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Anti-Predator Strategies in a Diurnal Prosimian, the Ring-Tailed Lemur (*Lemur catta*), at the Beza Mahafaly Special Reserve, Madagascar

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Introduction

With the dramatic increase in research on Madagascar's lemurs during the past few decades, it is now feasible to both document anti-predator behavior and to test predictions regarding the effect of predation pressure on the behavioral ecology of lemurs. In 1994 Goodman raised much interest by his suggestion that, in the absence of large, extant predators on Madagascar, anti-predator behaviors and strategies in lemurs were an artifact of a behavioral repertoire that existed before the extinction of a very large eagle, *Stephanoaetus mahery*. However, both before and subsequent to Goodman's argument, numerous studies of both diurnal and nocturnal lemurs revealed that both extant avian and mammalian predators pose a real predation threat. (Sauther, 1989, 2002; Overdorff & Strait, 1995; Wright & Martin, 1995; Gould, 1996; Gould et al., 1997; Wright, 1998; Schwab, 1999; Karpanty & Grella, 2001; Karpanty 2003). In this chapter, we first present information on predation risk, group size, and foraging in the ring-tailed lemur (*Lemur catta*), and then we examine sex differences in predator vigilance, canopy level differences in vigilance, and how alpha females contribute to anti-predator strategies in this species.

Ring-tailed lemurs inhabit a wide range of habitat in south and southwestern Madagascar, ranging from gallery (riverine) forest to xerophytic, spiny thorn scrub, and limestone forest, and a even a sub-alpine habitat in the central southeastern part of the island (Jolly, 1966; Budnitz & Dainis, 1975; Sussman, 1977; Tattersall, 1982; Mittermeier et al., 1994; Goodman & Langrand, 1996). Ring-tailed lemurs spend anywhere from 3–75% of their time on the ground, depending upon the month and season (Sauther, 2002), and they are therefore frequently exposed to both ground and aerial predators (Jolly, 1966; Sussman, 1972; Sauther, 1989, 2002; Gould, 1996).

L. catta is a medium-sized diurnal lemur with a mean weight of 2.2 kilograms (Sussman, 1991). Therefore, it is not as vulnerable to predation as much smaller, nocturnal lemur species; however, it is still under considerable predator pressure from a number of endemic and introduced species in their geographic range. These include the Madagascar harrier hawk (*Polyboroides radiatus*), the Madagascar buzzard (*Buteo brachypterus*), boa constrictor (*Boa mandtria*), hognose snake (*Leioheterondon madagascariensis*), and Indian civet (*Viverricla indica*) (Sauther, 1989, 2002; Goodman et al., 1993; Gould, 1996). Also, in some areas, the fossa (*Cryptoprocta ferox*), a medium-sized (7–12 kilogram) viverrid carnivore is a predator of *L. catta* (Goodman et al., 1993). In addition to these endemic predators, village dogs, feral domestic cats and a hybrid wild cat can be a serious predation threat to ring-tailed lemurs living in forests near human habitation (Sauther, 1989; Gould, 1996).

At the Beza Mahafaly Special Reserve in southwestern Madagascar actual predation has been observed and recorded. Infants have been taken by the Madagascar harrier hawk, and bones of both adults and juveniles have been found under the nests of this raptor (Ratsirarson, 1985; Goodman et al., 1993). Infants have also been preyed upon by Indian civets, feral cats, and dogs in the reserve (Sauther, 1989; Goodman et al., 1993). Numerous predation attempts by raptors have also been observed. For example, a migrating male sitting alone in an exposed spot near the top of a tree was nearly taken by a harrier hawk (Gould, 1994, 1996), and harrier hawks have been observed flying into the canopy where ring-tailed lemur groups were feeding or resting. An infant exploring in a tree away from the mother was followed by a small raptor until an adult lemur retrieved it (Gould, 1994, 1996). Sauther (2002) notes that the size of the harrier hawk (60–62 cm in body length) prevents it from moving easily in a closed canopy; however, harrier hawks have been observed in more open environments at Beza Mahafaly, flying above ring-tailed lemur groups or perched in dead trees watching groups of lemurs.

Dog and cat predation may also be especially important. On one occasion a feral cat was observed stalking a group of ring-tailed lemurs feeding on the ground, and on numerous occasions single ring-tailed lemurs have been "treed" by roaming dogs that wait at the base of the tree. We have also found both ring-tailed lemur and sifaka hair within dog scat as well as the predated remains of ring-tailed lemurs (Figure 13.1).

