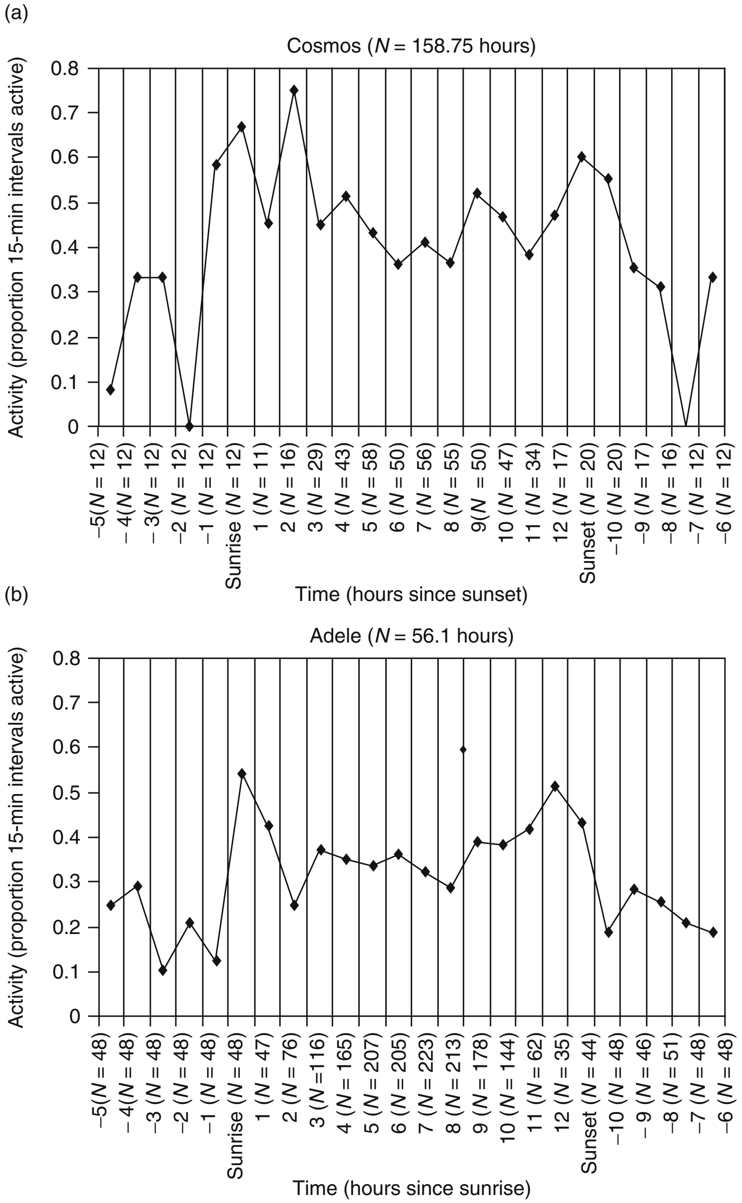

FIGURE 1.2. Relative activity patterns of two radio-collared leopards plotted as a function of onset of sunrise and sunset (Reprinted Jenny, D. & Zuberbühler, K., "Hunting behaviour in West African forest leopards," *African Journal of Ecology*, 43, 197–200, 2005, with permission from Blackwell Publishing)

range 85.6 km^2; the adult female had a total home range size of less than 28.5 km^2 (Jenny, 1996). The overall density of leopards in the Taï forest was estimated to be 0.1/km^2, suggesting a total population of about 400 individuals in the park (Jenny, 1996). This relatively high density, compared to other African forests, might be a direct consequence of the large population of forest duikers (*Cephalophus spp.*), frequent prey items of Taï leopards (see Table 1.3). The lowest monthly activity rates were observed during the rainy period (particularly in October), perhaps because heavy rainfall increased hunting success. During heavy rains, it could be more difficult for prey to detect an approaching or hiding leopard, a rationale that may also explain the increased hunting activity of chimpanzees during this time of the year.

Observations during direct follows of radio-tracked individuals revealed that individuals often hid in dense thickets. When in close vincinity of a resting leopard, the observer encountered significantly more monkey groups than when sitting alone at ten randomly chosen observation points throughout the study area, indicating that leopards selectively chose hiding spots close to monkey groups (Jenny, 1996; Jenny & Zuberbühler, 2005).

Forest leopards hide and attack by surprise, presumably from the lower branches of a tree. All eight species of monkeys occasionally come to the ground to forage or play (McGraw, 1998). Studies of leopard feces in the Taï forest allow some estimate of predation rates inflicted by leopards (Hoppe-Dominik, 1984; Zuberbühler & Jenny, 2002). Of the roughly 140 mammal species that have been

TABLE 1.3. Prey spectrum of Taï leopards.

Scientific Name	Common Name	Zuberbühler & Jenny (2002)	Hoppe-Dominik (1984)
Procolobus 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 atys	Sooty mangabey	6	9
Cercopithecidae	Unknown monkeys	10	3
Pan troglodytes	Chimpanzee	1	0
Perodicticus potto	Potto	0	1
Primates Total		**64**	**61**
Cephalophus spp. total	Duikers	82	82
Manis spp.	Pangolins	43	10
Sciuridae (undet.)	Squirrels	8	9
Panthera pardus	Leopards	6	6
Other mammals	Other mammals	18	62
Mammalia (undet.)	Unknown mammals	6	26
Non-Primates Total		**163**	**195**
Aves Total		**2**	**2**

described for the Taï forest, a wide variety has been found in leopard feces, most of them are mammals weighing less than 10 kg. Monkeys and duikers make up the largest proportion (Table 1.3). Leopards are known scavengers so a small proportion of leopard prey remains may have come from animals that died of other causes (Hart et al., 1996).

