

4

Predation on Lemurs in the Rainforest of Madagascar by Multiple Predator Species: Observations and Experiments

Sarah M. Karpanty and Patricia C. Wright

Introduction

Predation by raptors, snakes, and carnivores is a constant risk for most wild primates (Cheney & Seyfarth, 1981; Anderson, 1986; Cheney & Wrangham, 1987; Janson & van Schaik, 1993; Cowlshaw, 1994; Isbell, 1994; Hill & Dunbar, 1998; Treves, 1999; Bearder et al., 2002; Gursky, 2002a, b; Shultz & Noë, 2002). In Madagascar, the problem may be especially severe since prosimians are the largest, most abundant and conspicuous mammals in the forest (Wright, 1998). Lemur behavior may be strongly influenced in its avoiding predation by stealthy predators, such as Henst's goshawk (*Accipiter henstii*), the fossa (*Cryptoprocta ferox*), or the Madagascar boa constrictor (*Boa manditra*) (Sauther, 1989; Goodman et al., 1993a; Gould, 1996; Wright, 1998; Karpanty & Goodman, 1999; Karpanty & Grella, 2001; Fichtel & Kappeler, 2002; Goodman, 2004). Most studies of predator and prey concentrate on one taxon of predator, such as hawks or leopards (Isbell, 1990; Peres, 1990; Struhsaker & Leakey, 1990; Boesch, 1991; Shultz, 2001, 2002), while the forest reality is that an animal avoids several distinct predators simultaneously. This is certainly true in Madagascar, where day-hunting hawks and eagles hunt both sleeping nocturnal and active diurnal lemurs, and fossas and boas hunt day and night (Wright, 1998; Karpanty, 2006). Therefore, ability to develop foraging and resting strategy for risk avoidance might be a major factor in primate sociality (Janson & van Schaik, 1993; Janson & Goldsmith, 1995; Stanford, 1995).

Predation on primates is a factor governing patterns in species' social assembly, travel, resting tactics, and community composition (van Schaik, 1983; van Schaik & van Hooff, 1983; Janson, 1992; Isbell, 1994; Wright, 1998). It has been suggested that over evolutionary time predators may impact a change in the primate nocturnal or diurnal activity cycle (Wright, 1989; van Schaik & Kappeler, 1993; Wright, 1994; van Schaik & Kappeler, 1996). However, few authors have considered the real life complexity inherent in the avoidance of simultaneous

TABLE 4.1. Lemur species in Ranomafana National Park. The five nocturnal species are marked by asterisk. The two cathemeral species are marked with a C.

Species	Body Mass (g)	Biomass (kg/km ²)
<i>Avahi laniger</i>	900	20
<i>Propithecus edwardsi</i>	5,800	125
<i>Cheirogaleus major</i> *	320	18
<i>Microcebus rufous</i> *	45	4
<i>Daubentonia madagascariensis</i> *	3,500	?
<i>Lepilemur seallii</i> *	970	1
<i>Hapalemur griseus</i>	900	20
<i>Hapalemur aureus</i>	1,800	9.6
<i>Prolemur simus</i>	2,800	12
<i>Eulemur fulvus rufus</i> C	2,100	66
<i>Eulemur rubriventer</i> C	2,100	48
<i>Varecia variegata variegata</i>	3,500	4

predation by multiple species of predators with distinct hunting strategies (Lima & Dill, 1990; Sih et al., 1998; Wright, 1998).

Extensive fieldwork on the lemurs of Madagascar has shown that lemurs, once thought to have few predators, actually have multiple species of predators (van Schaik & Kappeler, 1996; Wright, 1998, 1999; Goodman, 2004; Karpanty, 2006). Little is known about the effects of multiple predators on lemur social and foraging behavior. It is possible that a lemur's response to one predator may bring a greater risk from another predator (e.g., risk enhancement or reduction, Sih et al., 1998). Wright (1998) outlined possible behaviors that would protect or decrease risk to lemurs from raptors and carnivores.

Twelve sympatric lemur species live in Ranomafana National Park (RNP) (Table 4.1). Of the five carnivore species observed at Ranomafana (Table 4.2), only two have been observed to prey on lemurs. The fossa is the largest extant carnivore in Madagascar and is found in forested areas in both the western dry and eastern rainforests. An agile mammalian predator in the trees, with retractile claws, strong mandible, and formidable canines, the fossa is able to kill prey nearly its own size (Wright et al., 1997). Fossas captured at RNP weighed 8.5 kg (adult male) and 6.5 kg (sub-adult male), and radio-collared fossas traveled 2–5 km per day (Dollar et al., 1997; Dollar, 1999). The ring-tailed mongoose (*Galidia elegans*) is a small (700 g) carnivore found in most forested areas throughout Madagascar (Garbutt, 1999). This diurnal carnivore eats birds, beetles, fruits, and small-bodied lemurs (Wright & Martin, 1995).

All four diurnal raptor species (Table 4.2) are large enough to take lemurs. The Madagascar harrier-hawk was observed to take lemur remains to its nest in gallery forest near spiny desert (Karpanty & Goodman, 1999). In contrast, in a study in the rainforest of Masoala peninsula of nest remains of *Buteo brachypterus*—Madagascar buzzard—no lemurs were found (Berkelman, 1994; Watson & Lewis, 1994). In the dry forests of Madagascar, owls eat small lemurs (Goodman et al., 1993a,b,c). There are no reports of the contents of owl pellet remains in the rainforest of Ranomafana.

TABLE 4.2A. Sympatric birds of prey, Ranomafana National Park. Raptors marked by an asterisk are known to eat lemurs in this region.