Types of Anti-Predator Behaviors

Ring-tailed lemurs exhibit a large repertoire of anti-predator behaviors, described below, which include both vocal signals and behavioral responses such as mobbing and vigilance.

Vigilance

Predator vigilance occurs when a ring-tailed lemur ceases the activity in which it is engaged, sits, or stands upright with ears facing forward and visually scans

FIGURE 13.1. Remains of a female ring-tailed lemur after predation, likely by a feral dog. Only portion of the stomach, fur, tail and vertebra remain (Photo: M.L. Sauther)

the surrounding environment (Gould, 1996). Animals engage in this "vigilance sequence" when sightings or vocalizations of predators occurred, and/or when they hear other groups of nearby ring-tailed lemurs or Verreaux's sifakas emitting anti-predator calls.

Vocalizations

Ring-tailed lemurs engage in "representational signaling," that is, they emit particular vocalizations for particular kinds of predators (Jolly, 1966; Sussman, 1972; Sauther, 1989; Macedonia, 1990). A "click" vocalization occurs when an animal is agitated or startled by the presence of a potential predator (Jolly, 1966). Sauther (1989) noted that if one or more animals engage in an initial click series they are immediately joined by much of the rest of the troop, which then move into the canopy or bushes and scan the ground. With terrestrial predators the clicking sequence can change to a series of sharp "yaps" while the group keeps watch on the potential predator until it has moved away (Jolly, 1966; Sussman, 1972; Sauther, 1989; Gould, 1996). If the predator is a low-flying or swooping raptor, a few individuals will click, the group will look up, scream, and quickly drop from high to lower canopy (Jolly, 1966; Sauther, 1989; Gould, 1996).

Sauther (1989, 2002) described anti-predator behavior in *L. catta* and examined the relationship between group size, anti-predator behaviors, habitat use, and predator sensitive foraging in two groups of wild ring-tailed lemurs at the Beza Mahafaly Special Reserve. She found that (1) when predation risk is high, ring-tailed lemurs avoided risky foraging areas, particularly terrestrial foraging; (2) that smaller groups of ring-tailed lemurs avoided open areas more frequently than animals in larger groups; and (3) that groups that avoided more open areas had reduced foraging/feeding measures.

Gould (1996, 1997) investigated sex differences in predator vigilance in two groups of ring-tailed lemurs, during the birth and lactation season at Beza Mahafaly Special Reserve, when risk of predation on infants is high. The goal of that study was to test whether males were benefiting females during this period, and to test costs and benefits to females of tolerating male residence in social groups, since female are dominant in this species and serve as the primary resource defenders (Jolly, 1966; Sussman, 1977; Sauther, 1992) The contribution of the alpha female to anti-predator vigilance was also examined.

Methods

Sauther collected predator sensitive foraging data on two groups of ring-tailed lemurs in the eastern part of the Beza Mahafaly Special Reserve as part of a larger study of feeding ecology on this species in 1988–1989 (1992, 1993, 1998, 2002). A total of 1,800 hours of focal animal data were collected. One group contained between 14 and 16 individuals, the other contained 6–8 animals. To examine predator sensitive foraging specifically, focal animal data (Altmann, 1974) were collected at 5-min intervals on all adult and sub-adult animals in the two groups and all behaviors were recorded. Nearest neighbor data were also collected every 15 min in order to examine whether animals were either more or less cohesive while foraging, and whether predator pressure affects cohesion. If an individual's nearest neighbor was <3 m, "group feeding" was recorded, as animals at this proximity were usually feeding in the same patch. If the nearest neighbor was 8 m or more away, "solitary feeding" was recorded. This was done because at a distance of 8 m the animal was usually outside of any other animal's food patch and thus it was truly feeding solitarily (Sauther, 1992). If nearest neighbors were between 3 and 7 m apart, intermediate foraging was recorded. Foraging location was recorded by a tree quadrat method, wherein a tree is divided into thirds along the vertical and horizontal axes and quadrats are numbered 1–9. Ground foraging was assigned the number 10. Each group's location was mapped every 15 min to determine ranging patterns and foraging effort. If the animals entered new areas of their home range each month, or if they foraged outside of their home range, a "new hectare" designation was recorded.

Predator pressure was determined by recording all encounters with potential diurnal predators throughout an annual cycle. Monthly predator encounters were

assessed as "low" if 0–3 encounters occurred in a one-month period, and "high" if the encounters numbered greater than 3. In addition, all instances of predator vigilance were recorded as defined earlier in this chapter.