Savannah leopards are typically described as opportunistic predators, hunting prey in proportion to abundance. However, at least one adult female monitored in Taï exhibited clear preferences (Fig. 1.3). This female consumed duikers and monkeys significantly more often, and pangolins less often than other leopards (Zuberbühler & Jenny, 2002). Also, after hearing drumming or screaming from a nearby chimpanzee party, she started moving in the opposite direction, while approach was never recorded (Zuberbühler & Jenny, 2002). It may be that such individual hunting preferences are only temporary, and that the female changed them again after some time. Nevertheless, the fact that the resident leopards can develop hunting preferences for particular prey species is evolutionarily relevant. Since leopards are territorial (Jenny, 1996), a particular monkey group is likely to interact with the same few resident leopards over many years. It may thus be of additional importance to actively dissuade leopards from hunting, not only to secure one's own survival and those of close genetic relatives, but also to avoid preference formation. The subsequent sections will show how the Taï primates have evolved specialised and highly conspicuous anti-predator behaviour in response to leopards.

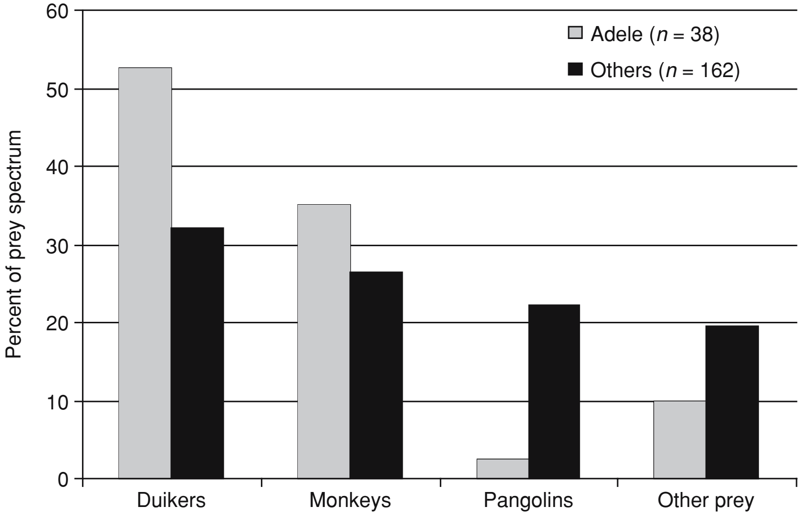

FIGURE 1.3. Prey selectivity of the focal animal Adele compared to other leopards in the Taï forest (Reprinted Jenny, D. & Zuberbühler, K., "Hunting behaviour in West African forest leopards," *African Journal of Ecology*, 43, 197–200, 2005, with permission from Blackwell Publishing)

Results

Adaptations to Predation

Predator-prey interactions lead to evolutionary "arms races," although the nature of co-adaptations will depend on various factors. The following section focuses on the possible effects of predation on primate evolution by the four predators just discussed, especially morphological, social, and cognitive adaptations.

The Effects of Human Predation

Red colobus monkeys are usually the first species to disappear in areas of high poaching (Refisch, 2001), suggesting that large multi-male groups, arboreal live, and large body size are ineffective measures in the face of human predation. All monkeys respond to approaching humans or playback of human speech with no or very few alarm calls, following their response by silent flight and prolonged cryptic behaviour (Zuberbühler et al., 1997; Zuberbühler, 2000). In Taï, poachers use deceptive tactics to localize and attract individuals, mainly by imitating the presence of a crowned eagle or a leopard, predators to which monkeys normally react with high calling rates and approach (Zuberbühler et al., 1997). Experimental work has shown that monkey groups frequently exposed to poachers are less likely to respond to these imitations than monkeys living in more protected areas. This work has demonstrated that adaptive discrimination can be acquired within the lifespan of individual monkeys using general learning abilities (Bshary, 2001).

The Effects of Chimpanzee Predation

Predatory chimpanzees have a bias towards the heavier arboreal monkeys, suggesting that large body size and arboreal live are ineffective deterrents against chimpanzee predation. Once a monkey group is located and a hunt is initiated by a group of chimpanzees, Taï monkeys no longer have very effective anti-predation responses. This is because chimpanzees can reach individuals in the high canopy and their multi-male hunting parties make escape difficult, especially for larger and less agile colobines. Not surprisingly, the presence or vocalisations of chimpanzees reliably elicits prolonged cryptic behaviour in all monkey species, sometimes lasting for several hours (Zuberbühler et al., 1999a). The pattern found in Taï is not necessarily representative for other parts of Africa, however. The Sonso chimpanzees of Budongo forest, for example, only hunt occasionally, and they have been observed to avoid black-and-white colobus monkeys, possibly because of their highly aggressive behaviour towards chimpanzees (Reynolds, 2005).