Species Name	Common Name
<i>Buteo brachypterus</i>	Madagascar buzzard
<i>Polyboroides radiatus</i> *	Madagascar Harrier-hawk *
<i>Accipiter henstii</i> *	Henst's goshawk*
<i>Eutriorchis astur</i>	Madagascar Serpent-eagle
<i>Tyto alba</i>	Madagascar barn owl
<i>Asio madagascariensis</i>	Madagascar long-eared owl

TABLE 4.2B. Sympatric viverrid carnivores in Ranomafana National Park. Viverrids marked by an asterisk are known to eat lemurs in this region.

Species Name	Common Name
<i>Euplores goudoti</i>	Falanouc
<i>Galidia elegans</i> *	Ring-tailed mongoose*
<i>Fossa fossa</i>	Fanalouc
<i>Galidictus fasciata</i>	Broad-striped mongoose
<i>Cryptoprocta ferox</i> *	Fossa*

Lemurs have several possible evolutionary strategies to avoid these predators, including (1) lowering susceptibility to predation via group defense, increased vigilance, or dilution of risk (Hamilton, 1971; Pulliam & Caraco, 1984; Janson, 1992); and (2) increasing crypsis and hiding (Vine, 1973; Janson, 1986, 1992; Cowlshaw, 1994; Terborgh & Wright, 1998). It has also been hypothesized that since predation rates vary with prey activity cycle, nocturnality may protect primates against diurnal raptor predation (Wright, 1989, 1994). Understanding the impact of predation on the evolution of lemur behavior and social systems as hypothesized above requires understanding the interactions of lemurs with all of their many predators.

As a first step in understanding the complex relationships between multiple predators and multiple lemur prey, we review and update information on direct observations of predator attacks on lemurs in the rainforest of Ranomafana National Park, and conduct an experiment to better understand how the lemurs react to and avoid multiple predators. By using audio playbacks, we compare the responses of three species of lemurs to experimental exposure to aerial and terrestrial predator vocalizations, and we examine whether differences in lemur responses to different predators are correlated with observed predation rates for these lemur species.

Methods

Study Site

Ranomafana National Park (RNP), established in 1991, contains 43,500 ha of continuous rainforest in southeastern Madagascar and is situated at 21°16' S latitude

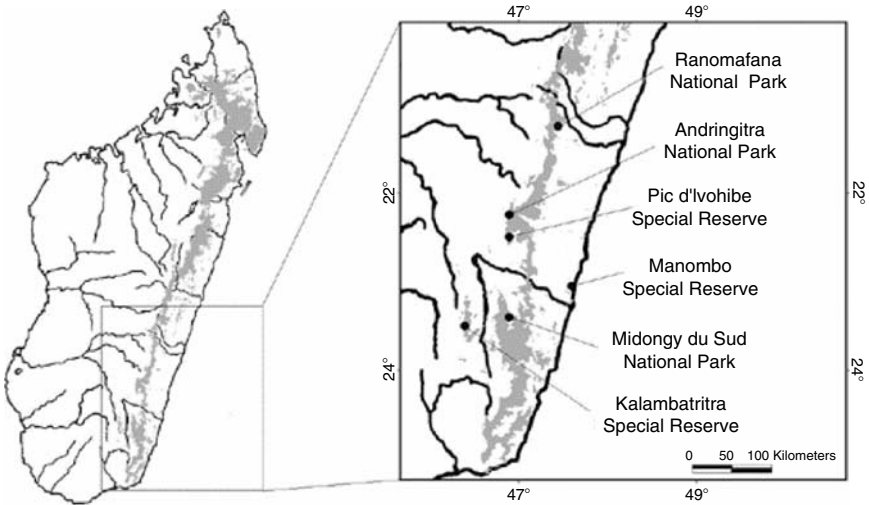


FIGURE 4.1. Map of Madagascar with study site, Ranomafana National Park, noted in the context of other protected areas in this region (Irwin & Arrigo-Nelson, pers. comm.)

and 47°20' E longitude (Wright, 1992; Wright & Andriamihaja, 2004). The park is 25 km from Fianarantsoa and 60 km from the Indian Ocean (Fig. 4.1). Elevations range from 500 to 1500 m, and annual rainfall ranges from 1600 to 3600 mm (RNP records). Most of the rainfall occurs during the months of December to March. Temperatures range from 4–12°C (June to September) to 30–32°C (December–February). The park contains moist evergreen forest and the canopy height range is 18–25 m. The study groups of lemurs were located in the 5 km² Talataky study site (TTS) which was selectively logged by hand in the period 1986–1989, and the Vatoaranana study site (VATO), 5 km south, which is undisturbed by humans. Human impact on predation rates has been minimal as there has been a non-hunting tradition in the last 50 years (Wright, 1997).

The faunal diversity in RNP is high for Madagascar (Wright, 1992), with 116 species of birds including six species of raptors, five species of viverrid, and twelve species of primates (Table 4.1). Total biomass of primates at this site was approximately 330 kg/km², comparable to *terra firme* forests in Central Amazon and Lope Reserve in Gabon, but roughly half the primate biomass of the alluvial floodplain forest of Manu, Peru or Kirindy dry forest in western Madagascar (Terborgh, 1983; Oates et al., 1990; Peres, 1993; White, 1994; Ganzhorn & Kappeler, 1996; Wright, 1998).

Review of Reported Kills

Although predation is difficult to quantify, we are lucky that at RNP, where 13 dissertations and 15 masters theses (DEA) have been completed on the behavior and ecology of lemurs, incidental observations have been recorded and accumulated

over time (Wright and Andriamihaja, 2004). We began by reviewing existing information, including reports from researchers and research technicians and data from field notebooks, with the objective of ascertaining all the known acts of predation on lemurs. We especially reviewed the data books from the long-term continuous behavioral study of *Propithecus edwardsi* (Wright, 1995; Pochron et al., 2004). In this study, predation events were scored as “kills” when the predator was near the corpse or when there were signs of predation (i.e., discarded entrails, or teeth or talon marks on bones) (Wright et al., 1997; Wright, 1998). Animals abruptly missing from a group and never seen again were scored as “possible kills.”