In Gould's study, 424 continuous time focal animal data sessions (Altmann, 1974) of 15-min duration were collected on 15 adult ring-tailed lemurs in two groups (Red group = 4 adult females, 2 adult males; Green group = 5 adult females, 4 adult males) at the Beza Mahafaly reserve between early October and mid-December, 1994. Females give birth from late September to late October at this site, and by four weeks of age, nursing ring-tailed infants begin to explore the environment on their own (Gould, 1990), becoming vulnerable to predation as the weeks progress.

Anti-predator vigilance was scored both when actual predators were seen or heard in the area and when the animals engaged in vigilance behavior toward anything in the environment that could have been a predator (e.g., a sudden unidentified sound occurring on the ground or in the trees, the spotting of an animal moving through the trees that was not a lemur, hearing a raptor in the distance, dogs barking). An instance of vigilance was scored when the animals engaged in the behaviors described as "vigilant" earlier in this chapter. Each focal animal's total frequency of anti-predator vigilance was divided by the number of focal animal sessions collected on that animal (which ranged from 27 to 30 sessions) to obtain a rate per focal animal session.

Sauther's interval data were analyzed using randomization tests (Edgington, 1980) in which a t-test with systematic data permutation was used to determine statistically significant differences between the two study groups. Gould's continuous-time data were analyzed using non-parametric analysis of variance tests for small samples to test sex differences in vigilance and the chi-square test to determine vigilance differences in canopy level.

Results

Predator Sensitive Foraging

When predator pressure was high, the smaller group foraged more often in the middle level of trees compared to periods of low predator pressure ($t = 2.76$, $p = 0.02$), and avoided terrestrial foraging. Predator pressure did not seem to affect foraging behavior or foraging level for the larger group. The larger group foraged in the low level of trees when predation risk was high,but they also continued to forage on the ground.

The smaller group, through avoiding terrestrial foraging when predation risk was high, had a significantly lower intake of leaves compared to when predation risk was low ($t = 2.40$, $p = 0.04$), as many of their leaf-food resources are found on the ground in the form of herbaceous vegetation. The smaller group also had a lower intake of fruit during periods of high predation risk ($t = 2.08$, $p = 0.04$). Food intake of the larger group was not significantly affected by predation risk.

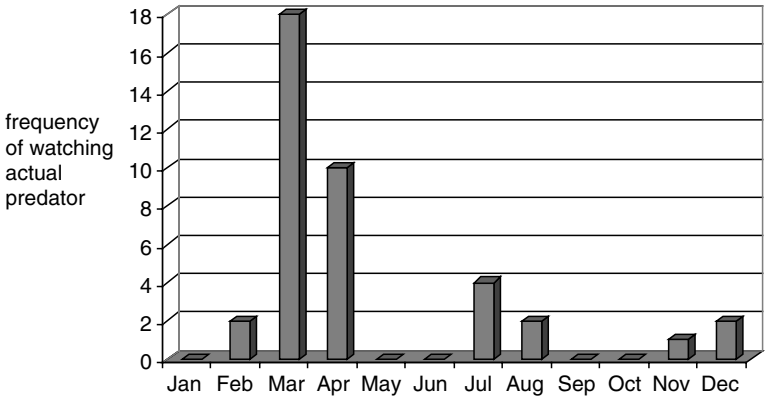

FIGURE 13.2. Frequency of vigilance towards an actual predator in the vicinity (predator watching) over a one-year period (1988–1989)

When entering new hectares of the home range or foraging outside of the home range, spatial cohesion, measured as "group nearest neighbor pattern" was positively correlated with number of new hectares entered for the smaller group ($r = 0.51$, $p = 0.049$). In other words, when smaller groups entered new areas they maintained close proximity to one another. In the larger group individuals actually spread out and fed some distance from one another.

In fact, there was a strong correlation between foraging without a nearest neighbor and new hectares entered ($r = 0.72$, $p = 0.008$). The larger group entered more new hectares when foraging than did the smaller group ($t = 2.60$, $p = 0.03$), and even though such behavior was correlated with a higher frequency of predator encounters ($t = 2.53$, $p = 0.03$), there was a positive correlation between foraging in these new areas and fruit feeding ($r = 0.75$, $p = 0.005$).

Comparing the total frequency of male versus female vigilance toward an actual predator by month ("predator watching") revealed no sex differences ($t = 0.633$, $p = 0.533$). However, total monthly vigilance behavior toward a predator did vary, peaking during March and April when infants are being weaned (Figure 13.2).