Playback experiments with red colobus monkeys have shown that, when hearing chimpanzee vocalisations nearby, individuals hide higher up the trees in positions where exposure to the forest floor is minimal and they become silent, often at close range (Bshary & Noë, 1997a, b). When a chimpanzee group is still at some distance, however, the monkeys move away silently through the canopy or they seek the presence of their Diana monkey group, if it is nearby, even if they have to move towards the chimpanzees. Interestingly, chimpanzees tend to refrain from hunting red colobus–Diana monkey groups, probably because Diana monkeys are excellent sentinels for predators approaching over the forest floor (Bshary & Noë, 1997a, b). Bshary (2007) found that in only about 5% of cases did a chimpanzee group approach a Diana–red colobus group if they heard Diana monkeys first. However, if the chimpanzees heard the red colobus first, then approach was much more common—almost 30% of occasions (Bshary & Noë, 1997a; Bshary, 2007). As mentioned previously, the situation in East Africa is somewhat different, suggesting that the Taï chimpanzees may not be representative for the species (Boesch, 1994).

The Effects of Eagle Predation

Crown living species, such as the Diana and red colobus monkeys, are underrepresented in the prey spectrum of crowned eagles, while the large, more terrestrial sooty mangabeys are strongly overrepresented (Shultz et al., 2004). The fact that mangabeys travel as large groups on the ground apparently makes them particularly easy targets for perched eagles. Mangabeys are the largest monkey species in the Taï forest and their large multi-male groups can surpass one hundred individuals, showing that neither group size nor body size of Taï primates was significantly related to crowned eagle prey preference. Crowned eagle predation has also been studied at other sites (e.g., Skorupa, 1989). In the Kibale forest, monkeys were also the predominant prey of crowned eagles, although hunting activity was apparently biased towards monkeys of an intermediate size, such as juvenile red colobus and adult guenons (Struhsaker & Leakey, 1990).

When detecting an eagle Taï monkeys responded with producing high rates of alarm calls. The continuous canopy of the Taï forest provides some protection from attacks and individuals often responded to eagle presence with rapid flight responses towards the middle of the tree or into thick vegetation. In several species, particularly in Diana monkeys, putty-nosed monkeys, black-and-white colobus and red colobus monkeys, males have been observed to attack a perched eagle, which then flies away and presumable leaves the area (Zuberbühler et al., 1997; Eckardt and Zuberbühler, 2004; Bshary & Noë, 1997a, b). Similar observations have been made in other parts of Africa (Gautier-Hion & Tutin, 1988).

The Effects of Leopard Predation

For leopards, the relationship between vulnerability to predation and morphological and behavioural traits has been analyzed (Zuberbühler & Jenny, 2002). Contrary to predictions, leopard predation rates were positively related to body size because the larger monkey species were preyed upon more often than smaller ones, even if population was controlled for overall density. Similarly, the relationships between leopard predation rate and monkey group size on the one hand and the number of adult males per group on the other hand were positive. Predation rates by leopards were unrelated to the reproductive rate of adult females and to a species' use of the lower forest strata, again suggesting that these traits are not very effective measures against leopard predation.

When they detect a leopard, monkeys react by giving myriad alarm calls and sometimes approaching the predator in the lower canopy. This has a striking effect on the leopard's hunting behavior: Radio-tracking data have shown that leopards typically give up hiding positions to move on and find another group. Zuberbühler et al. (1999a) reported 18 cases in which a group of monkeys detected a hiding leopard: The leopard's spent significantly less time hiding underneath a monkey group after detection the leopard usually abandoned its hiding spot within a few minutes to move onto another area (Fig. 1.4). The monkeys' strategy of signalling detection and making further hunting attempts futile is an adaptive response to leopard hunting behavior.

To further investigate the detection signalling hypothesis, we simulated predator presence by playing back typical vocalisations of two major ground predators of Taï monkeys—leopards and chimpanzees—from a concealed speaker (Zuberbühler et al., 1999a). Various monkey groups throughout a large 100-km^2 study area were tested this way, but never more than once on each stimulus type. Once a group was located, usually by the sound of its members' vocalisations, the speaker was hidden about 50 m from it and a trial conducted if no monkey had detected the observer or part of the equipment and no predator alarm calls had occurred for at least 30 minutes. The focal group's vocal response was recorded.

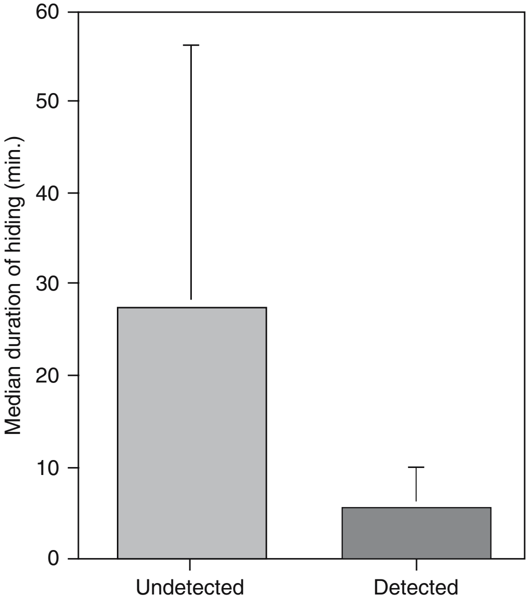

FIGURE 1.4. Median duration of hiding behaviour of the focal animal before and after detection by a group of monkeys (Reprinted from Zuberbühler, K., et al. "The predator deterrence function of primate alarm calls," *Ethology*, 105, 477–490, 1999, with permission from Blackwell Publishing)

