

## ADAPTATION AND PHYLOGENETIC CONSTRAINTS IN THE ANTIPREDATOR BEHAVIOR OF RINGTAILED AND RUFFED LEMURS

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### ABSTRACT

The antipredator responses of forest-living ringtailed (*Lemur catta*) and ruffed (*Varecia variegata*) lemurs were documented over a three-year period at the Duke University Primate Center (DUPC, Durham, NC, USA). Vocal and nonvocal responses to naturally-occurring and simulated predators are described, and their functions are considered with respect to species-specific differences in body size, ecology, and reproductive biology. Nonvocal responses of the two lemur species differed most conspicuously in propensity of predator-directed aggression: whereas ringtailed lemurs generally evaded predators, ruffed lemurs were likely to confront or attack them. Interspecific variation in vocal responses to predators included differences in call diversity, stimulus specificity, and function. Ringtailed lemur antipredator behavior (including large group size) is viewed as an adaptation to nontrivial levels of predator pressure that stem from being a relatively small-bodied, semi-terrestrial primate living in an open habitat. In contrast, the highly aggressive antipredator behavior of the ruffed lemur is seen in part as an effect of a somewhat larger body size, but also as a constraint of producing sessile offspring that do not cling to the mother. Thus, in contrast to ringtailed lemurs, ruffed lemurs with infants cannot flee predators without risking their reproductive success.

### INTRODUCTION

#### Effects of Predation on Primate Behavior

Avoiding predation has been argued to have had a profound impact on the evolution of social organization in primates (Alexander, 1974; van Schaik, 1983; van Schaik and van Hooft, 1983; van Schaik et al., 1983; Terborgh, 1983; Struhsaker and Leakey, 1990). Yet, the evidence available for predation on primates remains limited (see Cheney and Wrangham, 1987, for a review). Due to the swiftness with which predation typically occurs, the probability of observing a kill by chance is extremely low (Terborgh and Janson, 1986). Direct evidence of

predation is available in other forms, however, such as bones, teeth, and hair that can be matched to a prey species (Struhsaker and Leakey, 1990; Goodman et al., 1993). The veracity of predation on prey populations can be assessed indirectly as well. Just as astronomers and physicists identify the presence of forces that cannot be observed directly, but which are inferred from the behavior of the bodies they influence, stereotyped antipredator behavior serves as indirect yet compelling evidence that predation pressure has had a significant influence during a prey species' recent evolutionary past (Cheney and Wrangham, 1987).

Large group size in diurnal primates is one factor that has been argued to afford increased protection from predation due to there being "more eyes and ears" available for detecting the presence of predators (see Terborgh and Janson, 1986; Cheney and Wrangham, 1987, for reviews). For example, van Schaik et al. (1983) demonstrated in long-tailed macaques (*Macaca fascicularis*) that larger groups detected approaching observers at significantly greater distances than did smaller groups (though see Isbell, 1990). In another study, van Schaik and van Noordwijk (1988) found that long-tailed macaques lived in larger groups on Sumatra, where large felid predators include the tiger (*Panthera tigris*) and the arboreal clouded leopard (*Neofelis nebulosa*), than on the offshore island of Simeulue, where no felids occur. Thus, modulating group size appears to be one way that primates cope with the threat of predation.

Many species of birds and mammals, including primates, emit vocalizations in response to predators. In general, antipredator vocalizations (or, 'alarm calls') fall into one of three functional categories (see Klump and Shalter, 1984; Hasson, 1991 for reviews). *Alerting/Warning Calls* function to inform conspecifics of a predator's presence while minimizing their detection by the predator. *Mobbing Calls* are emitted during predator harassment. These vocalizations are predator-directed, repetitive, and solicit aggregation of the prey near the predator. *Perception Advertisement Calls* also are predator-directed, but unlike mobbing calls they do not function in predator harassment. These calls neither are repetitive in the absence of stimulation from the predator, nor do prey congregate near the predator during call emission. Rather, they serve to inform predators that they have been detected by the intended prey, thus causing some predators to abort the hunt.

Most primate species will mob mammalian predators, and some larger primates escalate to the point of direct combat with these carnivores. Baboons, for example, are known to kill domestic dogs, mob and chase cheetahs and jackals, and even fight to the death with leopards and lions (see Cheney and Wrangham, 1987). Primates characteristically mob perched raptors, though harassing truly large raptors usually is restricted to adult males in most monkeys. Eason (1989), for example, observed a cautious, yet determined, adult male red howler (*Alouatta seniculus*) physically harassing a Harpy eagle (*Harpia harpyja*), the largest living raptor. Even 6-8kg adult male howlers are not immune to harpy eagle predation, however (Sherman, 1991).

Among the five primate species described in an interaction with a crowned hawk-eagle (*Stephanoetus coronatus*), only adult males of the two largest species (white-nosed guenon: *Cercopithecus nictitans*; gray-cheeked mangabey: *Cercocebus albigena*) participated in chasing the eagle (Gautier-Hion and Tutin, 1989). As in the previous example, there is evidence that such behavior increases the vulnerability of these individuals to eagle predation (Struhsaker and Leakey, 1990).

Snake mobbing has been documented for several primate species, where individuals congregate around a snake and emit aggressive vocalizations (Heymann, 1987; Bartecki and Heymann, 1987; van Schaik and Mitrasetia, 1990). In addition, individuals sometimes will drop or throw branches at snakes (Chapman, 1986; van Schaik and van Noordwijk, 1989), and in one case an adult male used a branch to club a snake repeatedly (Boinski, 1988).

A few species employ antipredator tactics that are unusual for primates. When confronted by a snake in trees, pottos (*Perodicticus potto*) have been observed to drop to the ground, run a short distance and then freeze as if feigning death (Charles-Dominique, 1977). Although well-known for birds, 'predator

distraction displays' (Armstrong, 1949) also seem to be very rare in primates. Hall (1965) proposed, however, that a predator distraction display best characterized the behavior of adult male patas monkeys (*Erythrocebus patas*) when dealing with certain predators. In sum, primates are not defenseless against predators, and they employ a variety of techniques to avoid predation.