Anti-Predator Vigilance Towards Actual or Potential Predators

No sex difference was found in rates of vigilance behavior towards a real or potential predator in Gould's two study groups; however, females spent more time in anti-predator vigilance ($U = 11$, $p = 0.051$) than did males. Pooling the females and males from each group together, higher-ranking females were vigilant significantly more often than were lower-ranking females (U-test, $U = 0$, $p = 0.04$), but no relationship was found between rank and rates of anti-predator vigilance in males. The alpha female in each group was vigilant towards potential predators significantly more often than all other adults in her group (single sample against

the mean test, Green group, $t_s = 3.54$, df = 7, $p < 0.01$; Red group $t_s = 3.49$, df = 4, $p < 0.05$, Figure 13.3).

The study animals were significantly more vigilant when on the ground, compared with low, middle, or high canopy (chi-square goodness of fit, $\chi^2 = 128.59$, df = 3, $p < 0.001$, Figure 13.4). Red group contained three fewer adults than did Green group, but there was no between-group difference in overall rates of anti-predator vigilance, nor were there between-group differences in proportion of vigilance on the ground, or in low, medium or high canopy.

Discussion

Primates vulnerable to predation must be able to balance alertness toward potential predators with getting enough food to meet their nutritional needs and with conducting other daily activities. Different types of anti-predator strategies have evolved depending upon variables such as habitat, body size, density and types of predators in the area, group size, and degree of arboreality or terrestriality.

As *L. catta is* a medium-sized Malagasy primate, and the most terrestrial of all lemurs, it is vulnerable to both the large avian predators and the terrestrial predators described in the introduction. As with most primates, arboreal food resources are very important to ring-tailed lemurs; but this species also depends greatly upon terrestrial vegetation (Sauther, 2002) and thus, ring-tailed lemurs must be watchful at all levels of the forest.

Canopy Level and Vigilance

We found that ring-tailed lemurs at Beza Mahafaly reserve were markedly more vigilant while on the ground, compared to how vigilant they were at any canopy level. This pattern has been found in a number of primate species of similar or slightly larger body size which spend some time foraging terrestrially (e.g., wedge-capped capuchins (de Ruiter 1986; Miller, 2002); red-fronted brown lemurs in a dry forest (Rasolofoson, 2002); brown capuchins (Hirsch, 2002); red colobus and red-tailed monkeys (Treves, 2002). And, predictably, smaller-bodied saddleback and moustached tamarins exhibit heightened vigilance when in the lower canopy, even when found in mixed-species associations (Smith et al., 2004). Smith et al. (2004) and Peres (1993) suggest that in the Neotropics, increased vigilance on the ground or in low canopy relates to both numerous terrestrial predators as well as the fact that many raptors are ambush predators, which take their prey by swooping down from a stationary perch. The velocity with which these raptors swoop into the lower canopy could greatly increase the probability of a successful predatory attempt, which could explain why the tamarins in their studies were more vigilant at lower levels. Some of the smaller raptor species at Beza Mahafaly have been observed watching infant lemurs while on mid to low-canopy stationary perches (Gould, pers. obs). The large raptors at Beza commonly use the ambush method, swooping down on their prey (including chickens) from above

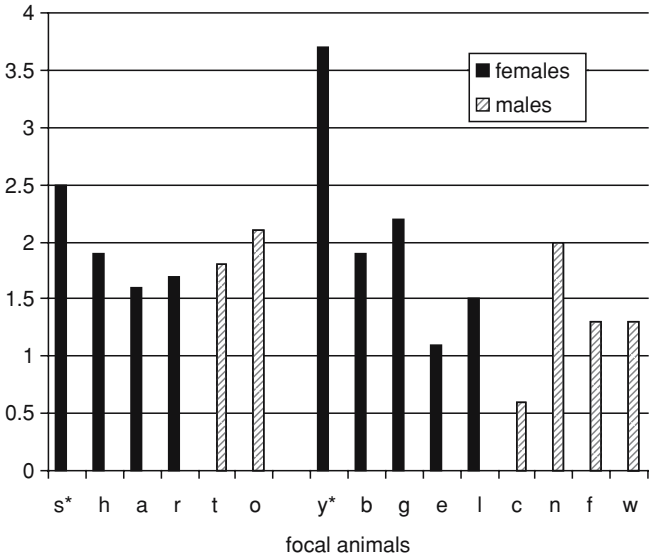

FIGURE 13.3. Rates of vigilance (rate per 15-min. focal session) towards an actual or potential predator by each focal animal in the two study groups over the birth/laction study period, 1994. The first animal presented for each group (s* and y*) were the alpha females in their respective groups