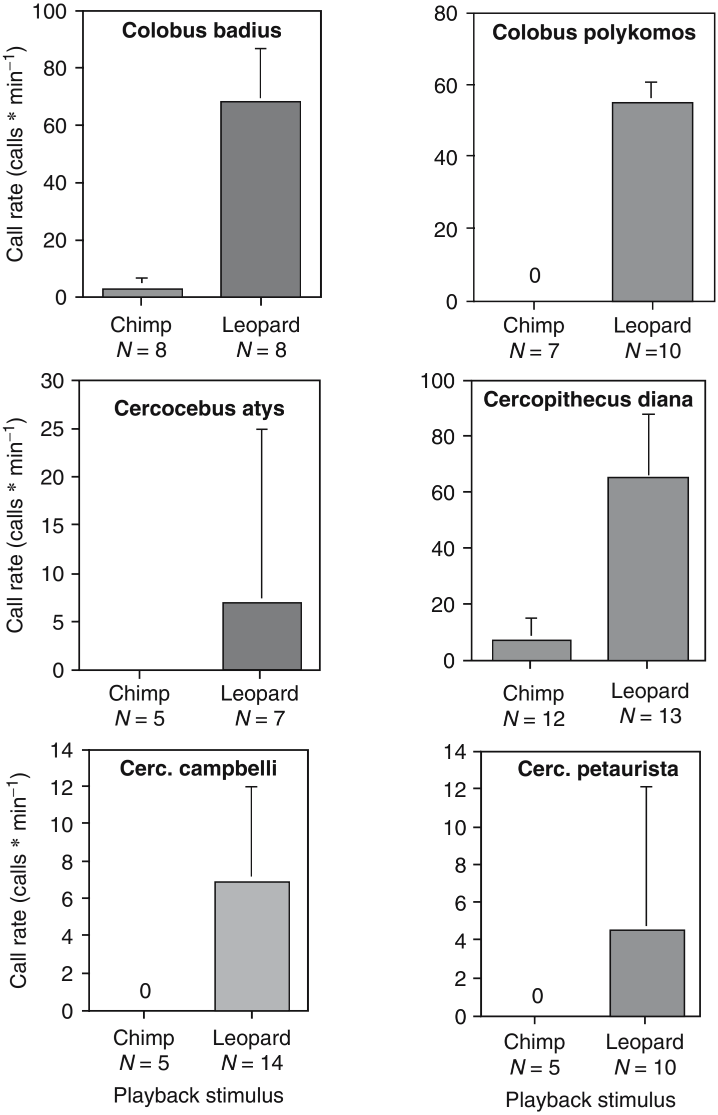

FIGURE 1.5. Alarm call behaviour of six Taï monkeys in response to chimpanzee pant hoots and leopard growls (Reprinted from Zuberbühler, K., et al. "The predator deterrence function of primate alarm calls," *Ethology*, 105, 477–490, 1999, with permission from Blackwell Publishing)

All tested monkey species gave significantly higher rates of alarm calls to playbacks of leopard growls than to playbacks of chimpanzee pant hoots (Fig. 1.5). Groups occasionally approached the speaker after hearing playback stimuli, but only during playback of leopard growls and never after playback of chimpanzee pant hoots, which typically caused flight away from the speaker. In sum, data support the hypothesis that monkey alarm calls to leopards have a predator deterrence function because leopards, in contrast to chimpanzees, elicited conspicuously high alarm call rates, which drove the leopards away.

Predation and Primate Cognitive Evolution

Behavioral and cognitive flexibility appear to be the crucial traits in dealing with Taï predators as compared to traits such as large body size, group size, number of males, inter-birth interval, and so on. A good deal of this flexibility becomes apparent in the monkeys' alarm call behavior. Diana monkeys, Campbell's monkeys, putty-nosed monkeys, and possibly most or all other primates have evolved acoustically distinct and predator-specific alarm calls that function, amongst other ways, to warn each other about the presence of specific types of predators (Zuberbühler et al., 1997; Zuberbühler, 2001; Eckardt and Zuberbühler, 2004; Arnold & Zuberbühler, 2006a & b; Wright, 1998).

Playback experiments have shown that individuals respond to the recordings of different alarm calls as if the corresponding predator were present. The alarm calls from other monkey species are just as effective in this respect as the calls of conspecific individuals (Zuberbühler, 2000b & c; Eckardt and Zuberbühler, 2004). Other work has shown that reactions to alarm calls are not simple responses to the acoustic features of the calls. Instead, monkeys associate the alarm calls of other individuals to the presence of a particular corresponding predator, rather than simply responding to the acoustic features of the calls (Zuberbühler et al., 1999a; Zuberbühler, 2000a & b), demonstrating a level of processing that goes beyond simple stimulus-response arithmetic.

Diana monkeys, and possibly other Taï monkeys, possess relatively detailed knowledge of their main predators' behavior. For example, chimpanzees produce various types of screams, which are given both in social situations (social screams) (Slocombe & Zuberbühler, 2005) and in response to leopards (SOS screams) (Goodall, 1986). Playback experiments have demonstrated that Diana monkeys are able to distinguish between the various types of chimpanzee screams, even though the acoustic differences are only very subtle (Zuberbühler, 2000b). Diana monkey groups whose home ranges were in the core area of a chimpanzee community responded with cryptic behavior to playbacks of chimpanzee agonistic screams and with their own leopard alarm calls when hearing playbacks of chimpanzee SOS-screams (indicating the presence of a leopard). In contrast, Diana monkey groups living in the peripheral areas of a chimpanzee group were more likely to respond cryptically to both types of screams (Zuberbühler, 2000b). Direct encounters between chimpanzees and leopards are probably quite rare events, suggesting that in core areas Diana monkey groups had more learning opportunities for forming these associations. These observations further stress the importance of cognitive abilities in dealing appropriately with these predators. Griffin and Galef (2005) have recently argued that predation has favoured the evolution of a specialised learning apparatus, which also accepts arrangements in which the conditioned stimulus follows, rather than precedes, the unconditioned stimulus.