### Evidence for Predation on Malagasy Lemurs

With land-hunting eagles (cf. fish eagles) being absent from Madagascar, and there being no truly large carnivores (such as leopards) on the island, predation on lemurs often is considered to have been negligible during the evolution of these primates (van Schaik and van Hooff, 1983). While it is true that there are only a few diurnal raptor species and a single type of carnivore (*Cryptoprocta ferox*) that are large enough to take adult lemurids as prey, predation on infants alone could have significant demographic effects on lemur populations (Sauther, 1989). Given that some lemur species produce only a single infant per year, and that sickness and lethal injuries take their toll of young, the loss of a progeny merely once or twice in a female's lifetime could dramatically reduce her reproductive success. Likewise, predator diversity is not necessarily a good indicator of predator pressure. Despite the fact that the leopard is the only East African carnivore whose preferred prey seems to include vervets, leopards have been responsible for more deaths of healthy vervets in Amboseli (during the years for which predation has been documented there by primatologists) than any other single cause (Cheney and Wrangham, 1987; Isbell, 1990). The compilation of information presented by Goodman et al. (1993), including the recent discovery of a large extinct Malagasy eagle (Goodman, in press), throws new light on the issue of predation on lemurs. It likewise helps to resolve the seemingly curious existence of formalized antipredator behavior in these primates - a phenomenon whose evolution would defy explanation had predation pressure actually been as trivial as has generally been claimed.

Below I describe the antipredator behavior of semi-captive, forest-living ringtailed (*Lemur catta*) and ruffed (*Varecia variegata*) lemurs. The responses of these lemurs to naturally-occurring and simulated predators are compared to those of free-ranging conspecifics, and species-specific antipredator tactics are viewed in terms of body size, ecology, and reproductive biology. By comparing these prosimians with anthropoids of similar physical and ecological characteristics, some insight into the evolutionary forces underlying primate antipredator behavior may be gained.

### MATERIALS AND METHODS

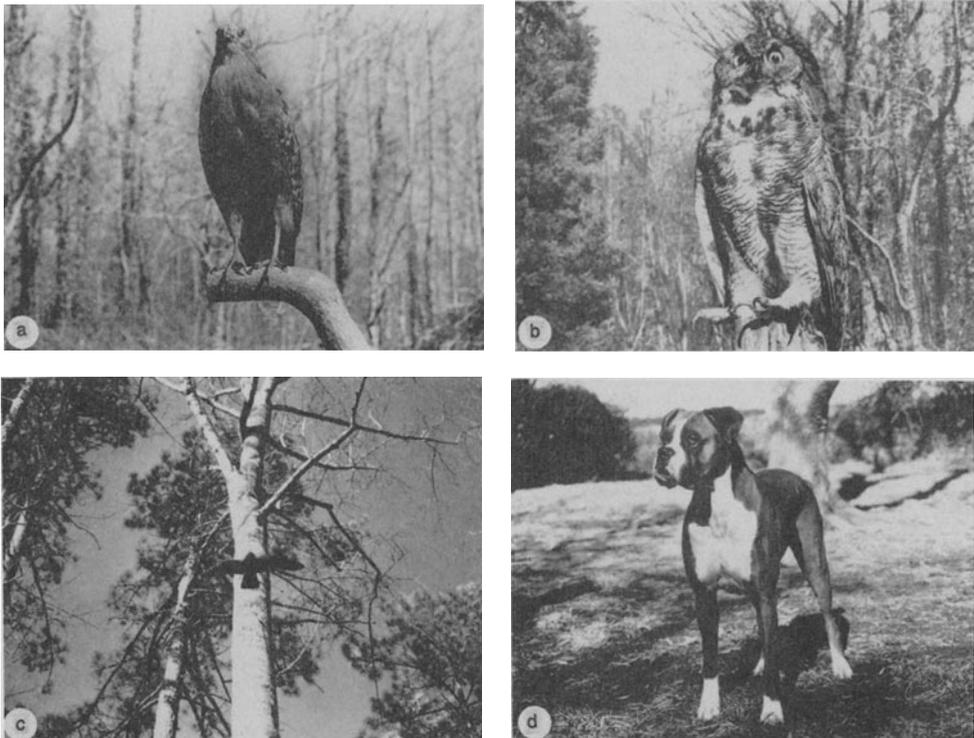
Antipredator behavior was documented in a group of ringtailed lemurs (*Lemur catta*, Lc1 Group) and a group of black-and-white ruffed lemurs (*Varecia variegata variegata*, Vv1 Group) between May 1986 and July 1989 at the Duke University Primate Center (DUPC, Durham, NC). These lemur groups lived year-round in a 3.5ha natural habitat enclosure (NHE-2) composed of mixed pine/hardwood forest surrounded by a mildly electrified fence. The groups were provisioned daily with monkey chow and twice per week with mixed cut fruit, but the lemurs spent much time foraging on local flora. All lemurs in the NHE's wore individually-identifiable collars and tags, excluding young infants who were identified by patterns of tail shaves. Adult (>3 yrs of age) ringtailed lemurs weighed roughly 2kg; adult ruffed lemurs weighed approximately 3.5kg (Kappeler, 1991). (For details of the study site, lemur group histories, and recording/analysis equipment, see Macedonia, 1990).

Observations of responses to naturally-occurring predators were recorded opportunistically. Raptors (e.g., red-tailed hawk: *Buteo jamaicensis*; red-shouldered hawk: *Buteo lineatus*; great-horned owl: *Bubo virginianus*), carnivores (gray fox: *Urocyon cinereoargenteus*; raccoon: *Procyon lotor*; weasle: *Mustela* sp.), venomous snakes (copperhead: *Agkistrodon contortrix*; cottonmouth: *Agkistrodon piscivorus*),

and a nonvenomous, semi-arboreal constrictor that could be dangerous to young infants (black rat snake: *Elaphe obsoleta*) inhabited or frequented the enclosures. By June 1992, a number of lemurs had been killed by these predators: 1 young adult female ringtailed lemur by a gray fox, 5 infant ringtailed lemurs by a great-horned owl, 1 infant and 1 young adult male ringtailed lemur by a copperhead, and 2 ruffed lemur newborns by a weasle. Whereas no lemur at the DUPC had been killed by a diurnal raptor, red-tailed hawks attack small mammals in the natural habitat enclosures (pers. obs.) and are capable of taking prey up to the size and weight of adult *L. catta* (e.g., jackrabbits, *Lepus californicus*; pers. obs.).

Because observations of responses to naturally-occurring predators were relatively rare (see Macedonia and Polak, 1989; Macedonia and Evans, in press), predator models were presented to Lc1 and Vv1 Groups to augment acquisition of opportunistic data. To observe responses to perched raptors, a museum specimen of a perched red-shouldered hawk (Fig. 1a) or great-horned owl (Fig. 1b) was placed along one of the paths routinely taken by the lemurs. Four presentations were conducted, one for each lemur species with each specimen. To document responses to attacking raptors, on two occasions a plywood raptor shape was hung on a guide wire and flown at the lemurs in a simulated 'stoop' (Fig. 1c).