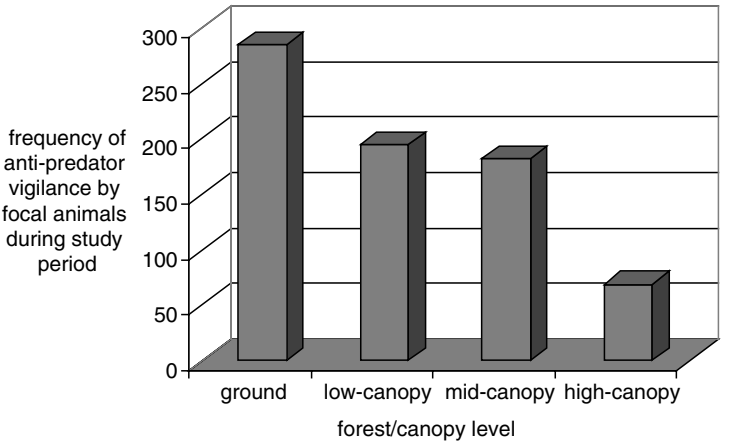

FIGURE 13.4. Frequency of vigilance towards an actual or potential predator (e.g. unfamiliar/unidentified sound or sighting) at different forest levels by all focal animals during the birth/lactation season in 1994

and especially within open areas (Sauther, 1989). Thus, when spending time in exposed terrestrial areas, of which there are many in this habitat, ring-tailed lemurs need to be vigilant toward these "ambush" avian predators.

Group-Size and Anti-Predator Strategies in Relation to Feeding and Foraging

Group size certainly plays a role in anti-predator strategies in ring-tailed lemurs. Larger groups might be able to take more foraging chances, particularly with respect to feeding on ground vegetation. Sauther (2002) found that 48% of the leaf diet of ring-tailed lemurs at Beza Mahafaly came from plants located on the ground. By not foraging terrestrially while predation pressure was high, the smaller group of ring-tailed lemurs in the study incurred a cost in terms of reducing leaf intake, thus, the benefits of engaging in predator avoidance foraging behaviors must be balanced against the cost of obtaining important protein resources (e.g., fewer leaves in the diet) at certain times of the year.

For the larger group, while fruit foraging efficiency increased in the new areas, the behavior of spreading out and therefore being less cohesive could potentially be costly in terms of predator spotting. It is also possible that by having more "eyes and ears" predator detection is enhanced in larger groups making the trade-offs more feasible. The smaller group, by being more spatially cohesive while foraging in new zones, was exhibiting predator sensitive foraging. Overdorff et al. (2002) found similar group-size effects on anti-predator strategies in rainforest lemurs. In three sympatric species (*Eulemur fulvus rufus* (rufous brown lemur), *Propithecus edwardsi* (Milne-Edwards' sifaka), and *Eulemur rubriventer* (red-bellied lemur)) at the Ranomafana site in the southeastern rainforest, the two species living in the larger, multi-male–multi-female groups (*E. f. rufus* and *P. edwardsi*) used all levels of the canopy and exploited a much wider range of food items than did the monogamous *E. rubriventer*. *E. f. rufus* and *P. edwardsi* also fed more on ground vegetation and soil, and were less likely to have a nearest neighbor when feeding, whereas the red-bellied lemurs primarily fed in the upper canopy were highly cohesive. Miller (2002) also found that in wedge-capped capuchins, members of larger groups utilize resources from risky areas and thus increase their foraging opportunities compared to animals residing in smaller groups.

Another strategy related to group size is that the smaller ring-tailed lemur group in Sauther's study formed a mixed-species association with groups of Verreaux's sifaka at the time of year when infants of both species had just been weaned, and thus were more independent but extremely vulnerable to predation.

Infant Vulnerability and Vigilance Behavior

While no sex differences were found in vigilance behavior during both studies, total vigilance behaviors toward actual predators did vary by month during the 1987–88 study. The highest frequency of vigilance behavior occurred during the

months of March and April. Peak weaning of ring-tailed lemurs occur during March, and by April most infants are weaned (Sauther, 1989). Thus, ring-tailed lemurs exhibit the most vigilance toward actual predators during a time period when infants are still not adult body size but are engaging in solitary feeding and presumably more vulnerable to predation.

