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Antipredator Behavior in Troops of Free-Ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar

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Observations of antipredator behavior in two troops of free-ranging Lemur catta *were made during a 13-month study of* L. catta *feeding ecology. Both responses to and frequency of encounters with other species were recorded. Ringtailed lemur antipredator calls differentiated between terrestrial and avian predators. L. catta responded to the Madagascar harrier hawk (*Polyboroides radiatus*) and the Madagascar buzzard (*Buteo brachypterus*) in a specific manner that differed from their reaction to the other bird of prey in the reserve, the Black kite (*Milvus migrans*), and to potential mammalian and reptilian predators. Encounters with avian predators peaked during the birth season and when infants were being weaned. These periods coincide with previously observed nesting periods for the Harrier hawk and the buzzard, and with times when their offspring are fledged. Both were periods when* L. catta *infants might have been especially vulnerable to predation.*

KEY WORDS: Lemur; predation; vocalization; communication.

INTRODUCTION

While some level of representational signalling has now been described in the vocalizations of free-ranging anthropoid primates (*Cercopithecus aethiops:* Seyfarth, *et al.*, 1980; *Macaca mulatta:* Gouzoules, *et al.* 1984) there is little information regarding this phenomenon in prosimian vocalizations Macedonia, 1988; in prep.). The most readily apparent vocalizations in which such a relationship can be examined are anti-predator calls. Studies on vervet alarm calling (Seyfarth, *et al.*, 1980) have correlated specific responses

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(e.g., look to the sky, search the ground) to calls given only in the presence of particular classes of predators. Rare accounts of free-ranging lemur vocal responses to predators are brief, but suggestive (*Indri indri,* Pollock 1975; *Lemur fulvus fulvus,* Harrington, 1975; *Propithecus verrerauxi,* Jolly, 1966; Richard, 1978; *Lemur catta,* Jolly, 1966).

There is also the question of what role predation may play in regulating primate populations. Recent focus has been on how human encroachment, via hunting and habitat destruction, has limited or eliminated primate populations. In the absence of human influence, the role of predation on primates is often assumed to be minimal (e.g., Raemakers and Chivers, 1980; Wrangham, 1980).

Although good estimates of predation rates are best obtained by watching the predators (Rettig, 1978; Terborgh, 1983), it is impractical to do so in most field studies focusing on primate behavior. Alternatively, the behavior of the primates themselves toward other species provides important information on the range of potential predators and the frequency of encounters, as well as their vocal responses to such stimuli. Observations of antipredator behavior in *Lemur catta,* and the frequency of its occurrence at Beza Mahafaly Special Reserve are described here.

METHODS

Research was conducted at Beza Mahafaly Reserve, located 33 km east of Betioky in southwestern Madagascar. The reserve was established in 1978 and was granted special reserve status by the Malagasy Government in 1985. It contains a wealth of birds, mammals, reptiles and insects representative of southwestern Madagascar. Field research was carried out on troops of *Lemur catta* which ranged freely within parcelle #1, a 80 ha fenced and guarded portion of continuous forest. This parcelle is a deciduous and semideciduous riverine forest which becomes more xerophytic as one moves from the east to the west. In the east, it is dominated by *Tamarindus indica* which becomes codominant with *Salvadora augustifolia* and *Euphorbia tirucalli* in the west. This habitat is very seasonal, with a specific hot/wet season and a cool/dry season.

The 13-month study focused on inter-individual variability in the feeding ecology of two troops of *L. catta.* All the adult lemurs of these two troops are collared and tagged with unique numbers so that each is individually identifiable (Sussman, in prep). The focal animal sampling method was used, (Altmann, 1974), with data being entered directly into hand-held portable computers (Tandy 102, Tandy Corporation, Fort Worth, Texas). Observations were stored on 1½″ diskettes. An assistant and I followed two different adult focal animals for at least 7 hours per sampling day. Each focal

animal in both troops was observed once per month. Over 1800 hr of observations were collected. Troops were habituated to both observers allowing close range observations (1-2 m). During each sample day, all responses to other species encountered by the ringtailed lemurs were recorded as *ad libitum* notes. Samples of alarm vocalization were recorded using a Sony WM-D3 professional cassette tape recorder.

