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Predation, Communication, and Cognition in Lemurs

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Introduction

Predation represents an important selective force shaping the evolution of primate behavior. Primates confronted with predators have evolved various strategies to minimize the probability of being eaten. Predation risk and hunting styles of predators should have selected for communicative and cognitive abilities linked to socioecology and life history. As studies on several socially cohesive mammals indicate, the study of anti-predator behavior represents an important tool for gaining insight into cognition, e.g., to understand how animals classify objects and events in the world around them (e.g., marmots: Blumstein, 1999; vervet monkeys: Seyfarth et al., 1980; Diana monkeys: Zuberbühler, 2000; suricates: Manser et al., 2002).

Malagasy lemurs belong to the most ancient extant primate radiation (Yoder, 2003). They show the largest variation in body sizes, activity, feeding patterns, locomotion styles, and sociality patterns among the strepsirrhine and provide, therefore, important models to explore the origin and evolution of primate behavior. Previously, Goodman et al. (1993) stated that predation pressure on lemurs was highly underestimated. Recent data supported that this pressure is comparable to, and in some cases even higher than, that of primates on other continents (Goodman, 2003). We therefore expected that lemurs would not only show crypsis to avoid predators, but would adapt to their predatory world by evolving distinct anti-predator strategies similar to those of anthropoid primates.

In this review we will have two major goals: We will estimate predation risk of lemurs based on current data on the number of predator species. By relating this information to the variation of life history and ecology in lemurs we will explore whether these traits are shaped by predation. Furthermore, we will summarize data on predation-related behavior of lemurs, including our own data on nocturnal lemurs, to investigate the general hypothesis that predation risk, perception abilities, and hunting styles of predators explain the variation of anti-predator strategies and associated communicative and cognitive abilities.

Methods

We have reviewed the literature on predation and anti-predation strategies in lemurs from 1940 to 2005 using PrimateLit (http://primatelit.library.wis.edu.). We also included unpublished predator-related information from the Ankarafantsika National Park in northwestern Madagascar obtained by our group and those of unpublished diploma and Ph.D. theses. In total, we included 49 references, 24 for diurnal, 10 for cathemeral, and 29 for nocturnal lemurs.

   Predation in primates is difficult to assess (Goodman et al., 1993; Goodman, 2003), in particular for nocturnal species. One possible approach toward estimating predation pressure for different lemur genera is to take as a rough indirect estimate the number of predator species to which lemurs are exposed. In this study we have used the number of predator species as an index to estimate predation risk in a respective lemur genus (see also Anderson, 1986). We summarized information of predator species for each lemur genus and displayed it in Table 5.1. We distinguished three different predation risk classes by taking the highest reported number of predator species ($N = 13$) and dividing it by three. The following classes were then set up: *low risk* (0 to 3 predator species), *medium risk* (4 to 8 predator species) and *high risk* class (9 to 13 predator species). To relate the information on predation risk to life history traits and ecology of lemurs, we extracted data on activity, body mass, number of predators, foraging group size, maximum female reproductive output per year (Mueller & Thalmann, 2000; Goodman et al., 2003; Zimmermann & Radespiel, in press). We calculated the mean for the following traits per genus across the number of those species for which this information was accessible: body mass, foraging group size, and female reproductive output per year (Table 5.2). We related the number of predator species to life history traits and ecology using Spearman rank correlation. We calculated a regression model (curve estimation procedure) according to SPSS 13.0 to explore the relation between predation risk and the particular trait being considered when values for the latter were normally distributed. We compared predation risk between nocturnal and diurnal/cathemeral lemurs using the Mann-Whitney U test for two independent samples.

Results

Predation and Its Relation to Variation in Life History and Ecology of Lemurs

More than twenty different predator species (ten raptors, six carnivores, five reptiles, as well as two lemur species) are reported to prey on lemurs (Goodman, 2003). Three lemur genera belong to the low predation risk class (*Daubentonia, Varecia, Indri*), eight to the medium predation risk class (*Mirza, Phaner*,

TABLE 5.1. Overview of known lemur predators based on Goodman (2003), [1]Schülke (2001), [2]Burney (2002), [3]Fietz & Dausmann (2003), [4]Dollar et al. (Chapter 3), [5]Karpanty & Wright (Chapter 4) and [6]Gould & Sauther (Chapter 13). Lemurs and predators are arranged according to body mass (data of lemurs and carnivores from Goodman et al., 2003; of birds from Langrand, 1990, and of reptiles from Glaw & Vences, 1996).