Although monkeys are able to attend to the meaning encoded by other individuals' alarm calls, this is not always possible, particularly if species do not encode information about the predator type when producing alarm calls. For example, crested Guinea fowls (*Guttera pulcheri*) forage in large groups on the forest floor and, when chased, produce conspicuously loud alarm calls that can be heard over long distances. These birds are not hunted by chimpanzees but may be attacked by leopards and humans (Zuberbühler & Jenny, 2002). Interestingly, the default response of Diana monkeys to Guinea fowl alarm calls is to behave as if a leopard were present. However, this kind of behavioral pattern is not the result of a rigid link between one particular acoustic structure and a behavioral response. Instead, monkeys appear to take into account the pragmatic information obtained from the environment before selecting a response (Zuberbühler, 2000a). Experiments have shown that if Guinea fowl alarm calls are caused by the presence of a human, then the Diana monkeys remain mostly silent to the birds' alarm calls. Cryptic behavior is the typical response of wild Diana monkeys to humans, suggesting that the monkeys assume the presence of humans when responding to the alarm calls. However, if the birds' alarm calls are given in response to a leopard, then the monkeys' response to the alarm calls is strong, that is, as if a leopard were present, suggesting that the monkeys' response is determined by the most likely cause of the birds' alarm calls. A number of control experiments were conducted to rule out simpler mechanisms. Since the same bird alarm calls were used in both the leopard and human situation, monkeys could not have been responding to some subtle acoustic cues unnoticed by the researcher.

Finally, some monkeys are able to alter the meaning of their alarm calls by constructing simple call combinations using existing elements of their vocal repertoire (Zuberbühler, 2002). As mentioned before, Campbell's males give acoustically distinct alarm calls to leopards and eagles and Diana monkeys respond to these calls with their own corresponding alarm calls (Zuberbühler, 2000). However, in less dangerous situations, Campbell's males often emit a pair of low, resounding 'boom' calls before their alarm calls. Playbacks of boom-introduced Campbell's eagle or leopard alarm calls no longer elicited alarm calls in Diana monkeys, indicating that the 'booms' have affected the semantic specificity of the subsequent alarm calls. Diana monkeys themselves do not produce booms and combining Campbell's booms with Diana monkey alarm calls had no effect, indicating that they were only meaningful in conjunction with Campbell's alarm calls.

Another surprising finding emerged from a field study on putty-nosed monkey alarm calls (Arnold & Zuberbühler, 2006a & b). In the Nigerian subspecies, males produced two types of alarm calls to leopards and eagles, but individual calls were given as parts of long sequences that often involved both alarm call types. However, playback experiments demonstrated that call production was not random, but that leopards and eagles elicited structurally unique call sequences. It is quite likely, therefore, that receivers are able extract semantic information from the structural features of a call sequence, as opposed to the individual calls.

Discussion

There is a large literature that suggests that a species' traits, including its morphology, group size, and so on, are a consequence of migration patterns that resulted from global climate changes. African rainforests have undergone dramatic changes in size in the relatively recent evolutionary past. Changing Pleistocene climate led to the compartmentalisation of the once continuous Upper Guinea forest, of which the Taï forest is part. During the dry and cold periods the forest contracted, forcing inhabitants into increasingly restricted refuges. The Taï forest sits in between two main West African refuges, one located in the border region of Sierra Leone and Liberia, the other one at the border of the Ivory Coast with Ghana (Booth, 1958a,b; Hamilton, 1988; Oates, 1988). When warmer, moister climates lead to forest expansion, the primate populations isolated in these refuges diverged and radiated outward to colonize new areas, including the Taï forest. However, it is likely that the newly emerging forests were limited in the number of available niches to fill in, resulting in inter-species competition (Fleagle & Reed, 1996; Tutin & White, 1999; Struhsaker, 1999; Reed & Bidner, 2004). The Taï primate fauna is fairly representative of most primate communities in other parts of Africa. These communities typically consist of a several arboreal frugivores, 2–3 arboreal folivores, terrestrial cryptic foragers, and some nocturnal prosimian species, suggesting that the number and types of available niches a tropical forest can offer is limited and roughly the same throughout the tropical forest belt (Reed & Bidner, 2004; Fleagle & Reed, 1996, 1999; Chapman et al., 1999). Phylogenetic history and the constraints of a rainforest habitat, in other words, may explain the current trait differences in the Taï monkeys much better than predation alone.