RESULTS

Responses To Predators

Human predation on lemurs does not occur at Beza Mahafaly Reserve because of the presence of guards and long-standing cultural taboos. However, there are a number of potential predators on *L. catta* and *Propithecus verreauxi,* the other diurnal lemur in the reserve (Table I). *L. catta* responded to predators with specific vocalizations, which were easily differentiated by ear (Table II). The "Click" (Andrew, 1963) and click series (Jolly, 1966) occurred when they were agitated by the presence of an uncertain stimulus. If one or two animals gave this vocalization, they were soon joined by other troop members, which responded by moving into the trees or bushes and by scanning the ground. These vocalizations and behaviors continued until the lemurs had visually located the disturbance. If the stimulus was an innocuous species, such as a tortoise or flock of sheep and/or goats (which

Table I. Predators and Non-predators That Elicit Vocalizations in *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar.

	Common Name	Vernacular Name[1]
Potential Predators		
Polyboroides radiatus	Madagascar harrier hawk	Fihiaka
Buteo brachypterus	Madagascar buzzard	Bemanana
Milvus migrans parasitus	Black kite	Papango
Cyrptoprocta ferox	Fossa	Fosa
Canis familiaris	Dog	Alika
Leioheterodon madagascariensis	Malagasy Giant Hognose Snake	Menarana
Felis sp.	Feral Cat	Piso
Non-predators		
Coracopsis vasa	Vasa Parrot	Boloky
Coua gigas	Ground Coua	Eoke
Numida meleagris	Helmeted Guinea-fowl	Akanga
Geochelone radiata	Radiated Tortoise	Sokaka
Potamochoerus larvatus	Forest Pig	Lambo
Ovis aries	Sheep	Ondry
Capra hircus	Goat	Osy

[1]Source: Richardson, J. (1885) A *New Malagasy-English Dictionary,* The London Missionary Society, Antananarivo.

Table II. Alarm Calls and Accompanying Behavior Exhibited by *Lemur catta* at Beza Mahafaly Special Reserve

Call	Intensity	Directed at	Accompanying Behavior
Click/Click Series	Low-level	All General Ground Disturbances	Enter Trees, Bushes, Visually Search Ground
Yap	High-level	Dogs, Fossa, Feral Cat, Unfamiliar Humans	Enter Trees, Bushes, Visually Search Ground, Low Trees and Bushes
Chirp and Moan	Low-level	Madagascar Harrier Hawk, Other Troops	Approach
Shriek	High-level	Madagascar Harrier Hawk, Madagascar Buzzard	Watch Predator

sometimes entered the reserve), the lemurs would either continue to click and watch the animal move away or move off themselves. They also emitted clicks in response to the presence of the Malagasy Giant Hognose Snake (*Leioheterodon madagascariensis*). If the stimulus was an unknown human, dog, cat or fossa, then clicking would escalate into emissions of "Yaps" (Jolly, 1966). The ringtailed lemurs yapped once at wild pigs which were noisily crashing through the underbush. *L. catta* were never observed yapping at snakes. Yapping animals would orient toward the disturbance; but they made no attempt to approach the stimulus. Yapping was interspersed with clicking so that at any one time, some animals were yapping while others were clicking. As with clicking, yapping by one individual stimulated others. If no disturbance was determined, the calls dissipated and the lemurs returned to their former activities.

A distinctive sequence of vocalizations and behaviors was elicited from *L. catta* by the Madagascar harrier hawk (*Polyboroides radiatus*) and the Madagascar buzzard (*Buteo brachypterus*). These raptors often appeared to be waiting in "ambush" for prey by perching in low trees (7–8 m.) and bushes (2–3 m.). They were normally encountered when the lemurs were travelling on the ground. In such cases, the ringtailed lemurs would rapidly approach the tree, in which the bird was perched, while "Chirping", (Macedonia in prep.), and "Moaning", (Andrews, 1963). Some lemurs even climbed trees near the bird. This "harassment" always resulted in the raptor flying off, at which time the ringtailed lemurs emitted "Shrieks" (Jolly, 1966), an extremely loud vocalization which could be heard clearly up to 500 m away. The lemurs also shrieked if either raptor flew near them. After the bird had flown away, troop males often scent-marked the trees in the immediate area; and, all animals engaged in allogrooming.

In comparison to *P. radiatus,* and *B. brachypterus,* the response of the ringtailed lemurs to Black kites (*M. migrans*) were quite different. These raptors frequently flew in large flocks and often soared over or landed en masse in a tree occupied by *L. catta.* The lemurs responded by jumping to the center

Table III. Percentages of shrieks directed at various disturbances by *Lemur catta* at Beza Mahafaly Special Reserve.

Disturbance	Proportion of Shrieks	
Raptors (*P. radiatus, and B. brachypterus)*	(*n* = 16)	85%
"Mistakes" (falling branch hook-billed vanga Vasa parrot)	(*n* = 3)	15%

of the tree and either waited for the kites to leave or eventually descended to the ground and silently moved into the bushes. During this time no vocalizations were emitted.