Two presentations of a large carnivore (27kg dog; Fig. 1d) were conducted. For the 'low urgency' presentation, the dog was walked slowly toward the lemurs from a distance of roughly 50m. For the 'high urgency' presentation, the (tethered) dog was permitted to ambush the lemurs from behind a blind (see Pereira and Macedonia, 1991, for details).



**Figure 1.** (a) Perched specimen of red-shouldered hawk (*Buteo lineatus*); (b) perched specimen of great-horned owl (*Bubo virginianus*); (c) raptor model on test apparatus; (d) dog used as mammalian predator.

**Table 1. Ringtailed and Ruffed Lemur Vocalizations Emitted in the Predator Context.**

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**a. Ringtailed Lemur**

<b>Vocalization</b>	<b>Context and/or Function</b>
Gulp	general context group alert call (Fig. 2a)
Rasp	conspecific-directed raptor alarm call (Fig. 2b-d)
Shriek	predator-directed antiraptor call (Fig. 2f-h)
Chirp	elicits, and may mediate, rapid group relocation (Fig. 2i)
Plosive Bark	high-intensity threat vocalization (Fig. 2j)
Click	'location marker' in response to low/moderate arousal disturbances (Fig. 2k)
Closed-Mouth Click Series	mammalian disturbance; also during rapid locomotion, particularly arboreal; location marker in response to moderate/high arousal disturbances (Fig. 2k)
Open-Mouth Click Series	location marker in response to high arousal disturbances; may aid in synchronization of Yaps (Fig. 2k)
Yap	mammalian predator 'mobbing call' (Fig. 2k)
Howl	individual/group 'advertisement call', emitted in series' by males (Fig. 2l)

**b. Ruffed Lemur**

<b>Vocalization</b>	<b>Context and/or Function</b>
Abrupt Roar	avian predator mobbing call; also emitted in some other contexts of high-level aggression (Fig. 4a)
Roar/Shriek Chorus	group advertisement call (Fig. 4b)
Growl-Snort	location marker in high arousal disturbances (Fig. 4c)
Growl	location marker in low/moderate arousal disturbances (Fig. 4d)
Pulsed Squawk	mammalian predator mobbing call; may signal high-urgency desire for group reaggregation (Fig. 4e)
Wail	'all clear' call in antipredator contexts; may signal low-urgency desire for group reaggregation (Fig. 4g)

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## RESULTS

### Responses of Ringtailed Lemurs to Avian Predators

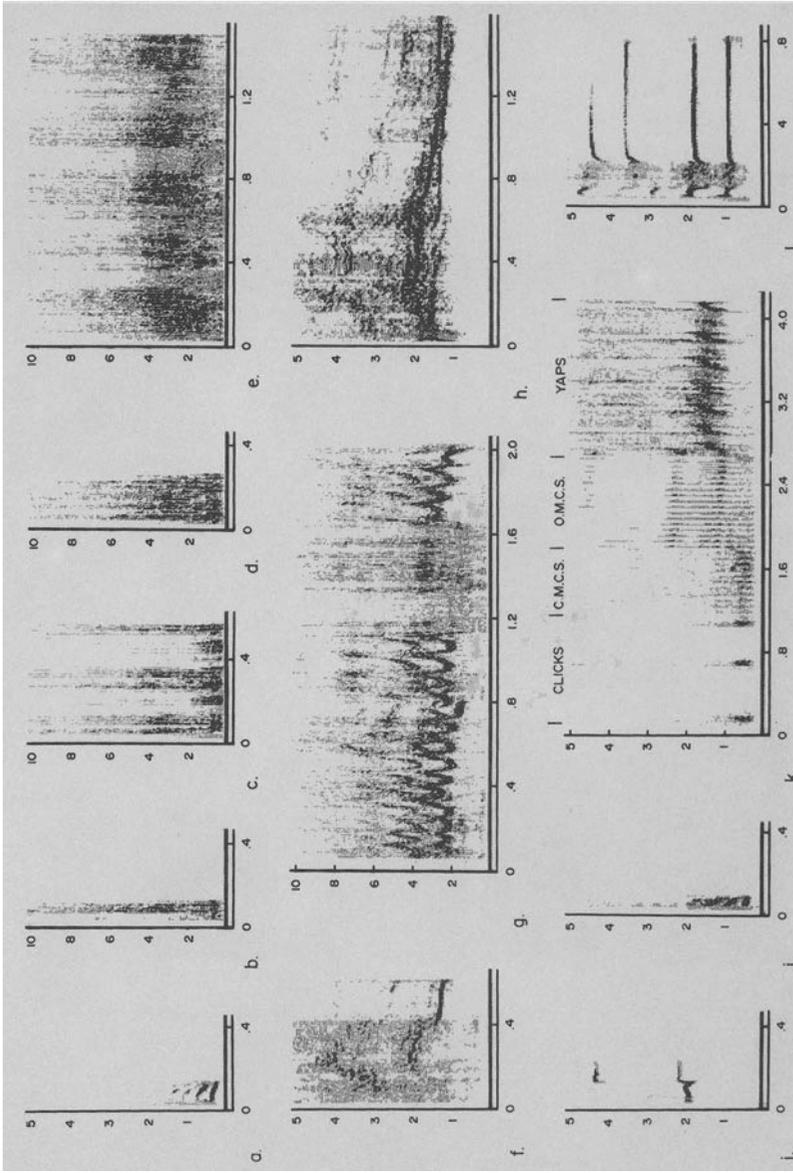
**Natural Encounters.** The initial response to the sight of large hawks or to their calls was to emit one or more kinds of vocalizations (Table 1). 'Gulps' (Fig. 2a) typically were given first, and were elicited in other contexts by any kind of startling stimulus (e.g., loud or unusual sounds, sudden movements). In the case of airborne birds, if an antiraptor call (see below) was not forthcoming, gulps often continued to be issued until the bird passed from view. Individuals responded to gulps by looking quickly toward the caller while becoming poised for locomotion. This response presumably allows individuals to track the direction of the caller's gaze and to observe the caller's reaction to the eliciting stimulus. The low emission amplitude and very broad range of eliciting stimuli suggest that the gulp functions as a generalized alerting/warning call.

'Rasps' (Fig. 2b-d), were given by one or several individuals when a large aerially-approaching bird reached a proximity to the group where its identity (apparently) could be ascertained as a potential threat. Although gulps usually preceded rasps, gulps sometimes were foregone when raptors appeared suddenly. For example, on one occasion a pair of red-tailed hawks appeared just above the tree tops in NHE-2 grappling with their talons in courtship. The first Lc1 Group member to vocalize emitted a brief rasp (Fig. 2b). The courting hawks, now below the canopy, then turned in the direction of the lemur group. The same caller responded again, this time with three consecutive brief rasps (Fig. 2c), followed approximately two seconds later with a long rasp (Fig. 2d).