Observations at Raptor Nest Sites

During four raptor nesting seasons (August–January) between 1999 and 2002, 11 nests of *B. brachypterus* were observed for a total of 1,204 hrs with 204 observed prey deliveries; 7 nests of *A. henstii* were observed for a total of 1,703 hrs with 284 observed prey deliveries; and 7 nests of *P. radiatus* were observed for a total of 1,007 hrs with 186 observed prey deliveries (Fig. 4.2). Nest observations included behavioral sampling of a nest through continuous recording of prey deliveries, feeding behavior and instantaneous sampling every 5 min for nest attendance by the adult male and female. Focal nest observations on all three raptor species were conducted from sunrise to sunset with each nest being observed one to two days per week throughout the four-year study from a distance of at least 150 m, to minimize nest disturbance (Karpanty, 2005, 2006).

Experiments

Playback experiments were conducted on five previously habituated groups (n = 15 groups total) of *Eulemur fulvus rufus*, *Hapalemur griseus griseus*, and *P. edwardsi* in the Talatakely and Vatoharanana trail systems of RNP. The three diurnal lemur species were chosen as they represent a range in body size, group size, and anti-predator tactics. Individuals in most groups were collared to allow the researcher individual recognition. The design of this experiment was modeled after Zuberbühler et al. (1999) and Hauser & Wrangham (1990).

Vocalizations used included the fossa, Henst’s goshawk, Madagascar harrier-hawk, Madagascar buzzard, Madagascar serpent eagle (*Eutriorchis astur*), and the greater vasa parrot (*Coracopsis vasa*), the latter as a control. To avoid pseudoreplication, a collection of four different vocalization tapes was made for predator and control species, with each tape containing a different individual from RNP. Raptor calls were recorded from birds near their nest sites. Calls of *E. astur* were provided by the Peregrine Fund and were recorded from two nesting birds in the Masoala Peninsula of northeastern Madagascar. The tapes were then merged for each species so that each playback consisted of calls from different individuals of the same species. Two tapes of the common vocalizations of the fossa were provided by Deutsches Primatenzentrum, recorded from one individual from Zoo



FIGURE 4.2. Map of study site and raptor nests

Duisburg in Germany, and by Animal Sound Archives (Tierstimmenarchiv), from a collection of calls from three individuals. Vocalizations were broadcast using a SONY WMD6C with Nagra DSM speakers. Sound level was set to mimic natural intensity (85–105 dB SPL) and was calibrated using a Radio Shack sound level meter planned one meter from the speaker.

All subjects and groups were tested only once with each of the six stimuli in a randomized order in either September to December of 2001 or the same period

in 2002. The playback trial was only conducted if (1) no lemur had detected the observer as a predator risk (e.g., they were engaged in normal activity) and (2) no predator alarms had occurred within thirty minutes. Statistical independence was maintained within species by sampling different groups and by using groups from both the Talatakely and Vatoharanana trail systems of RNP, which are separated by approximately 5 km of contiguous rainforest. It was assumed that the natural predation risk and predator experience were constant between the groups of the same species. Human presence was minimized and experiments separated by at least seven days so lemur subjects would not habituate to predator calls. Playback stimuli in the rainforest generally can only be detected up to 300 m, so other groups and species should not have been affected by the playback.

When a lemur was located, its location was marked on a map and behavioral observations were conducted on two adult focal individuals (one male, one female) chosen at random from the group. Twelve 5-minute focal samples on each male and female individual were collected before the playback (pre-playback time period), the playback occurred during the 13th focal sample, and 12 more focal samples were collected after the playback (post-playback period), giving a total of 2 hr 5 min of sampling per playback experiment. While the animals were in an observable location during the 13th focal sample and engaging in normal activities, the speaker was hidden 50 m away from the groups, and an observer conducted the playback. Immediately before the playback, the speaker was raised with a stick to 4 m above the ground to control for speaker-induced downward vigilance. Four observers stayed within viewing distance of the group and continued conducting the focal sample and documenting the response of the group to the playback. Two observers were responsible for writing the data and checking the observations of the primary observers and two for continuously watching the lemurs and verbally reporting the data. The focal group and individuals' responses included vigilance type and duration, height, activity, vocal alarm responses, nearest neighbor distance and individual. Vigilance types were defined to be fixed stares either greater than 3 sec duration in an upward direction; greater than 3 sec downward; or greater than 3 sec in a horizontal direction (from the lemur's point of view) with cessation of other activity. Height was classified as low (<5 m), medium (5–15 m) and high (> 16 m). Activity classes included feeding, traveling, grooming, resting, sleeping, and playing. Any aerial predator alarms, terrestrial predator alarms, general predator alarms, contact calls, or lost calls were also recorded. Finally, ad libitum notes were made when animals dropped or ascended in the canopy or approached the speakers. Vigilance, height, and activity behaviors were recorded through focal individual sampling and continuous recording in 5-minute intervals. Proximity data and trail locations were recorded at the end of each 5-min interval by instantaneous recording.

Analysis of Experimental Data

Data were summarized from each focal sample to give the percentage of each 5-min sample that a focal animal spent vigilant (summing upward, downward

and horizontal vigilance; fixed stares >3 sec duration), active (summing feeding, playing, traveling, and grooming), and low (<5 m high). The effects of time in relation to the playback sex, playback type, lemur species, and all possible interactions on percent time vigilant, active, and low were tested by ANOVA and adjusted for multiple comparisons while controlling for variation across groups. The effect of time in relation to playback was coded as the pre-playback period (behavioral samples 1–12), the short-term post-playback period (0–15 min after playback, samples 14–16), and the longer-term post-playback period (16–60 min after the playback, samples 17–25).