Although shrieks were primarily directed at Harrier hawks and buzzards, other exceptions were noted (Table III). In one case a juvenile responded with an abbreviated shriek when a hook-billed vanga, (*Vanga curvirostris*), guarding its nest, swooped at it. An adult female ringtailed lemur also gave an abbreviated shriek as a Vasa parrot (*Coracopsis vasa*) flew over the troop; and in one other instance, a young adult female shrieked and leaped backwards when a large branch fell by her. No other troop members shrieked which they normally do but instead, along with the agitated female, approached the branch and smelled it. Because harrier hawks occasionally and Madagascar buzzards normally capture prey on the ground by swooping down from above (pers. obs.; Pidgeon, pers. comm.; Brown and Amadon, 1968), this female may have interpreted the falling branch as one of these raptors.

Variability in other responses to potential predators also occurred. Three young adult females and one young adult male were seen, on numerous occasions, to "tail mark" while staring at a perched harrier hawk. Tail marking, an agonistic behavior, has been observed only in adult male *L. catta* (Jolly, 1966) and has not been previously noted in response to a potential predator. In tail marking, the animal sits or stands with the tail drawn between its legs and strokes caudally between the wrists. These three females often tail marked in response to mild annoyances such as buzzing flies and mosquitos. One young female was also observed giving a facial threat and a threat-yawn while staring at a perched Harrier hawk.

Table IV. Frequency of Diurnal Encounters Between *Lemur catta* and Potential Mammalian and Reptilian Predators at Beza Mahafaly Special Reserve

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	3	1	1	1	0	0	0	2	1	0	3

Felis sp. = 1
Leioheterodon madagascariensis = 2
Canis familiaris = 9
Cryptoprocta ferox = 1

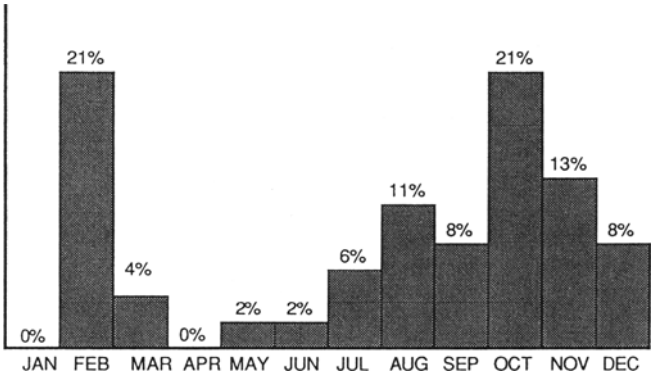

Fig. 1. Monthly proportions of encounters between *Lemur catta* and the Madagascar Harrier Hawk and Madagascar Buzzard at Beza Mahafaly Special Reserve, Madagascar.

Actual frequency of diurnal encounters with potential mammalian and reptilian predators was low, (n = 13) though there was at least one sighting for most months (Table IV). Frequency of encounters with avian predators was much higher (n = 48), with the number of encounters peaking in October and again in February (Fig. 1).

Inter- and Intra-specific Responses to Alarm Calls

Verreaux's sifaka (*Propithecus verreauxi*), the second large diurnal lemur at Beza Mahafaly, often rested or fed in trees near troops of *L. catta*. During one third of these associations ringtailed lemurs or sifakas responded to each otner's alarm calls (Fig. 2). *L. catta* reacted to the sifaka's roaring bark (Jolly, 1966) by clicking and rapidly moving to the center of the tree. Another response was to look skyward. Sifakas reacted to ringtailed lemur shrieks by roaring. *L. catta* responded to alarm calls of Ground coua (*Coua gigas*) and the Helmeted Guinea fowl (*Numida meleagris*) by clicking and either moving into the trees, if on the ground, or toward the center of a tree. Ringtailed lemurs responded to shrieks from nearby troops of *L. catta* by looking skyward.

DISCUSSION

The Semantics of *Lemur catta* Antipredator Responses

Representational signalling in nonhuman primates has been suggested for vervets; (Seyfarth *et al.*, 1980), rhesus macaques; (Gouzoules *et al.*, 1984)

pig-tailed macaques, (Gouzoules and Gouzoules, 1989) toque macaques (Dittus, 1984); and spider monkeys (Masataka, 1986). Likewise, *L. catta* at Beza Mahafaly were able to distinguish between potential predators. Avian predators evoked an entirely different repertoire of vocalizations and behaviors from those evoked by mammalian and reptilian predators. Intensity of response also varied, depending on the presumed threat of the stimulus, e.g. clicking at tortoises but yapping at dogs. Recent experimental work by Macedonia (1988; in prep.) also indicates that representational signalling is present in ringtailed lemur alarm calls; but may be absent in the alarm calls of some other lemur species.