When raptors were detected at some distance from the group (including high-altitudes directly overhead), usually only one or two rasps were uttered. Very distant raptors elicited, at most, gulps. In contrast, raptors suddenly appearing close to the group elicited a flurry of rasps and rasp-shriek intermediates (Fig. 2e; see below) from numerous individuals as they ran for cover. The rasp's broadband acoustic structure, its low-to-moderate amplitude, and its restriction as a vocal response to large aerial stimuli (Macedonia and Polack, 1989), suggests that this call functions as an alerting/warning call specific for aerial predators.

A third vocalization elicited by large avian stimuli was the 'shriek' (Andrew, 1963; Fig. 2f). Unlike gulps and rasps, shrieks were emitted at very high amplitudes (Sauther, 1989; Macedonia, 1990). Shrieks sometimes were emitted in synchrony (Fig. 2g) in cases where group members had been aware of a raptor's presence for some time (e.g., > 5s). For example, on one occasion the members of Lc1 Group were feeding on items in the leaf litter, or were grooming or sitting quietly. One individual began to emit gulps as it stared skyward. In the distance was a large soaring bird, about five meters above the treetops, that was moving on a trajectory toward the group. About ten seconds later, when the bird (a red-tailed hawk) was almost directly overhead, single brief rasps were emitted by two unidentified individuals. Before the second rasp had terminated, the group erupted in a synchronous shriek, during which time group members stared skyward toward the soaring hawk. All individuals remained still and appeared calm throughout the entire event, and continued to track the flight of the hawk until it disappeared from view before resuming prior activities. The restriction of this call as a response to large avian stimuli, its high amplitude level, and the demeanor of individuals emitting it suggests that the shriek functions as a perception advertisement call specific to aerial predators.

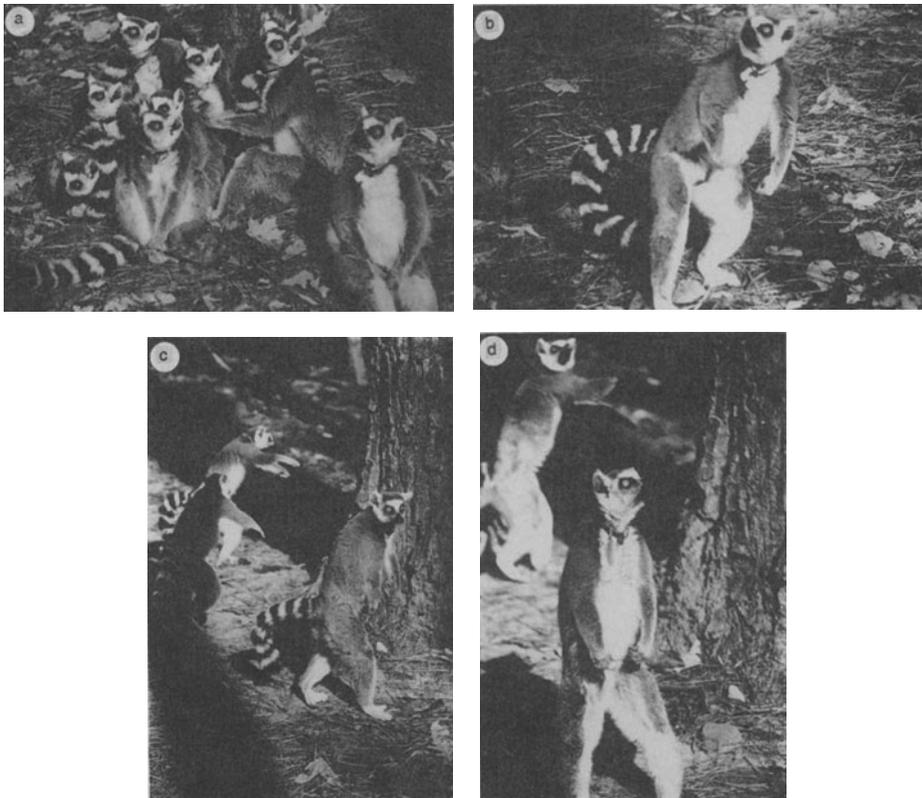
If Lc1 Group was on the ground when detecting a raptor whose proximity seemed potentially threatening, the group often proceeded quickly to a new location (usually one with increased overhead cover). Hurried group relocation always was accompanied by the emission of 'chirps' (Table 1; Fig. 2h) from most group members. If in trees when a raptor was seen or heard, the ringtailed lemurs moved from the peripheral branches toward the trunk. Often, this was followed by the group climbing down to the ground and moving to a new location.



TIME IN SECS

**Figure 2.** Antipredator calls and related vocalizations of the ringtailed lemur (*Lemur catta*): (a) gulp; (b) chort rasp; (c) three consecutive rasps; (d) long rasp; (e) five rasp/shriek intermediates; (f) typical shriek (Type I); (g) multiply-frequency-modulated shriek (Type II); (h) group synchronous shriek; (i) chirp; (j) plosive bark; (k) anticarnivore call series: click, closed-mouth click series, open-mouth click series, yaps; (l) howl.

A peculiar behavior sometimes exhibited by Lc1 Group in the context of avian predators was 'bipedal locomotion' (Fig. 3a-d). When a large hawk was sighted or its call heard, a number of individuals would assume a bipedal stance before walking or trotting bipedally away from the area (Macedonia and Yount, 1991; Pereira and Macedonia, 1991). This behavior has not been reported for *L. catta* in Madagascar (Jolly, 1966; Sauther, 1989) nor did it occur in other lemur species at the DUPC. Bipedal locomotion in response to raptors seems to be a culturally-propagated phenomenon unique to the DUPC forest-living ringtails.



**Figure 3.** Several Lc1 Group members when (a) sighting a soaring raptor overhead, (b) standing bipedally, then (c-d) locomoting bipedally away from the area.

The responses of infant ringtailed lemurs to the antipredator calls of conspecific adults also deserve mention. The emission of gulps by any group member would cause mothers and infants (that were not in close proximity) to begin searching for one another. Young infants gave 'infant contact calls' (Macedonia, in press) at this time, followed with running to and leaping onto their mothers' backs, once they located them. If the gulps had been elicited by a visible carnivore, young infants did not climb into trees along with adults and older immatures, but waited for their mothers to retrieve them. By the age of three

months, however, infants first would leap into trees and then begin trying to locate their mothers. On several occasions a stereotyped response to antiraptor calls was observed in young infants (about 4-8 wks of age) that were clambering about in saplings or on sturdy ground vegetation at a height of 1-2m. These infants responded to rasps or shrieks by immediately letting go of the branches and dropping to the ground (pers. obs.; M. Pereira, pers. comm.). Once on the ground, the infants remained motionless while calling for retrieval.