Polyspecific Associations

Rather than tolerating more conspecific group members, forest primates appear to prefer living with members of other species. In some cases they may even be forced to do so because their own rigid social system prevents them from increasing group size. What keeps these mixed-species groups together is difficult to understand, particularly if two species have similar feeding requirements. A number of observations are consistent with the idea that monkeys trade their services in predation defence for increased tolerance by a more dominant partner at the feeding site, a prerequisite of a biological market game (Noë et al., 2001). An important feature of a biological market is that there is an element of choice and that the partners can adjust the benefits they offer each other. Some species, such as the Diana monkeys and putty-nosed monkeys, are astonishingly tolerant towards each other, despite a high degree of feeding competition (Eckardt and Zuberbühler, 2004). In this case, biological market theory predicts that interspecies tolerance should be determined by differences in predation pressure and food availability, as well as level of competition between the two partner species. The mechanisms governing mixed-species groups are thus fundamentally different from those determining monospecific groups. In polyspecific groups individuals have a large degree of control over how many partner individuals they want to associate with simply by refusing to form a group with other species. Individuals can thus change their effective group size on an almost ad hoc basis, allowing rapid adjustments to changes in the environment. Successful living in poly-specific groups thus requires a cognitive apparatus that can deal with the signals of the partner species, especially its alarm call and anti-predator behavior. The studies reviewed in this chapter have illustrated this capacity extensively. Predation, in other words, has lead to the formation of polyspecific associations, whose value is multiplied by adequate semantic abilities. The forest may thus have been the breeding ground for advanced communicative abilities.

Interaction Effects

It is unclear how the various behavioral and morphological traits interact with one another in their efficiency in predation aversion. For instance, the habitat may put a limit on how much biomass it can support, leading to a trade-off between body size and group size. However, that is not what is observed in Taï. Sooty mangabeys and red colobus are amongst the heaviest Taï primates but they also form the largest groups, while the smaller guenons and olive colobus monkeys live in substantially smaller groups. It may also be that different predators put opposing selection pressures on a particular trait. For instance, small body size may be advantageous to escape pursuit hunters, such as chimpanzees, but it may provide a substantial disadvantage when interacting with crowned eagles. Although this is interesting, the finding was that all predators consistently preferred the larger monkeys, and that multi-male groups seemed to provide little or no protection for other group members.

It would be desirable to analyze within species differences. For example, it would be useful to ask, “Are individual red colobus monkeys living in larger groups attacked less often by chimpanzees, eagles, or leopards than individuals living in smaller groups?” Hill & Lee (1998) have found some evidence for this sort of relation, but no such data are available for the Taï monkeys. Nevertheless, differences among the various Taï monkey species with respect to vulnerability to predators need to be explained. If predation did play a crucial role in the monkeys’ morphological and behavioral evolution, then the outcome of this process was not very simple or straightforward. There seem to be two options: (a) predation was the main factor in the evolution of these traits, but its effects were so intricate and complex that it is impossible to see any clear effects in the species’ current traits; (b) predation played some role during evolution as part of a more general adaptation process, which was mainly determined by interspecies competition and the colonization history of the habitat. The latter scenario seems to be the more likely one.

Evolution of Cognitive Abilities

The idea that the principal evolutionary effect of predation was on primate cognitive evolution is obviously a controversial one, and it will be nothing short of a challenge to think of studies capable of providing conclusive evidence. The generally accepted view is that predation selected for sociality (e.g., van Schaik, 1983) and that living in groups then resulted in selective pressure that lead to advanced cognitive abilities: the 'social' or 'Machiavellian' intelligence hypothesis (Humphrey, 1976). What is proposed in this chapter is a more direct route, one in which predation directly affected primate cognitive evolution, independent of social structure. It is noteworthy that some of the monkey species described in this chapter, particularly the Diana monkeys, live in very primitive mammalian social systems with small groups consisting of one adult male and several philopatric adult females and their offspring. Their social behavior is decisively unremarkable, and classic indicators of social complexity, such as differentiated grooming and social relationships or complex triadic interactions, are not normally observed in these animal (e.g., Buzzard & Eckardt, 2007).

What exactly are 'advanced' communicative abilities? A useful way of addressing this problem is to invoke the notion of 'flexibility' (Tomasello & Call, 1997). In the vocal domain this relates to the flexible, context- and audience-dependent meaningful use of vocalisations, rather than a reflex-like direct response to some sorts of stimuli. The various examples discussed in this chapter suggest that much of the monkey behavior in the predation context is of the former kind.

Conclusions

The Taï forest primate fauna is the product of a series of evolutionary events. It is not completely clear for how long each species has existed at Taï, nor is the exact order of their arrival known. Just like in other African forests, the different monkey species in Taï occupy specific niches, as defined by body size, diet, locomotion, or activity patterns, which suggests that there is a deterministic element to the composition and structure of the primate community at Taï and elsewhere in Africa (Fleagle et al., 1999). The various species were probably forced to adapt to one of the few available ecological niches and this process may better explain the interspecies differences in their traits than predation alone. Predation may have been an important factor in this process, but it fails to account for many of the observed patterns: There was no evidence that the four predators drove the evolution of traits, such as group size, body size, multi-male grouping pattern, inter-birth interval, stratum use, and so on, in the predicted way.

Instead, the most striking adaptations displayed by the monkeys are highly predator-specific behavioral strategies, apparently designed to interfere with a predation event at various levels. Several field experiments have demonstrated that some of these behavioral responses are based on relatively sophisticated cognitive processes. Monkeys use their alarm call behavior not only to warn each other about the type of predator present but also to interfere with some of the predators' hunting techniques. They are attuned to responding to the alarm calls of other individuals, which are interpreted by flexibly taking into account a variety of additional information.

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References

Anderson, C.M. (1986). Predation and primate evolution. *Primates*, 27: 15–39.