Owings and Hennessy suggested that alarm calls may serve to alert troop members to ground or aerial disturbance due to the time constraints associated with those predators instead of predator types *per se*. At Beza, clicks were given to many types of disturbances; and, were also used during agonistic encounters with other troops. However, Yapping was directed almost exclusively at potentially threatening mammalian predators. Likewise, while chirps and moans were also emitted before intertroop encounters, the approach and shriek sequence of behaviors was directed only at avian predators, specifically the Madagascar Harrier hawk and the Madagascar buzzard.

Study of the ontogeny of vervet alarm calling behavior (Seyfarth and Cheney, 1980; Seyfarth and Cheney, 1986) indicate that "mistakes" in responding to stimuli (e.g., giving an eagle alarm call in response to a falling leaf) occur most often among immatures. Observations of ringtailed lemur responses to potential predators at Beza revealed a similar pattern. Only young animals responded to innocuous species such as tortoises; and, the only observed incident of yapping at an avian predator involved two juveniles. Two of the three mistakes in use of the shriek also involved younger animals. Mistakes by older individuals were more rare at Beza, with a single observed occurrence of an adult female shrieking at a flying Vasa parrot. At Berenty, a private reserve which contains a number of lemur species, Black Kites and Pied crows (*Corvus albus*) are the two birds most often mistaken for Harrier hawks or buzzards by ringtailed lemurs, though the age of the responders is not known in these cases (Pidgeon, pers. comm.).

Potential Predators at Beza

Several factors suggest that the Madagascar harrier hawk and the Madagascar buzzard may be perceived as greater immediate threats to ringtailed lemurs than Black kites are. The presence of perched harrier hawks or Madagascar buzzards always invoked a very intense pattern of reactions from the lemurs which seemed to enable the entire troop to quickly locate the raptor. Calls by perched harrier hawks also initiated searching behaviors by the lemurs, which then visually established the hawk's position. The

response to large flocks of Black kites was either to move to the center of the tree and wait until the birds flew off or to retreat silently, Calls by Black kites never elicited specific behaviors in the ringtailed lemurs during the study period.

The Black kite is reported to be unable to kill any mammal larger than a rat (Brown and Amadon, 1968), which would limit them to preying on newborn lemur infants. Black kite pellets, which have been examined at Berenty, largely contained invertebrate remains such as beetles, grasshoppers, and locusts (Pidgeon, unpublished data). Black kites are also scavengers, often attacting other carrion eaters to a carcass (Brown and Amadon, 1968).

Ringtailed lemurs at Beza can best be described as "semi-terrestrial," (Sauther, in prep.); nearly all their travel is done on the ground. Because they are so terrestrial, *L. catta* may be especially vulnerable to predation by harrier hawks and buzzards. The Madagascar harrier hawk, which is endemic to Madagascar (Dee, 1986), is a large raptor, 60–62 cm in length, (Milon, *et al.,* 1973) and is unable to move easily in closed environments such as closed canopy forests (pers. obs.). Observations of the behavior of the harrier hawk at Beza suggests that it may favor more open environments where terrestrial prey may be attacked from above. These hawks were commonly observed in fields; they preyed on chickens in open areas of local villages by swooping from above (pers. obs.). All encounters with the harrier hawk occurred in more open terrain such as meadows or clearings, with the hawk perched in a dead standing tree, and the ringtailed lemurs either travelling on the ground or foraging in low bushes. This raptor is a confirmed predator on *L. catta,* with the predation of a live infant ringtailed lemur occurring on the grounds (Ratsirarson, 1985). The Madagascar buzzard is a slightly smaller raptor, 48–51 cm (Milon, *et al.,* 1973); and, it is more adept at maneuvering in closed environments than the harrier hawk (Pidgeon, pers. comm.). It is also commonly found perched in trees and takes all its prey on the ground either from the air or from a stationary perch (Brown and Amadon, 1968). At Beza, these hawks were encountered in closed canopy forest. At Berenty, buzzards have been observed to swoop at ringtailed lemur troops containing infants (Jolly, pers. comm.).