Three types of a priori contrasts were conducted on the data set: (1) contrasts of responses over time: pre-playback versus longer-term post-playback (significance indicative of slow reaction to the playback and a delayed reaction) and pre-playback and longer-term playback responses versus the short-term response (significance indicative of a quick reaction to the playback and a quick decay of the reaction); (2) contrasts of playback type by risk or predator category: Control versus All Predators, Control vs. Aerial Predators, Control vs. Ground Predators, Aerial vs. Ground Predators, *A. henstii* vs. other aerial predators; and (3) contrasts of lemur species effects (*Eulemur* vs. *Haplemur* vs. *Propithecus*).

Results

Observations of Predation on Lemurs from Reported Kills and Scat

Long-term studies have resulted in observations of corpses immediately following fossa kills for four species of lemurs, *Eulemur rubriventer*, *Varecia variegata*, *Avahi laniger*, and *Propithecus edwardsi* (Andrea Baden, pers. comm.; Overdorff & Strait, 1995; Overdorff et al., 1999; Stacey Tecot, pers. comm.; Wright et al., 1997; Wright, 1998). Including data from behavioral ecology studies between 1986 and 2005, we observed both actual kills and possible kills in four groups of *P. edwardsi* that we followed year round (Table 4.3). During the 19-year study of the 87-member *P. edwardsi* community (four groups), a maximum of 19 and minimum of 9 individuals were killed and eaten by the fossa. The fossa ate all age, sex classes (see Table 4.3) with the minimum toll: 1 adult male, 3 adult females, 1 three-year old female, 1 one-year old female, and 2 infants that died with their mothers (Wright, 1995, 1998, unpubl. data). The data show that predation on *Propithecus* is seasonal, and all verified fossa kills occurred in May–September, the cold, dry season and the season when infants are 1–3 months old. *Propithecus* has been observed giving a ZZUSS! call at ground predators including the fossa (Wright, 1998).

Additionally, five species of lemurs have been identified from fossa scats found at Ranomafana National Park, including two diurnal (*P. edwardsi* and *Haplemur simus*), two cathemeral (*E. rubriventer* and *E. fulvus rufus*) (Wright et al., 1997), and one nocturnal (*Microcebus rufus*) (Goodman, 2004, Table 4.4).

TABLE 4.3. *Cryptoprocta ferox* kills (corpse observed) and suspected kills of *Propithecus edwardsi* at Talatakely Trail System (TTS) in Ranomafana National Park during a 19-year continuous study of two groups (1986–2005), as well as two additional groups since 1993 (Group III) and 1996 (Group IV).

<i>C. ferox</i> kills	Suspected <i>C. ferox</i> kills	Yr/month	Group
adult male (RR)		1990/Jul	I
adult female (BY)		1994/Aug	III
2 month infant (BYI)		1994/Aug	III
1 year old female (PYI)		1994/Sep	
3 yr old female (BB)		1994/Sep	I
3 year old male (PS)		2003/May	I
adult female (Radio Silver)		2005/May	II
	adult male (I)	1987/Jan	I
	one yr old male (GGI)	1987/Oct	II
	adult female (RG)	1989/Feb	II
	6 mo old (GGI)	1989/Dec	II
	adult female (Y)	1993/Sep	I
	3 mo infant (YI)	1993/Sep	I
	adult female (GG)	1993/Jun	II
	6 mo old (BYI)	1993/Jan	III
	one yr old (GGI)	1992/Jun	II
	2 yr old female (TSI)	2000/Jul	I
	2 yr old female (BI)	2000/Jul	III
	1 yr old male (BGI)	2000/May	IV
	adult female (TS)	2001/Jun	I

TABLE 4.4. Lemur remains identified in *Cryptoprocta ferox* scats within RNP. Each asterisk represents a separate scat. These scats were found by Luke Dollar (Wright et al., 1997; Goodman, 2004), Summer Arrigo-Nelson, pers. comm., and Deborah Overdorff, pers. comm.

Species	Common Name	MNI
<i>Propithecus edwardsi</i>	Milne Edwards' sifaka	***
<i>Haplemur griseus</i>	Lesser bamboo lemur	***
<i>Avahi laniger</i>	Eastern woolly lemur	*
<i>Cheirogaleus major</i>	Greater dwarf lemur	*
<i>Microcebus rufus</i>	Brown mouse lemur	*
<i>Eulemur fulvus rufus</i>	Red-fronted brown lemur	***
<i>Eulemur rubriventer</i>	Red-bellied lemur	**
<i>Haplemur simus</i>	Greater bamboo lemur	*
<i>Varecia variegata</i>	Black and white ruffed lemur	*

All *P. edwardsi* group members give the aerial predator call, a very loud, low-pitched series of roars and barks, which can continue for 5–15 minutes (Wright, 1998). In observations we made during follows, we saw sifakas react to raptor sightings, or to group members alarm-barking in response to raptors by looking up, alarm barking, and dropping to lower levels of the forest. During the 19 years of sifaka follows, the four species of raptors observed to elicit alarm barking were *B. brachypterus*, *P. radiatus*, *A. henstii*, and *E. astur*. Other large birds such as the crested ibis, vasa parrot, or blue coua occasionally received an

alarm bark. Only one attack on *P. edwardsi* by raptors was observed. The hawk, talons extended (*A. henstii*, although it happened too fast for positive identification), swooped at a mother with infant during July.

During the long-term study of *H. simus* (Tan, 1999), C. Tan and P. Wright observed an *A. henstii* attempt an attack on an eight-month old infant. The group of nine individuals gave an alarm call, dropped to the forest floor and hid for over two hours. The infant (3/4 the size of the mother) leaped into his mother's arms and remained ventrally cradled for over an hour, low in the understory.