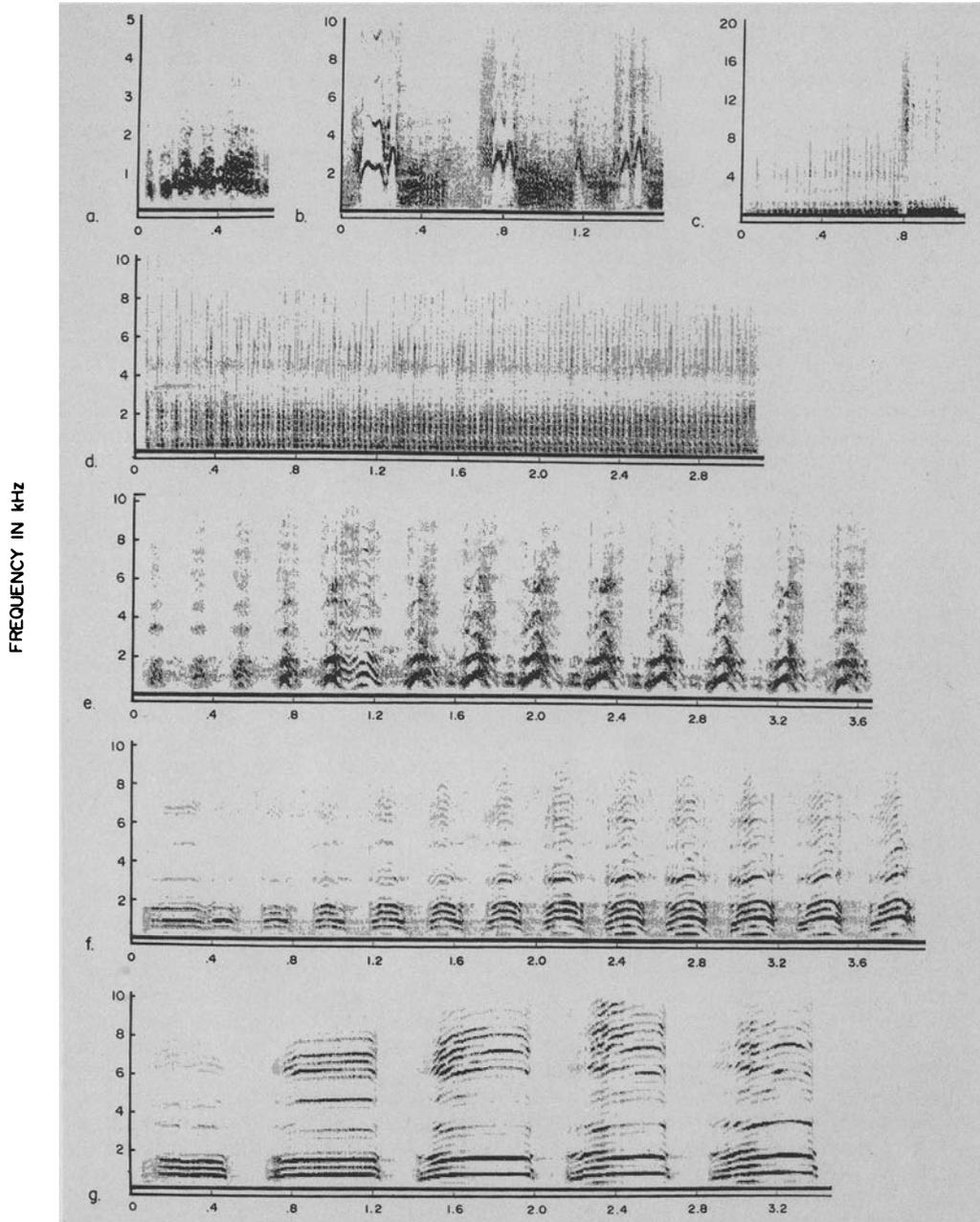
**Experimental Manipulations.** Responses to the two presentations of the 'stooping hawk' model were similar in all important respects. In the first presentation, numerous rasps and Type II shrieks (Fig. 2g) were emitted upon its release. One adult female stood bipedally and shrieked directly toward the descending model, and an unidentified immature was observed pushing itself underneath an adult. Other individuals crouched close to the ground and rasped loudly before running for cover. As Lc1 Group scattered, chirping began. Several individuals trotted and hopped bipedally away from the test site. Though many group members ran rapidly from the immediate area, some individuals looked back toward the apparatus, after having taken positions behind tree trunks, and emitted plosive barks (Fig. 2i). A few subjects leapt a short distance up tree trunks while clinging to the trees' far sides, but did not move up to the level of the lowest branches. Chirping reached choral proportions as the lemurs regrouped some distance away, continuing to move rapidly on the ground away from the test site.

During presentations of the perched raptor specimens to Lc1 Group, subjects emitted plosive barks toward the birds as a threat. Typically, several group members (often adolescent and adult males) would approach cautiously to within 1-2m of the raptors and lunge toward them, without making contact, while emitting plosive barks. Each time a plosive bark was uttered in this context, many of the more timid individuals, some 5-15m distant, would begin to emit chirps and move further away, sometimes bipedally. Numerous males engaging in this threat behavior, as well as those that remained at a distance, were observed rubbing their tails with scent secretions (see also Sauther, 1989). In nonpredator contexts, male tail-rubbing precedes tail-waving in an assertive display (Jolly, 1966; Evans and Goy, 1968; Schilling, 1979). Elsewhere, plosive barks were emitted most often by young infants (frequently from their mother's backs) to threaten closely-approaching adult conspecifics and humans.

### **Responses of Ruffed Lemurs to Avian Predators**

**Natural Encounters.** Whenever large hawks were seen or heard nearby, ruffed lemurs responded vocally with 'abrupt roars' (Fig. 4a). These are high-amplitude, noisy calls (Macedonia, 1990) that appear to serve as threat signals. The equally powerful 'roar/shriek chorus' (Fig. 4b), an extended series of roars and shrieking sounds that appears to function as a group advertisement call (Pereira et al., 1988), often was mixed with abrupt roars at the outset of calling. Abrupt roars were used as hawk mobbing calls, and continued to be produced at irregular intervals long after the eliciting stimulus had disappeared from view. Once high-arousal levels began to subside, bouts of abrupt roars were punctuated with 'wails' (Fig. 4g). In this context, wails seemed to serve an 'all clear' function (Pereira et al., 1988). The duration of wail emissions (from less than a minute to more than 45min) appeared to reflect the level of arousal reached in response to a given predator.