Sex and Rank Differences in Anti-Predator Behavior

One prediction in relation to sex differences in vigilance in female philopatric species is that males should offer females enhanced predator protection through vigilance in exchange for tolerance in a social group (Baldellou & Henzi, 1992). In similar-sized primates such as vervet monkeys, white-faced capuchins, and rufous brown lemurs (in a dry forest), males are often more vigilant than females (Baldellou & Henzi, 1992; Rose, 1994; Rose & Fedigan, 1995; Rasolofoson, 2002), although in brown capuchins, sex differences in vigilance were not detected (Hirsch, 2002). Since female *L. catta* are dominant to males and are the primary resource defenders (Jolly, 1966; 1984), theoretically, males should benefit females by being more vigilant against potential predators, but they were not more vigilant, at least not during the birth and lactation season when this study was conducted.

The lack of a sex difference in vigilance in this case may relate to a phylogenetic trend in dominance patterns—white capuchin males are dominant to females and rufous brown lemurs are co-dominant (Fedigan, 1990; Pereira & McGlynn, 1997; Overdorff, 1998), and perhaps the dominant sex in a species is the more vigilant. Lewis (2005) found that female Verreaux's sifaka, also a female dominant species, were more likely to alarm call in the presence of a predator than were males. Nonetheless, male ring-tailed lemurs in this study did devote a similar percentage of time to anti-predator vigilance as did females, and it can be argued that they still contribute to group protection through their vigilance (Gould, 1996). We also suggest that males may serve as low-cost sentinels in the group, since females have priority of access to all resources (Sauther, 1993; Gould, 1996). Also, females may be more vigilant toward actual or potential predators in the birth and infant-rearing season and may relax their vigilance when offspring are not as vulnerable. Information on total vigilance by adult females and males at other times of the year would be useful toward determining if this is the case.

During this study the alpha females from both groups exhibited significantly more anti-predator vigilance than did other group members. In white-faced capuchins, alpha males are significantly more vigilant (Rose, 1994; Rose & Fedigan, 1995). Such heightened vigilance by these individuals has prompted Gould et al. (1997) to suggest that there may be certain behaviors that alpha animals engage in either more often or uniquely, and that these are characteristically found in any animal occupying the top rank in a group. For example, on one occasion when one of the study groups was drinking from standing water on the road just outside of the reserve, the alpha female stood guard, sometimes bipedally, while each group member that was on the road at the time drank. Thus, although the alpha female has priority of access to all resources in her group, which may

incur a cost to lower-ranking group members, she is providing a benefit to those animals through a high degree of vigilance.

The "Startle Response": An Innate Anti-Predator Strategy?

Researchers who have studied ring-tailed lemurs in both wild and semi-free-ranging captive situations have noted that, no matter how habituated, when groups are on the ground, any sudden or unfamiliar sound in the environment causes the animals scatter immediately. Usually the individuals jump into the nearest tree, where they will often remain for some time. Taylor (1986) has termed such behavior the "startle response," and it can occur even at the slightest sound, such as that made by a researcher stepping on a stick in the forest. Since this response is also found in animals in captivity, it could be innate and makes sense as an anti-predator strategy that has evolved in a relatively small primate that spends considerable time on the ground.

In summary, we can suggest several anti-predator strategies in ring-tailed lemurs:

(1) Ring-tailed lemurs exhibit heightened vigilance while foraging or engaging in other activities on the ground. (2) Larger groups may take more chances while foraging on both the ground and in new areas, as more animals are available to watch for predators in a larger group. Smaller groups may be more cohesive and exhibit heightened predator sensitive foraging, such as avoiding terrestrial food patches, a response that is beneficial with respect to avoiding predation, but can also incur a nutritional cost. (3) Smaller groups may form a mixed-species association with Verreaux's sifaka in geographic areas where they are sympatric and respond to each other's alarm calls. (4) Group members appear to be most vigilant toward actual predators during periods of high infant vulnerability, e.g., during and just after weaning. (5) Males provide a low-cost sentinel service, particularly during the lactation and infant-rearing season when offspring are most vulnerable, even though males are not significantly more vigilant than females during this period. (6) Alpha females may provide a high degree of vigilance in their female-philopatric groups, thereby enhancing survival of their own and their female relatives' offspring. (7) When ring-tailed lemurs are terrestrial they exhibit the "startle response" at the first sign of potential danger. This response is possibly an innate anti-predator behavior, which arose during the evolution of this relatively small, semi-terrestrial primate species.

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