Sightings of the serpent eagle (*E. astur*) are rare, but L. Rasabo reports a serpent eagle eating an adult *A. laniger* (Wright, 1998). A nest of this eagle was not found for this study, and no further observations of kills of lemurs by the serpent eagle have been made.

Raptor Nest Site Observations

The remains from seven species of lemur were observed taken to the nests of *A. henstii* and *P. radiatus* for ingestion by chicks and parents during October–December 1999–2002. Three of these lemur species are nocturnal, two are diurnal and two are cathemeral (active equally in day and night hours). No lemurs were observed to be delivered to nests of *B. brachypterus* during this same time period. Predation rates on these lemurs were calculated by taking the percentage of the lemur population killed per year by each raptor predator or by a combination of the two hawk species (Figs. 4.3, 4.4). The highest predation rate was on the 1-kg primates, *Hapalemur* (diurnal) and *Avahi* (nocturnal). The 2-kg *E. rubriventer* and *E. fulvus rufus* (cathemeral) were also eaten at a high rate.

The diet of *A. henstii* (Table 4.5) comprises at least 26 different prey species, including three nocturnal, two diurnal, and two cathemeral lemur species. The largest component of the prey profile in terms of individuals is avian prey (59%); however, lemurs are second in terms of percent individuals (23%). In terms of percent of total biomass, the trends hold the same with avian prey accounting for 70.51% of all biomass delivered to the nest, primates 28.43% of all biomass, and reptiles 0.32% of all biomass. The diet of *A. henstii* is highly variable, ranging from endangered species such as *Varecia variegata* (black and white ruffed lemur) and *Lophotibis cristata* (crested ibis)—found only in old-growth forest—to domestic chickens and rats. Both *A. henstii* and *P. radiatus* delivered lemurs to the nest only during the nestling and fledgling stages of the nesting cycle. During this period, *A. henstii* individuals delivered a lemur to the nest every 21 hrs, or 0.047 lemur per hr of observation. Extrapolating this prey delivery rate to the incubation period, we would have expected to see at least 15 lemur prey deliveries during our observations at the nest during incubation, instead of the zero we did observe.

The diet of *P. radiatus* (Table 4.6) is composed of at least 24 different prey species, including 3 nocturnal and 1 diurnal species of lemur. The diet of this generalist predator ranges from prey relying on high quality forest (*Accipiter madagascariensis*) to prey associated only with human disturbance (*Rattus rattus*). The largest percentage of prey deliveries is avian (27%), followed by reptiles

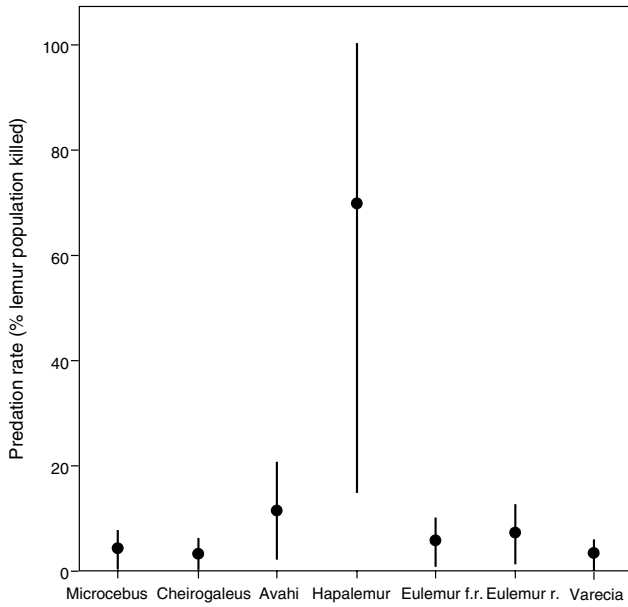


FIGURE 4.3. Predation rates on lemurs by *Accipiter henstii* and *Polyboroides radiatus* as calculated from direct nest observations in this study. Predation rates equal percentage of the lemur population killed per year by a combination of the two hawk species. The filled black dot is the median of the possible projected rates

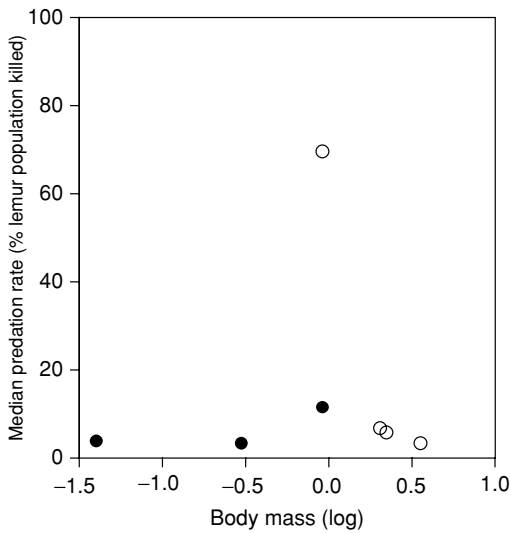


FIGURE 4.4. Predation rates on lemurs by raptors with the weights of the lemurs log transformed. The filled black dot is the median of the possible projected rates

TABLE 4.5. Primate prey of *Accipiter henstii* at RNP from direct nest observations 1999–2002. Data are combined from observations at 7 nest sites. MNI is the minimum number of individuals. Additional prey includes primarily birds with a few amphibians, reptiles, tenrecs and rodents (see Karpanty, 2005, for a complete list of prey taxa).