Predator	Primate Species Preyed Upon												
	Microcebus	Cheirogaleus	Mirza	Phaner	Lepilemur	Avahi	Hapalemur	Eulemur	Daubentonia	Lemur	Varecia	Propithecus	Indri
BIRDS													
Vanga curvirostris	+												
Tyto soumagnei	+												
Tyto alba	+	+[3]			+								
Asio madagascariensis	+	+	+		+	+	+						
Aviceda madagascariensis				+									
Buteo brachypterus		+	+	+	+							+	
Accipiter henstii	+	+[5]			+[5]	+	+[5]	+			+[5]	+[5]	
Accipiter francesii							+[5]						
Eutriorchis astur						+							
Polyboroides radiatus	+	+			+	+[5]	+[5]			+		+	
CARNIVORES													
Mungotictis decemlineata	+	+			+								
Galidia elegans	+	+											
Viverricula indica*										+			
Felis sylvestris*										+			
Cryptoprocta ferox	+	+	+	+	+	+[4]		+	+	+	+	+	
Canis lupus*	+									+[6]			
REPTILES													
Ithycyphys miniatus	+		+[1]										
Sanzinia madagascariensis	+	+		+[1]			+						
Acrantophis madagascariensis								+				+[2]	
Acrantophis dumerilii		+[3]											
Crocodylus niloticus								+					
PRIMATES													
Mirza coquereli	+												
Eulemur fulvus										+			
TOTAL NUMBER OF PREDATORS	**13**	**10**	**5**	**4**	**7**	**5**	**5**	**4**	**1**	**6**	**2**	**5**	**0**

* introduced predators

TABLE 5.2. Predation risk, life history traits and ecology of lemurs (according to [1]Goodman et al. (2003), [2]Zimmermann & Radespiel (in press), [3]Müller & Thalmann (2000); mean value of trait across all species of a genus was calculated.

Genus	Family	Activity[1]	Body Mass[1] (g)	Number of Predators[1]	Foraging Group Size[1]	Maximum Female Reproductive Output/Year[2]	Social System[3]
Microcebus (n = 8)	Cheirogaleidae	n	53	13	1	2	dispersed MM
Cheirogaleus (n = 2)	Cheirogaleidae	n	281	10	1	2	dispersed monogamy
Mirza (n = 1)	Cheirogaleidae	n	294	5	1	2	dispersed MM
Phaner (n = 1)	Cheirogaleidae	n	327	4	2	?	dispersed monogamy
Lepilemur (n = 4)	Lepilemuridae	n	740	7	1	1	dispersed monogamy
Avahi (n = 2)	Indriidae	n	1012	5	3.25	1	gregarious monogamy
Hapalemur (n = 3)	Lemuridae	c	1644	5	4.83	1.09	gregarious MM
Eulemur (n = 5)	Lemuridae	c	2081	4	5.70	0.75	gregarious monogamy gregarious MM gregarious monogamy
Daubentonia (n = 1)	Daubentoniidae	n	2516	1	1	0.6	dispersed MM
Lemur (n = 1)	Lemuridae	d	2678	6	16.9	0.86	gregarious MM
Varecia (n = 1)	Lemuridae	d	3548	2	11.0	2	gregarious MM
Propithecus (n = 3)	Indridae	d	4196	5	5.47	1	gregarious MM
Indri (n = 1)	Indridae	d	6480	0	3.10	1	gregarious monogamy

N = number of species; n = nocturnal;

c = cathemeral; d = diurnal; MM MF = multimale-multifemale system

Lepilemur, Avahi, Hapalemur, Eulemur, Lemur, *Propithecus*) and two genera belong to the high predation risk class (*Microcebus, Cheirogaleus*) (Table 5.2).