If on the ground when an airborne raptor was detected, ruffed lemurs typically emitted explosive rounds of abrupt roars while assuming a posture in which the head was held low, the back arched, and the shoulders hunched. Nearby group members, unaware of the location of the stimulus, exhibited a 'scan-and-roar' behavior (Macedonia, 1990). This consists of turning the body sharply about the horizontal plane in short jumps of roughly 45 to 90 degree arcs (often in alternating directions), while producing one or more abrupt roars during each shift in position. When engaged in this behavior, individuals appeared as if they were attempting



**Figure 4.** Antipredator calls and related vocalizations of the black-and-white ruffed lemur (*Varecia variegata variegata*): (a) abrupt roar; (b) roar/shriek chorus; (c) growl-snort; (d) growl; (e) pulsed squawk; (f) pulsed squawk-wail intermediate; (g) wail.

to confront an unseen threatening stimulus from whichever direction it might be approaching. Foot movement was more restricted when exhibiting this response in trees. Occasionally, airborne raptors also were 'pursued' by ruffed lemurs as they climbed toward the treetops while emitting abrupt roars in the direction of the bird.

**Experimental Manipulations.** Two Vv1 Group members were present at the test site for the first stooping hawk silhouette presentation. Both individuals emitted abrupt roars in the direction of the model immediately upon its release. Other group members, between 50 and 150m away, responded to the abrupt roars with the same call as they ran in the direction of the first callers. The relocation of these more distant individuals was interrupted periodically as each would stop to emit one or more abrupt roars while scanning the environment, run several meters further, stop and roar again, and so on, until they arrived at the test site. One of the two adults present at the start of the trial had a 20 day-old infant. Upon release of the hawk silhouette, the mother rushed to the infant, put her mouth around its midsection, and transported it orally approximately 4m up into a tree where she 'parked' it in the fork of a large branch (see Pereira et al., 1987). The adult female then returned to the ground to join other group members (all seven of which now were at the test site) who were emitting abrupt roars toward the model. When the silhouette was lowered for removal and reached the ground, one ruffed lemur leapt out from behind a tussock of grass directly onto the model's 'back'. Two other group members then lunged toward the model while they emitted abrupt roars. These calls continued for five to ten minutes before wails (and 'pulsed squawk-wail' intermediates: Fig. 4f) began to punctuate the bursts of abrupt roars.

Adult ruffed lemurs usually approached the perched raptor specimens closely, whereas if immatures approached at all they did so briefly and maintained a distance of several meters. An adult male and two juveniles were present for the presentation of the perched red-shouldered hawk specimen. The adult first saw the bird from approximately 10m away, and began moving slowly toward it, stopping occasionally to emit 'growl-snorts', a high-arousal location indicating call (Fig. 4c; Pereira et al., 1988). When just over a meter from the stimulus, the adult paused while averting his gaze, and then lunged suddenly toward the hawk giving it a powerful, sharp shove with his hands followed with an abrupt roar. The immatures joined in with abrupt roars, but did not approach the bird. Frequent brief bouts of scratching with the 'grooming claw' of the foot also occurred in all individuals throughout the presentation, apparently a reflection of anxiety (Diezinger and Anderson, 1986; Easley et al., 1987).

### **Responses of Ringtailed Lemurs to Mammalian Predators**

**Natural Encounters.** Mammalian stimuli elicited antipredator vocalizations from ringtailed lemurs consisting of four call types. 'Clicks' (Andrew, 1963; Fig. 2k) are uttered in circumstances of minor mammalian disturbances, including disturbances caused by arboreal movement of the lemurs themselves. Emission of these calls appears to reflect a mixed motivational state of 'curious-but-wary' on the part of the caller. Clicks preceded the 'closed-mouth click series' (CMCS: Fig. 2k), which also occurs during rapid (individual) locomotion, particularly when in trees. Unlike clicks and the closed-mouth click series, the 'open-mouth click series' (OMCS: Fig. 2k) and 'yaps' (Fig. 2k; Jolly, 1966) were observed, with rare exception, only as a response to mammals that seemed to be perceived as threatening. Occurrences of OMCS' outside the context of mammalian stimuli were limited to a few instances of equivalently-high arousal.

The transition from closed-mouth to open-mouth clicks may inform nearby group members that yapping is about to begin, thus allowing participants to synchronize their yaps. The accuracy of call synchronization appeared to covary with the proximity of callers. Only carnivores elicited yaps in this study, but one researcher (D. Wheeler, pers. comm.) observed Lc1 Group emitting yaps upon their first sighting of Lc2 Group in the trees of an adjacent enclosure. Unfamiliar humans also elicited yaps from free-ranging *L. catta* in Madagascar (Jolly, 1966;

Sauther, 1989). The group-coordinated use of the yap, its high emission amplitude, and its restriction to mammalian stimuli perceived as threatening indicates the function of this vocalization as a carnivore mobbing call.

A characteristic of the ringtailed lemur anticarnivore call sequence (clicks, CMCS, OMCS, yaps) is its repetitive nature. Emissions of these calls frequently continued until either the predator or the lemurs left the vicinity. As pointed out by Jolly (1966), individuals out of visible range of the stimulus often yapped 'sympathetically' with the rest of the group. In contrast to ruffed lemurs, however, repetitive calling dissipated quickly in ringtailed lemurs once the carnivore was no longer in view. Jolly (1966) also noted that extended bouts of yapping sometimes stimulated male ringtailed lemurs to howl (Fig. 21). This occurred in Lc1 and Lc2 Groups as well, as did the rare, reverse case where several yaps were evoked by enthusiastic howling.

When on the ground, the primary non-vocal response of ringtailed lemurs to the appearance of a carnivore was to leap immediately into the trees. Once above the ground, clicks and CMCS' accompanied movement through the branches and between trees. On many occasions ringtailed lemurs were observed to mob raccoons, and young raccoons were mobbed with particular fervor. Raccoons never were observed to lunge toward or attack the ringtails; either they fled high into the crowns of trees or they remained motionless, appearing to ignore the vocal threats. Although the DUPC ringtailed lemurs became increasingly habituated to the presence of raccoons from spring through fall of each year, large adult raccoons generally continued to be treated as potential threats whenever detected.

**Experimental Manipulations.** When a large dog (Fig. 1d) was walked slowly toward Lc1 Group from a distance, group members stayed on the ground for 5-6s, stared at the approaching carnivore, and emitted gulps. All group members then leapt into the trees and began emitting clicks and CMCS' while continuing to monitor the dog's approach. Emission of yaps began just over a minute from the time the first gulps had been issued. The first clearly-audible OMCS was heard 2min after the first gulps. Several howls also occurred at this time and again 9min after the dog first had been seen approaching. Individuals nearest the dog stared at it while vocalizing, whereas more distant group members that were calling were not necessarily facing the carnivore. Calling continued for about a minute after the dog was removed from the enclosure (approx. 20min after it had been introduced). Less than 10min later, most Lc1 Group members were back on the ground engaged in normal daily activities (e.g., foraging, grooming, resting).