It is pertinent to note that there were two peaks of encoutners with harrier hawks and buzzards, (Fig. 1). The first of these was in October, which was also the peak of the birth season of *L. catta* at Beza. Young *L. catta* are very precocial and actively move about the mother soon after birth. Between the second and third week of life, infants beging environmental exploration, such as hopping off their mothers and climbing independently (Gould, in press). During October, when temperatures can reach 35°*C, L. catta* spend much of their time resting on the ground at the bases of trees. On more than one of these occasions a sudden disturbance resulted in all

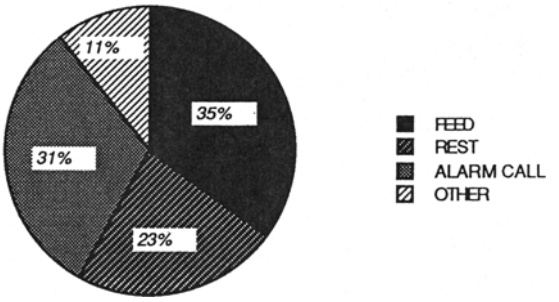

Fig. 2. Context of associations between *Lemur catta* and *Propithecus verreauxi* at Beza Mahafaly Special Reserve, Madagascar.

the mothers leaping into the tree, leaving their infants loudly calling on the ground. Thus, October may be a time of high vulnerability for infant ringtailed lemurs. This period also coincides with the nesting season of both harrier hawks and buzzards at Berenty and Beza (Pidgeon, unpublished data). During this time an increased food supply is necessary for their egg-laying and incubation. The second peak of encounters with avian predators was in February. By this time, infants were still small but were nearly weaned and spent most of their time off their mothers. Danger from avian predation, especially during terrestrial travel along open trails, meadows, and open canopy forest may have been even greater during this period because the infants were moving independently of their mothers. At this time, harrier hawk and buzzard chicks are fledged and still require feeding until they leave the nest (Pidgeon, unpublished data). Peaks in encounters with avian predators thus occur at a time when ringtailed infants may be more vulnerable to predation, and when these predators may be more inclined to seek out such prey.

While the frequency of encounters with potential mammalian predators was low, observations of the remains of adult ringtailed lemurs showed signs of predation by mammalian predators (e.g., puncture wounds at the back of the skull). The fossa (Albignac, 1984) and presumably feral cats kill prey in this manner. It is not surprising that few of these predators were encountered during the day because both fossa (Albignac, 1984) and feral cats (pers. obs.) are crepuscular and nocturnal hunters. Ringtailed lemurs can be active after dark (Jolly 1966); and, yapping by *L. catta* was often heard at night, suggesting the presence of some disturbance. Nocturnal yapping toward a cat by a ringtailed lemur troop at Berenty is reported by Jolly (1966). The most frequent diurnal encounters with potential mammalian predators were with dogs; and, one carcass of a freshly dead *Propithecus verreauxi* showed bite wounds at the base of the spine, which indicates a large mam-

malian carnivore. To summarize, it is possible that avian predators are primarily a threat to young animals, especially infants, while the mammalian predators pose a threat to both infant and adult lemurs.

CONCLUSION

It has been proposed that predation pressure on large Malagasy primates is low because there are no large carnivores (van Schaik and van Hooff, 1983). This largely ignores the impact of predators on vulnerable classes such as infants. Because all of the Malagasy primates are seasonal breeders (Tattersall, 1982), and all diurnal lemurs (excluding *Varecia variegata*) normally have only one infant per birth in the wild, (Shively and Mitchell, 1986) even low-level predation can be expected to have an important effect on demography. Certain types of avian predation (diurnal, hunting by sight) provide one explanation for the existence of social groups in diurnal lemur species and the absence of such groups in nocturnal lemur species (Terborgh, 1983). Alexander (1974) originally suggested that predation pressure is the primary factor which could select for group living in primates. Since then, Van Schaik and Van Hoof (1983) and Terborgh (1983; Terborgh and Janson, 1986) independentally proposed the Optimal Group Size model, which states that optimal group size in primates is a balance between predator pressure and feeding competition. A number of recent studies on anthropoid primates provide some evidence for this (van Shaik, 1983; van Shaik, *et al.* 1983a; van Shaik *et al.*, 1983b; de Ruiter, 1986; but see Wrangham, 1980, 1983, Cheney and Wrangham, 1986); and, similar factors may affect group size in the diurnal Malagasy lemurs. The recent focus on habitat destruction as a potential cause of the extinction of lemurs is important from a conservation standpoint; but it has tended to de-emphasize investigation of the factors which regulate lemur populations in the wild and may, indeed, have obscured the importance of predation. To give a more complete picture, complementary research on the feeding ecology of the Malagasy raptors is needed.

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