Life history traits are supposed to be an adaptation to predation in anthropoid primates (Isbell, 1994; Janson, 2003), therefore we explored to what extent this is also true for lemurs by relating particular life history and ecological traits to predation risks.

It is predicted that predation shapes group size in anthropoid primates (e.g., Van Schaik, 1983). Individuals living in large groups are assumed to be less threatened by predation because of safety-in-number effects and/or improved predation detection (Alcock, 1997). Lemurs living in cohesive groups that forage together should consequently be eaten by fewer numbers of predators than those foraging in pairs or solitarily. If grouping pattern at a sleeping site protects against predators, as assumed by various studies (e.g., Radespiel et al., 1998, 2003), lemur species forming sleeping groups should be exposed to a lesser predation risk than those sleeping solitarily. The first part of this hypothesis is not supported by our data. Thus, foraging group size and predation risk are neither correlated for nocturnal (Spearman correlation: $r = -0.360$, $N = 7$, $P = 0.428$) nor for diurnal/cathemeral genera (Spearman correlation: $r = 0.464$, $N = 6$, $P = 0.354$) nor for the whole lemur sample (Spearman correlation: $r = -0.278$, $N = 13$, $p = 0.357$). The second part of the hypothesis is hard to investigate since up until this time, only two genera were described in which individuals of both sexes sleep solitarily (*Mirza, Daubentonia*).

A further hypothesis established for anthropoid primates predicts that high female reproductive output per year is an adaptation to predation (e.g., Hill & Dunbar, 1998). According to this hypothesis, genera with a high number of offspring per year should be exposed to a higher number of predator species than those with a lower reproductive rate. Reproductive rate and predation risk are, however, not significantly related neither in the whole lemur sample (Spearman correlation: $r = 0.408$, $N = 12$, $p = 0.188$) nor in nocturnal (Spearman correlation: $r = 0.705$, $N = 6$, $p = 0.188$) or diurnal/cathemeral lemurs (Spearman correlation: -0.279, $N = 6$, $p = 0.592$).

Others discuss that predation selects for activity mode (e.g., Clutton-Brock & Harvey, 1980; Terborgh & Janson, 1986; Bearder et al., 2002). Nocturnal activity is assumed to be a response to high predation pressure during the day. According to this hypothesis, lemurs foraging during the night should be exposed to a lower predation risk than those foraging during the day. Instead, nocturnal lemurs seem to suffer a similar predation risk to diurnal/cathemeral lemurs (Mann-Whitney $U = 12, 5$, $N = 13$, $p = 0.218$).

Body size (or body mass) is often assumed to be an adaptation to predation (e.g., Isbell, 1994), in so far as larger species are less vulnerable than smaller ones. This hypothesis is supported by data in lemurs. Variation of body mass is indeed significantly related to predation risk and can be best explained by a logarithmic model ($r^2 = 0.639$, df $= 11$, $p = 0.001$, Figure 5.1). Accordingly, the small-bodied mouse lemurs (*Microcebus ssp.*) were found to be eaten by the highest number of predator species, from smaller to larger ones and from nocturnal to
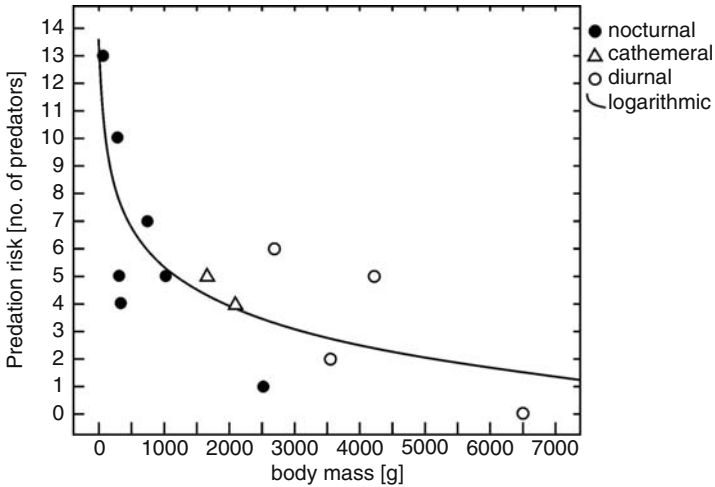
FIGURE 5.1. Relationship between mean adult body mass and predation risk in 13 lemur genera

crepuscular to diurnal ones, including aerial and terrestrial predators, whereas the largest extant lemur, the indri (*Indri indri*), does not seem to have a single extant predator (except human poachers, who represent evolutionarily new predators that cause an increasing threat to all extant lemurs).