Upon seeing the dog in the 'ambush' presentation, all Lc1 Group members dashed toward the trees without vocalizing, and were between 10 and 15m up into the trees 5s or so after the dog's appearance. The ringtailed lemurs began to emit clicks and CMCS's as soon as they were arboreal, but did not start to emit yaps for about 40s after the start of the presentation. The dog was in view of the lemurs for approximately two minutes, and the ringtails ceased emitting anticarnivore calls several minutes after the dog had been led out of the enclosure.

### **Responses of Ruffed Lemurs to Mammalian Predators**

**Natural Encounters.** When detecting a potentially-threatening mammal, ruffed lemurs typically first responded with growls and growl-snorts, followed by their mammalian predator mobbing call, the pulsed squawk (Fig. 4e). Like ringtailed lemur yaps, group emission of pulsed squawks was more or less synchronized, and accuracy of call synchrony seemed to depend on interindividual proximity (ruffed lemur groups housed in smaller quarters at the DUPC frequently exhibited tight synchrony in the emission of these calls).

Ruffed lemurs typically leapt into the trees before emitting any pulsed squawks. Once in the trees, an arched-back posture was assumed while calling. All group members did not always leap into the trees, however; ruffed lemur group matriarchs sometimes remained on the ground and confronted carnivores. An unusually large influx of raccoons into the DUPC enclosures in the summer of

1989 evoked a remarkable level of aggression from the matriarch of Vv2 Group. This female regularly chased the raccoons from the provisioning areas and, on several occasions, leapt onto the backs of raccoons and slapped them with her hands (L. Balko, pers. comm.).

It is intriguing that after pouncing on raccoons, this female often would run 10m or more away, stop, and lie still on the ground (L. Balko, pers. comm.). This behavior gave the impression that she was attempting to incite these carnivores to chase her, in the sense of predator distraction displays of nesting birds (Armstrong, 1949). The matriarch of Vv1 group exhibited similar 'luring' behavior, minus the attack, in response to the approach of museum specimens of mammals mounted on a radio-controlled toy vehicle (Macedonia and Shedd, unpubl. data). In contrast to *L. catta*, avian-like distraction displays would seem particularly adaptive for *Varecia*, given their means of rearing young (see Discussion).

**Experimental Manipulations.** In response to the introduction of the slowly approaching dog, many Vv1 Group members responded initially with growls. Most (or all) individuals then leapt into the trees, emitting growl-snorts. Approximately 30s later, the ruffed lemurs began to respond with pulsed squawks. These three call types persisted throughout the 20-minute stimulus period and, unlike the ringtailed lemurs which had ceased calling less than a minute after the dog had been removed, the ruffed lemurs continued to call for at least 20min post-presentation (at which time observations were terminated). Interestingly, the group matriarch either had remained on the ground or had returned to it shortly after the dog had reached the lemurs' location. At one point the dog was allowed to approach to within 10m of the adult female. This lemur did not flee, but kept her head lowered and her shoulders hunched forward as she emitted growls toward the dog (which was more than seven times the lemur's weight).

In response to the dog's ambush attack, Vv1 Group members ran rapidly and silently up into the nearest trees. Emission of growl-snorts began about 10s later and pulsed squawks at about 15s. Although the dog was in view of the lemurs for only two minutes, the ruffed lemurs continued calling for more than 45min post-presentation.

### **Responses of Ringtailed and Ruffed Lemurs to Snakes**

Encounters by ringtailed and ruffed lemurs in the NHE's with snakes corroborate similar observations of ringtailed lemurs in Madagascar (Jolly, 1966; Budnitz and Dainis, 1975; Sauther, 1989). The lemurs responded to snakes as minor disturbances (emission of clicks by ringtailed lemurs, and growls or growl-snorts by ruffed lemurs). As of 1992, only two of the DUPC semi-captive lemurs had been killed by snakes (see Methods). Were this number to increase dramatically, however, the lemurs might be expected to begin responding to snakes as a predatory threat, as has been seen for some other primates (Gouzoules et al., 1975; Masataka, 1983; see also Mineka et al., 1984).

## **DISCUSSION**

One way to understand the adaptive differences in ringtailed and ruffed lemur antipredator behavior is to compare them with other primates for which relevant data are available. The nearby African continent harbors some monkey species that are analogous in several respects to ringtailed and ruffed lemurs. Ecologically, the vervet monkey (*Cercopithecus aethiops*) is a good anthropoid analog to the ringtailed lemur: both species are relatively small in comparison to their primary predators, both species live in large groups and typically live in open habitats, and although both spend much time in trees, they are the most terrestrial members of their respective genera (Kingdon, 1988; Ward and Sussman, 1979). The ruffed lemur does not have such a direct ecological analog in Africa, though it is in some ways comparable to the arboreal and frugivorous mangabeys (*Cercocebus* sp.).

Although these monkey species are larger than ringtailed and ruffed lemurs in absolute size, one variable of concern here is primate body size relative to predator body size. Also, whereas cercopithecids are sexually dimorphic in body size, with males often being much larger than females, there is no significant difference in body size between the sexes in lemurs (see Kappeler, 1993). This aspect of phylogenetic heritage could explain the lack of a male bias in predator defense among lemurs.

Because exposure to predation from raptors is severe for most mammals when foraging in the terminal branch milieu, moving toward tree trunks and/or out of trees in response to raptors or antiraptor calls is widespread among relatively small diurnal primates (capuchins: van Schaik and van Noordwijk, 1989; crowned lemurs: Wilson et al., 1989). Accordingly, when arboreal, the typical response of ringtails and vervets to raptors is to move away from peripheral branches and out of trees; likewise, these primates move away from open areas in response to raptors when on the ground (Struhsaker, 1967; Jolly, 1966; Seyfarth et al., 1980; Sauther, 1989; Macedonia, 1990; Macedonia and Yount, 1991). Notably, adult male vervets are the only age/sex class that is far above the average prey size taken by one of the common large raptors that are encountered by this species: the martial eagle, *Polemaetus bellicosus* (Cheney and Seyfarth, 1981). Yet, adult male vervets are not large enough to be too bold toward these raptors, and only once was one seen by Struhsaker (1969) to lunge aggressively toward a martial eagle. Experiments with raptor models showed that ringtailed lemurs also respond with 'contained aggression' toward avian predators. Like vervets, this aggression was limited primarily to perched raptors which, once detected, may pose less of a threat than raptors already on the wing.