Species	Common Name	MNI	% Total Individuals	% Total Biomass
<i>Hapalemur griseus</i>	Lesser bamboo lemur	28	9.86	9.96
<i>Avahi laniger</i>	Eastern woolly lemur	13	4.58	7.37
<i>Cheirogaleus major</i>	Greater dwarf lemur	10	3.52	2.41
<i>Microcebus rufus</i>	Brown mouse lemur	8	2.82	2.56
<i>Eulemur fulvus rufus</i>	Red-fronted brown lemur	5	1.76	5.59
<i>Eulemur rubriventer</i>	Red-bellied lemur	1	0.35	1.01
<i>Varecia variegata</i>	Black and white ruffed lemur	1	0.35	1.83

TABLE 4.6. Primate prey of *Polyboroides radiatus* at RNP from direct nest observations 1999–2002. Data are combined from observations of 7 nests. MNI is the minimum number of individuals. Additional prey include mainly reptiles and birds with a few frogs, bats, rodents, tenrecs (see Karpanty, 2005, for a complete list of taxa).

Species	Common Name	MNI	% Total Individuals	% Total Biomass
<i>Microcebus rufus</i>	Brown mouse lemur	14	7.53	3.73
<i>Avahi laniger</i>	Eastern wooly lemur	4	2.15	18.86
<i>Cheirogaleus major</i>	Greater dwarf lemur	3	1.61	6.02
<i>Hapalemur griseus</i>	Lesser bamboo lemur	3	1.61	8.88

(18%) and primates (13%). In terms of percent of total biomass, the trend is reversed, with the most important taxa being primates (37.49%), followed by reptiles (24.65%) and birds (19.05%). All deliveries of lemurs occurred during the nestling and fledgling stages of the nesting cycle. During this study, a lemur was delivered to the nest every 31 hrs (0.0327 lemur/ hour of observation). If the delivery rate were to be the same during incubation, we would expect to have seen at least 6 lemurs (instead of zero) delivered to the nest during the hours that *Polyboroides* nests were observed.

Playback Experiments

Intra-species responses to playback experiments

Eulemur fulvus rufus

After the playbacks of predator vocalizations, *Eulemur* individuals generally exhibited a cryptic anti-predator strategy by increasing vigilance, moving to higher portions of the canopy, and decreasing activity levels in the hour after the playback. Changes were most marked in the last 45 min of the experiments, indicating that *Eulemur* have a delayed, but long-term, cryptic response to predator vocalization exposures.

Changes in vigilance were generally short term for *Eulemur*, with overall levels of vigilance highest in the first 15 min after the playback and lowest in the last 45 min, when the lemurs were quiet and cryptic (*Percent Time Vigilant*: Pre-Playback: 33.1%; Short-term Post-Playback: 35.1%; Long-term Post-Playback: 18.5%; $F_{2,119} = 29.63$, $p < 0.001$). As another indication of the cryptic response, the activity levels of *Eulemur* did decrease during the last 45 min of the playback experiments (*Percent Time Active*: Pre-Playback: 45.7%; Short-term Post-Playback: 43.9%; Long-term Post-Playback: 32.4%; $F_{2,119} = 8.20$, $p < 0.001$). *Eulemur* individuals did move up in the canopy during the last 45 minutes of the experiments (*Percent Time Low in Canopy*: Pre-Playback: 3.7%; Short-term Post-Playback: 14.1%; Long-term Post-Playback: 11.9%; $F_{2,119} = 6.81$, $p < 0.01$).

Hapalemur griseus griseus

Hapalemur individuals exhibited an even greater cryptic response than *Eulemur* by decreasing vigilance and activity levels for the entire one hour after the predator playbacks. (*Percent Time Vigilant*: Pre-Playback: 22.9%; Short-term Post-Playback: 17.5%; Long-term Post-Playback: 16.4%; $F_{2,119} = 3.32$, $p < 0.05$. *Percent Time Active*: Pre-Playback: 52.9%; Short-term Post-Playback: 23.9%; Long-term Post-Playback: 38.4%; $F_{2,119} = 18.29$, $p < 0.0001$). Instead of moving up in the canopy to hide, *Hapalemur* generally moved lower and were significantly lower in the canopy following playbacks of the aerial predators. (After Aerial Predators: 40.6 % Time Low) than the terrestrial predator (After Fossa: 31.1% Time Low; $F_{1,119} = 8.67$, $p < 0.01$). *Hapalemur* individuals decreased their activity levels in response to all predator playbacks versus the control. (*Percent Time Active*: After Predator Playbacks: 29.9%; After Control Playbacks: 41.2%; $F_{1,119} = 13.42$, $p < 0.001$).

Propithecus edwardsi

In contrast to the smaller lemur species, *Propithecus* individuals altered vigilance only following playbacks of the most important aerial predator in this rainforest system, *A. henstii*. (*Percent Time Vigilant*: After *A. henstii*: 31.9%; After Other Predators: 25.7%; After Control Playback: 22.3%; $F_{1,119} = 6.47$, $p < 0.01$.) There were no overall effects of the playbacks on vigilance or height choice

for this species. The only general effect observed was that *Propithecus* exhibited higher activity levels following the control playbacks than those of the aerial predators. (*Percent Time Active*: After Control Playback: 63.1%; After Aerial Predators: 48.0%; $F_{1,119} = 15.72$, $p < 0.001$.)

Inter-species responses to playback experiments

The effect of species identity on the behavioral responses of lemurs to the predator playback experiments was tested along with the effects of time since playback, playback type, and all possible interactions.

Vigilance

Both *Eulemur* (24.7% more vigilant) and *Propithecus* (25.9%) were significantly more vigilant than *Hapalemur* (17.9%; $F_{2,395} = 20.61$, $p < 0.001$), but there were no differences between *Eulemur* and *Propithecus*.