Arnold, K., and Zuberbühler, K. (2006a). The alarm calling adult male putty-nosed monkeys, Cercopithecus nictitans martini. *Animal Behaviour*, 72.

Arnold, K., and Zuberbühler, K. (2006b). Semantic combinations in primate calls. *Nature*, 441: 303.

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

Boesch, C. (1994). Chimpanzee-red colobus monkeys: A predator-prey system. *Animal Behaviour*, 47, 1135–1148.

Boesch, C. (1994). Hunting strategies of Gombe and Taï chimpanzees. In R. Wrangham, W. McGrew, F. de Waal, and P. Heltne (Eds.), *Chimpanzee Cultures* (pp. 77–92). Cambridge: Harvard University Press.

Boesch, C. (2002). Cooperative hunting roles among Taï chimpanzees. *Human Nature*, 13: 27–46.

Boesch, C., and Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *Am. J. Phys. Anthr.*, 78: 547–573.

Boesch, C., and Boesch-Achermann, H. (2000). *The chimpanzees of the Taï forest. Behavioural ecology and evolution*. Oxford: Oxford Univ. Press.

Brown, L. (1982). The prey of the crowned eagle *Stephanoaetus coronatus* in Central Kenya. *Scopus*, 6: 91–94.

Bshary, R. (2001). Diana monkeys, *Cercopithecus diana*, adjust their anti-predator response behaviour to human hunting strategies. *Behav. Ecol. Sociobiol.*, 50: 251–256.

Bshary, R. (2007). Interactions between red colobus monkeys and chimpanzees. In W.S. McGraw, K. Zuberbühler & R. Noë (Eds.), *Monkeys of the Taï forest: An African primate community* Cambridge: Cambridge Univ. Press.

Bshary, R., and Noë, R. (1997). Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. *Behavioral Ecology and Sociobiology*, 41: 321–333.

Bshary, R., and Noë, R. (1997). Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour*, 54: 1461–1474.

Buzzard, P., & Eckardt, W. (2007). Social systems of the Taï guenons (*Cercopithecus spp.*). In R. McGraw, K. Zuberbühler & R. Noë (Eds.), *Monkeys of the Taï forest*: *An African monkey community*. Cambridge: Cambridge Univ. Press.

Cheney, D.L., Seyfarth, R.M., Fischer, J., Beehner, J., Bergman, T., Johnson, S.E., Kitchen, D.M., Palombit, R.A., Rendall, D., and Silk, J.B. (2004). Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology*, 25: 401–428.

Cheney, D.L., and Wrangham, R.W. (1987). Predation. In B. Smuts, et al. (Eds.), *Primate societies* (pp. 227–239). Chicago: Univ. of Chicago Press.

Cords, M. (1990). Vigilance and mixed-species association of some East African forest monkeys. *Behavioral Ecology and Sociobiology*, 26: 297–300.

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

Eckardt, W., and Zuberbühler, K. (2004). Cooperation and competition in two forest monkeys. *Behavioral Ecology*, 15: 400–411.

Enstam, K.L., and Isbell, L.A. (2004). Microhabitat preference and vertical use of space by patas monkeys (*Erythrocebus patas*) in relation to predation risk and habitat structure. *Folia Primatologica*, 75: 70–84.

Gautier-Hion, A., and Gautier, J.P. (1974). Les associations polyspecifiques de Cercopitheques du Plateau de M'Passa (Gabon). *Folia primatol.*, 22: 134–177.

Gautier-Hion, A., and 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.

Gil-da-Costa, R., Palleroni, A., Hauser, M.D., Touchton, J., and Kelley, J.P. (2003). Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. *Proceedings of the Royal Society of London Series B—Biological Sciences*, 270: 605–610.

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

Hart, J.A., Katembo, M., and Punga, K. (1996). Diet, prey selection and ecological relations of leopard and golden cat in the Ituri forest, Zaire. *African Journal of Ecology*, 34: 364–379.

Herbinger, I., Boesch, C., and Rothe, H. (2001). Territory characteristics among three neighbouring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *Int. J. Primatol.*, 22: 143–167.

Hill, K., Boesch, C., Pusey, A., Williams, J., and Wrangham, R. (2001). Mortality rates among wild chimpanzees. *J. Hum. Evol.*, 40: 437–450.

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

Hill, R.A., and Lee, P.C. (1998). Predation risk as an influence on group size in cercopithecoid primates: Implications for social structure. *J. of Zoology*, 245: 447–456.

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.

Humphrey, N.K. (1976). The social function of intellect. In P.P.G. Bateson and R.A. Hinde (Eds.), *Growing points in ethology* (pp. 303–317). Cambridge, UK: Cambridge Univ. Press.

Isbell, L.A., Cheney, D.L., and Seyfarth, R.M. (1993). Are immigrant vervet monkeys, *Cercopithecus aethiops*, at greater risk of mortality than residents? *Animal Behaviour*, 45: 729–734.

Janmaat, K.R.L., Byrne, R.W., and Zuberbühler, K. (2006a). Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour*.

Janmaat, K.R.L., Byrne, R.W., and Zuberbühler, K. (2006b). Primates take weather into account when searching for fruits. *Curr. Biol.*, 16: 1232–1237.

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., and Zuberbühler, K. (2005). Hunting behaviour in West African forest leopards. *African J. of Ecology*, 43: 197–200.