The fact that ringtailed lemur and vervet monkey infants cling to their mothers from birth confers an advantage against predation over species whose young do not cling. Once infants of clinging species begin to explore and play at a distance from the mother, however, they become more vulnerable to predation. In Madagascar, for example, some species of large hawks (e.g. *Polyboroides radiatus* and *Buteo brachypterus*) perch motionless on the low branches of dead trees, apparently in wait to ambush passing prey (Sauther, 1989; pers. obs.). Young infants who are engaged in play or are exploring on peripheral branches of saplings and bushes must be prime targets for raptors hunting in this manner. Observations of infant ringtailed lemurs dropping from exposed low branches to the ground in response to antiraptor calls suggests that this may be an adaptive response against raptorial predation, once infants begin to distance themselves from direct maternal protection. Intriguingly, a similar response to antiraptor calls has been reported for vervet monkeys (Struhsaker, 1967).

Vervet monkeys and ringtailed lemurs both respond to potentially threatening mammalian predators by running up into the branch network of trees, where their grasping hands and feet give them an advantage in maneuverability over that of clawed carnivores (Struhsaker, 1967; Seyfarth et al., 1980). When on the ground, however, this advantage is lost and the probability of being killed by a carnivore is increased (Seyfarth et al., 1980). The fact that carnivores can place themselves between these primates and access to trees poses an additional level of threat that is less commonly experienced by forest-living primates. The increased predator pressure imposed on relatively small-bodied, highly-terrestrial primates like vervet monkeys (Cheney and Wrangham, 1987) and ringtailed lemurs (Sauther, 1989), in conjunction with the fact that avoiding predation from raptors and carnivores often involves responses that are diametrically opposed, may explain the high level of stimulus specificity witnessed in some of the antipredator calls of these primates (Macedonia and Evans, in press). For ringtailed lemurs at least, larger group size also can be seen as a response to increased predator pressure, given that this species is descended from bamboo-lemurs that live in smaller groups (Macedonia and Stanger, unpubl. data).

Because adult ruffed lemurs weigh about 75% more than adult ringtailed lemurs, the former undoubtedly are less easily dispatched by raptors. Like large monkeys, adult ruffed lemurs not only threaten but probably attack raptors. Yet, at 3.5kg, the ruffed lemur is not a large primate and its aggressiveness towards

predators seems out of proportion for its size. This behavior may be a consequence of phylogenetic constraints in ruffed lemur reproduction and infant care.

Unlike other diurnal lemurs, ruffed lemurs retain ancestral features of prosimian reproduction, including a comparatively short gestation period, possession of three functional pairs of mammary glands, and giving birth to litters of young (Foerg, 1982; Tattersall, 1982). Infant ruffed lemurs are kept in nests, and later are 'parked' in tree forks by the mother when she leaves them (Pereira et al., 1987; Morland, 1990). During this time, these infants must be exceedingly vulnerable to predation. Moreover, simultaneous escape from predators via transport by the mother is not an option for ruffed lemur infants, as they must be carried orally to safety one at a time. Thus, if ruffed lemurs are not to lose their reproductive investments they must defend their sessile progeny by confronting predators rather than fleeing from them. Consequently, aggressive defense against raptors year-round might maintain a level of deterrence toward these predators that would enhance the survivorship of infants when present (Klump and Shalter, 1984). In this study, ruffed lemur parents and their adult offspring chased and threatened raptors year-round. Clearly, both parents and siblings would stand to gain fitness by deterring predation on infant kin.

Although adult ruffed lemurs may be largely immune to raptorial predation, their demeanor toward carnivores (excluding that of one group matriarch) was rather similar to that of ringtailed lemurs in being defensive rather than aggressive. This may stem in part from the fact that carnivores not only take larger prey per their own body weight than do raptors, but also because the size range of prey taken is much broader (Cheney and Seyfarth, 1981). The lack of sexual size dimorphism in lemurs (Kappeler, 1993), however, still raises the question of why there should be a matriarchal bias in defense against carnivores in ruffed lemurs. It is, perhaps, that the potential cost associated with confronting carnivores may be too high for individuals other than multiparous adult females. Ruffed lemur fathers were, in fact, among the first to flee during naturally-occurring and staged encounters with carnivores, which seems to highlight the vast differential in reproductive investment between the sexes that is characteristic of mammals.

Finally, with regard to vocal antipredator behavior, ruffed lemurs called repetitively after encounters with predators for a far longer period than did ringtailed lemurs. Though many predators give up the hunt after being discovered by their intended prey (see Klump and Shalter, 1984, for a review), such resignation is not guaranteed, and extended bouts of antipredator calling may provide a margin of safety against renewed hunting efforts from discovered predators (Owings and Hennessy, 1984; Loughry and McDonough, 1988). Considering the helplessness of ruffed lemur neonates, extending the period of predator awareness through repetitive calling could be crucial to their survival.

## SUMMARY

The responses of semi-captive, forest-living ringtailed lemurs and ruffed lemurs to avian predators differed considerably. Whereas ringtailed lemurs responded to the sight or sound of airborne raptors by fleeing peripheral branches and by moving downward and/or out of trees, ruffed lemurs entered the trees and pursued raptors and raptor models with overt displays of aggression. Comparative data on responses of some African monkeys to raptors suggest that the differences in antiraptor behavior between these two lemur species stem partly from differences in their body sizes. The overall responses of ringtailed and ruffed lemurs to carnivores were more similar than their responses to raptors, and this may be due to the larger prey size per predator body weight that carnivores can accommodate as compared to raptors. Because the hallmark traits of grasping hands and feet confer to primates an advantage over carnivores when in the branch network of trees, most primates habitually seek or maintain an arboreal location when dealing with dangerous carnivores. Indeed, both lemur species typically entered the trees before beginning to mob carnivores vocally. An exception to this rule would be expected when, as in ruffed lemurs, progeny do not

cling to their mothers and when prior to locomotor independence infants are kept in nests or parked on branches. Adult ruffed lemurs therefore may not always flee into trees in response to carnivores because deterring predators that are still on the ground (and thus who still are at a distance from arboreally-located immatures) may be more effective than waiting until the carnivore has entered the trees before attempting to fend it off. Unlike ringtailed lemurs, ruffed lemur group matriarchs confronted, chased, and sometimes attacked carnivores on the ground, and performed what seemed to be predator distraction displays. This suggests that, like many avian species, the ruffed lemur has evolved such antipredator behavior as an adaptation to the phylogenetic constraint of possessing sessile young.

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