Activity

For all species, activity decreased significantly from the pre-playback through the hour after the playbacks. *Propithecus* spent significantly more time active (51.9%) than either *Eulemur* (37.4%) or *Hapalemur* (38.4%; $F_{2,395} = 8.32$, $p < 0.001$), but the latter two species did not differ significantly from each other. *Hapalemur* individuals were significantly less active after the playbacks than both of the other lemur species.

Height

Hapalemur spent significantly more time at a low height, under 5 m in canopy, (36.6%) than either *Eulemur* (10.7%) or *Propithecus* (18.2%; $F_{2,395} = 58.68$, $p < 0.001$), while *Propithecus* spent significantly more time low than *Eulemur*.

Playback type

There were no consistent responses across the three lemur species with regard to vigilance levels to the playbacks. For all species, the percent of time spent active was significantly greater following playbacks of the control than of the other aerial predators ($F_{2,395} = 11.62$, $p < 0.001$). Further, for all three lemur species, the percent of time spent low was greater after playbacks of *A. henstii* than of the other aerial predators ($F_{2,395} = 5.21$, $p < 0.05$).

Discussion

Predation Rates and Lemur Anti-predator Tactics

Long-term data on raptor predation on lemurs in Ranomafana, including this study on raptor nest prey, show that no individuals of *Propithecus* were observed in the

diets of *A. henstii* or *P. radiatus*, or any other raptor. In comparison, *E. fulvus rufus* experienced a minimum predation rate of 1.25% of the population killed per year by *Accipiter* and *Polyboroides*, while *H. griseus* experienced a predation rate of at least 15.12% per year by these two raptor species (Figs. 4.3, 4.4). The cryptic habits of *Eulemur* and *Hapalemur* documented in the experimental part of this study did not appear to be totally effective in protecting these lemurs from raptor predation.

Lemur Behavioral Responses to a Multiple-Predator Community

In general, the results of these experiments are in agreement with previous research using playbacks of predator vocalizations in showing that the initial responses by lemurs are often predator specific (Macedonia & Polak, 1989; Macedonia, 1990; Zuberbühler et al., 1999; Fichtel & Kappeler, 2002). All species of lemurs recognized aerial vs. terrestrial predators and all three lemur species became more vigilant after the playbacks of calls. As reported in Karpanty & Grella (2001) and Wright (1998) and observed in these experiments, the initial response of each of these lemurs is most frequently to search the sky, drop in the canopy, and alarm or flee from the source of the vocalization when the playback is of a raptor predator. When the playback is of the fossa, the lemurs more frequently ascend in the canopy, increase downward vigilance, and give a general excitement alarm.

The data on vigilance, height, and activity choice from this experiment indicate that after the initial alarm and flight reaction, *Eulemur* and *Hapalemur* switch behavior to employ a cryptic anti-predator strategy, while *Propithecus* individuals respond very specifically only to predators that pose a serious threat (*C. ferox* and *A. henstii*). Studies of nests of the diurnal raptors reveal that *A. henstii* kills more lemurs than other raptors in this system (this study, Karpanty, 2006). *Propithecus* increased their vigilance more significantly to playbacks of *Accipiter* than to other raptors.

These findings that lemurs may alter vigilance, height, and activity after the initial alarm response according to general predator type and specific level of risk provide new information on the anti-predator strategies of diurnal and cathemeral lemurs. The contrast in the general cryptic strategy of *Hapalemur* and *Eulemur* versus the predator-specific strategy of *Propithecus* may have important implications in this multiple-predator community. Lima (1992) and Matsuda et al. (1993, 1994, 1996) demonstrate that predator-specific, anti-predator behaviors, such as those exhibited by *P. edwardsi*, may lead to greater predation rates than what would be expected if one simply extrapolated the predation rates of single predators alone.

Lemur Social Aggregations and Risk of Predation

Primates may join in larger groups to reduce risk from predators (Hamilton, 1971; Alexander, 1974; van Schaik, 1983; Terborgh & Janson, 1986; Janson, 1992).

Compared to many primates on other continents, group size in lemurs is small, ranging from monogamous groups of 3–6 and polygynous groups of 3–25 (Wright, 1999). In this study of a community of lemurs of different social group sizes, we have begun to understand the nuances of variability in group size as a predator deterrent or protection by comparing the effects of predation on two same-sized lemurs, *E. rubriventer* (monogamous groups of 3–5) and *E. fulvus rufus* (polygynous groups of 5–18, Overdorff, 1996). We would predict that larger group size would be a more successful strategy due to dilution effect, as well as having “more eyes and ears” for an early warning alert. Both lemur species are taken by the goshawk and the fossa. The prediction based on socio-ecological theory would be that the species with smaller group size would be preyed upon more. However, our data suggest that five times as many *E. f. rufus* were eaten by Henst’s goshawk as *E. rubriventer*. When the predation rate is calculated to equal the percentage of the lemur population killed per year, this difference evens out. The sample size is not large and should be taken with caution, but there is a suggestion that commonness rather than group size may be a factor in predator choice. There may be a slight advantage to large group size in the “dilution effect,” but there is also the possibility that larger, noisier, groups may attract predators.

Body Mass and Risk of Predation

The absence of adult *Propithecus* from the diets of raptors may be accounted for by *Propithecus*’ large body mass: three times the body mass of *Eulemur* and six times the body mass of *Hapalemur*. However, infants only reach the body mass of *Hapalemur* at six months, and of *Eulemur* after a year, and yet these vulnerable infants are not preyed on by the raptors; perhaps because of the high levels of vigilance of the adult *Propithecus*. This strategy makes sense in light of the life history of the lemurs. *Propithecus* females give birth only once every two years, on average (Wright, 1995; Pochron et al., 2004), and each offspring is perhaps more valuable than infants of species that reproduce every year, such as *Eulemur* and *Hapalemur* (Overdorff et al., 1999, Tan, 1999). Vigilance may be well worth the foraging cost to *Propithecus*.