Korstjens, A.H. (2001). *The mob, the secret sorority, and the phantoms*: *An analysis of the socio-ecological strategies of the three colobines of Taï. Unpublished Ph.D.*, Utrecht.

Krebs, J.R., and Davis, N.B. (1993). Predator versus prey: Evolutionary arms races. In J.R. Krebs and N.B. Davies (Eds.), *An introduction to behavioral ecology* (pp. 77–101). Oxford: Blackwell Scientific Publications.

Lehmann, J., and Boesch, C. (2003). Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Côte d'Ivoire. *Behavioral Ecology*, 14: 642–649.

Malan, G., and Shultz, S. (2002). Nest-site selection of the crowned hawk-eagle in the forests of KwaZulu-Natal, South Africa, and Taï, Ivory Coast. *Journal of Raptor Research*, 36: 300–308.

Marchesi, P., Marchesi, N., Fruth, B., and Boesch, C. (1995). Census and distribution of chimpanzees in Côte -Divoire. *Primates*, 36: 591–607.

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 Taï Forest, Ivory Coast. *Am. J. Phys. Anthrop.*, 105: 493–510.

McGraw, W.S. (2000). Positional behavior of *Cercopithecus petaurista*. *Inter. Jour. of Primatology*, 21: 157–182.

Mercader, J., Panger, M., Scott-Cummings, L., and Boesch, C. (2003). Late Holocene archaeological remains from chimpanzee and human sites in the rainforest of Côte d'Ivoire. *American Journal of Physical Anthropology*, 150–151.

Noë, R., and Bshary, R. (1997). The formation of red colobus–Diana monkey associations under predation pressure from chimpanzees. *Proceedings of the Royal Society of London Series B—Biological Sciences*, 264: 253–259.

Refisch, J. (2001). Einfluss der Wilderei auf Affen und die sekundären Effekte auf die Vegetation im Taï Nationalpark, Elfenbeinküste. In: *Bayreuther Forum Ökologie* (pp. 1–189). Bayreuth: Bayreuth.

Refisch, J., and Kone, I. (2005). Impact of commercial hunting on monkey populations in the Taï region, Côte d'Ivoire. *Biotropica*, 37: 136–144.

Reynolds, V. (2005). *The chimpanzees of the Budongo forest—Ecology, behaviour, and conservation*. Oxford: Oxford Univ. Press.

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

Shultz, S. (2002). Population density, breeding chronology and diet of crowned eagles (*Stephanoaetus coronatus*) in Taï National Park, Ivory Coast. *Ibis*, 144: 135–138.

Shultz, S., Faurie, C., and Noë, R. (2003). Behavioural responses of Diana monkeys to male long-distance calls: Changes in ranging, association patterns and activity. *Behavioral Ecology and Sociobiology*, 53: 238–245.

Shultz, S., and Noë, R. (2002). The consequences of crowned eagle central-place foraging on predation risk in monkeys. *Proceedings of the Royal Society of London Series B—Biological Sciences*, 269: 1797–1802.

Shultz, S., Noë, R., McGraw, W.S., and Dunbar, R.I.M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society of London Series B—Biological Sciences*, 271: 725–732.

Shultz, S., and Thomsett, S. (2007). Interactions between African crowned eagles and their primate prey community. In W.S. McGraw, K. Zuberbühler and R. Noë (Eds.), *Monkeys of the Taï forest: An African monkey community.* Cambridge: Cambridge Univ. Press.

Skorupa, J.P. (1989). Crowned eagles (*Stephanoaetus coronatus*) in rainforest: Observations on breeding chronology and diet at a nest in Uganda. *Ibis*, 131: 294–298.

Slocombe, K.E., and Zuberbühler, K. (2005). Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *J. Comp. Psych.*, 119: 67–77.

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

Struhsaker, T.T., and Leakey, M. (1990). Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behav. Ecol. Sociobiol.*, 26: 435–444.

Tomasello, M., and Call, J. (1997). *Primate cognition*. New York: Oxford Univ. Press.

Treves, A. (1999). Has predation shaped the social systems of arboreal primates? *International Journal of Primatology*, 20: 35–67.

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, 60: 711–722.

Uehara, S. (1997). Predation on mammals by the chimpanzee (*Pan troglodytes*). *Primates*, 38: 193–214.

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

Wachter, B., Schabel, M., and Noë, R. (1997). Diet overlap and polyspecific associations of red colobus and Diana monkeys in the Taï Park, Ivory Coast. *Ethology*, 103: 514–526.

Waser, P.M. (1982). Primate polyspecific associations: Do they occur by chance? *Animal Behaviour*, 30: 1–8.

Wolters, S., and Zuberbühler, K. (2003). Mixed-species associations of Diana and Campbell's monkeys: The costs and benefits of a forest phenomenon. *Behaviour*, 140: 371–385.

Wright, P. (1998). Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rainforest of Madagascar. *Behaviour*, 135: 483–512.

Zuberbühler, K. (2000). Causal cognition in a non-human primate: Field playback experiments with Diana monkeys. *Cognition*, 76: 195–207.

Zuberbühler, K. (2000). Causal knowledge of predators' behaviour in wild Diana monkeys. *Animal Behaviour*, 59: 209–220.

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

Zuberbühler, K. (2000). Referential labelling in Diana monkeys. *Animal Behaviour*, 59: 917–927.

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. *Animal Behaviour*, 63: 293–299.

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

Zuberbühler, K., and Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, 43: 873–886.

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

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