Both goshawks and harrier hawks preferred primates that were 1 kg in body weight. There are three lemur species—*Hapalemur griseus*, *Avahi laniger*, and *Lepilemur seallii*—with this adult body weight at RNP, but *Lepilemur* was not observed eaten by the raptors, perhaps because of their rarity or their habit of sleeping deep in tree holes during the day (Porter, 1998). *Avahi* was the preferred choice by the harrier hawk and *Hapalemur* was the preferred choice of the goshawk. When predation rate was calculated, taking into account percentage of lemur population killed by raptors, *H. griseus* had the highest predation rate at three and a half times the rate of *A. laniger*. Body mass is equal in *Avahi* and *Hapalemur*, so the higher rate of *Hapalemur* cannot be accounted for by body mass alone. This difference in observed predation rate might be related to differences in anti-predator strategies, group size, activity patterns, or habitat use patterns.

Species Rarity and Hibernation

A factor in predation rate that is obvious, but not often discussed as a strategy, is patchiness or rarity in the environment. In this community there are two endangered (*P. edwardsi* and *V. variegata*) and two critically endangered species (*H. aureus* and *P. simus*) (IUCN, 2005) lemurs in the RNP community. Three of these species (*Varecia*, *Haplemur*, *Prolemur*) have populations that are extremely patchy in all forests (Arrigo-Nelson & Wright, 2004; Balko & Underwood, 2005; Irwin et al., 2005). These lemurs were rarely eaten by raptors, partially because they were difficult to find. Making oneself “scarce” may be a strategy in the case of two lemur species that are commonly eaten, *Microcebus rufus* and *Cheirogaleus major*. For many weeks or months of the year, these species go into torpor, and because they are not active they are not easily found by aerial and terrestrial predators. However, during periods of torpor, these lemurs may be more vulnerable to snake predation (Wright & Martin, 1995). The avoidance of predation by certain species of predators may be another advantage of torpor.

Birth Synchrony of Lemurs

One strategy to help alleviate the risk of predation is the synchronization of births, which results in a “dilution” effect (Boinski, 1989). Same-size lemurs do synchronize their birth seasons (Wright, 1999; Wright et al., 2005). More research would be needed to determine if birth synchrony is successful against predation.

Activity Cycle and Risk of Predation

During the 1990s a lively scientific controversy arose regarding lemur evolution and raptor predation. With the discovery of two extinct genera of large eagles in the sub-fossil record, Goodman (1994a,b) and Goodman & Rakotozafy (1995) suggested that present-day raptor alarm calls by lemurs could be remnants of behaviors evolved to avoid the giant extinct raptors. A series of papers expanded on this idea to suggest that diurnal lemurs had only recently become day-active, after day-active giant raptors went extinct (van Schaik & Kappeler, 1993, 1996; Kappeler & Heyman, 1996). This change would have been quite recent since sub-fossil lemur bones are dated 500–20,000 yrs BP (Simons, 1997). Field evidence on present-day raptor predation on lemurs was sparse (Goodman et al., 1993a,b,c), but lemur studies cast doubt on this theory of lemur evolution (summarized in Wright, 1999).

Recent evidence, including the results from this paper, confirms that in present-day Madagascar, nocturnal, diurnal, and cathemeral lemurs are vulnerable to both raptors and carnivores (Table 4.7). We show that in the Ranomafana rainforest, diurnal raptors such as *A. henstii* and *P. radiatus* eat almost equal numbers of nocturnal, cathemeral, and diurnal prey. In addition, *C. ferox*, active in all hours of the day and night, eats nocturnal and diurnal lemurs (Wright, 1998; Dollar, 1999; this study). However, the most eaten prey of the raptors by a factor of 10 was a diurnal primate (*H. griseus*), and the second most popular menu item was *A. laniger* of equivalent body mass and social system, but with a nocturnal lifestyle. Therefore, the advantage of being nocturnal to avoid diurnal raptors, as seen in

TABLE 4.7. Activity cycle of lemurs and predation evidence in Ranomafana National Park, ranked high, medium or low. Population density (P) is ranked common (C) or patchy and rare (R). Common species of possible size are preferred by all predators. Note that no data have been collected for owls at this site.

Activity Cycle	Species	P	<i>Accipiter</i>	<i>Polyboroides radiatus</i>	<i>Cryptoprocta ferox</i>	<i>Galidia elegans</i>
Diurnal	<i>Propithecus edwardsi</i>	C	–	–	medium	–
Diurnal	<i>Varecia variegata</i>	R	low	–	low	–
Diurnal	<i>Prolemur simus</i>	R	–	–	low	–
Diurnal	<i>Hapalemur aureus</i>	R	–	–	–	–
Diurnal	<i>Hapalemur griseus</i>	C	high	medium	–	–
Cathemeral	<i>Eulemur rubriventer</i>	C	medium	–	low	–
Cathemeral	<i>Eulemur fulvus rufus</i>	C	medium	–	low	–
Nocturnal	<i>Daubentonia</i>	R	–	–	–	–
Nocturnal	<i>Lepilemur seallii</i>	R	–	–	–	–
Nocturnal	<i>Avahi laniger</i>	C	medium	medium	low	–
Nocturnal	<i>Cheirogaleus major</i>	C	medium	medium	–	low
Nocturnal	<i>Microcebus rufus</i>	C	medium	high	low	low

the South American owl monkey (Wright, 1989, 1994), may be important to the rainforest primates of Madagascar as well, but will not offer complete protection from predation by diurnal predators. Future research is needed to determine if this is true of other sites or at all times of year as the raptor predation data reported here were collected during the raptor nesting season alone.

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