These findings imply that predation risk and body mass are closely linked to each other in lemurs. Consequently they should act as important selective forces shaping the evolution of sensory and brain mechanisms and related antipredator behaviors minimizing the risk to be eaten.

Strategies and Alarm Call Systems

Current theory suggests that different hunting styles of predators shape escape behaviors as well as communication and cognitive abilities of anthropoid primates (e.g., Seyfarth & Cheney, 2003). "Alarm calls" were thereby defined as calls given by the prey when they encountered a predator. Calls may not only inform about the presence of a predator, but may also encode information about the urgency of escape (urgency-based alarm call system sensu: Owings & Hennessy, 1984) and the type of predator (functionally referential alarm call system sensu: Seyfarth & Cheney, 2003). A researcher needs to perform audio playback experiments to make the differentiation between an urgency-based and a functionally referential alarm system.

Lemurs face different risks of predation related to body mass. Here, we will transfer the theory outlined for anthropoid primates for the first time to lemurs to explore whether different perception abilities and hunting styles of evolutionarily old lemur predators have selected for particular predation recognition and signaling systems in the lemur's brain. How lemurs express and recognize fear

evoked by predators and how they will categorize their predatory world we will assess by their predator-advertisement and -avoidance behavior. Based on the previously described lemur predators, we expect four major anti-predator strategies:

1. *Terrestrial snake anti-predator strategy*: Snakes locate prey by olfactory cues and boas additionally by infrared detection of body heat (e.g., Neuweiler, 2003; Safer & Grace, 2004). They are usually sit-and-wait hunters, but may also actively search for their prey on the ground, in dense vegetation or in nests or tree holes. Snakes cannot hear, do not seem to see well, and are not able to move too fast, especially when temperatures are low, but they can climb well on bushes and trees. A prey living in a dispersed or cohesive social system with kin, mate, or social partners nearby, will bear almost no cost, but may benefit (with regard to fitness), if snake detection will induce acoustic and visual snake advertisement, e.g., pointing to the snake while circling around and steering at the snake from a safe distance while giving alarm calls. Not only group members at visual distance but also visually separated ones profit from receiving alerts and from searching for the sender and the alerting stimulus. A snake confronted by several mammals moving around will most probably get distracted and retreat.

2. *Terrestrial carnivore anti-predator strategy*: Carnivores such as viverrids locate prey by olfaction, audition, and vision (e.g., Neuweiler, 2003) and are therefore not easy to avoid. Viverrids hunt either by surprise attacks from hidden places, by pursuing their prey on the ground as well as through bushes and trees, or by grabbing it out of vegetation, nest, or tree hole (Goodman, 2003). Different anti-predator responses may be evolutionarily beneficial, depending on body size of prey and its actual location. During foraging, small-bodied prey should be expected to retreat as cryptically as possible into dense strata of the forest without any calling, whereas larger-bodied prey should flee to cover and advertise predator detection by loud mobbing calls (Curio, 1993), in this way recruiting mobbing conspecifics. A carnivore predator mobbed by loud calls of a number of mobile animals will most likely give up and retreat (e.g., Curio, 1993; Zuberbühler & Jenny, 2002). During resting at the sleeping site, e.g., when being grabbed out of a hole, a surprised prey should produce a loud and noisy threat display to distract the predator (e.g., Owings & Morton, 1998).

3. *Aerial anti-predator strategy*: Diurnal raptors, e.g., hawks, buzzards, or eagles, locate prey primarily by vision while flying around and scanning their territories from the sky and by surprise attack, whereas nocturnal raptors such as owls, for example, locate their prey primarily by audition (e.g., Konishi, 1973; Gaffney & Hodos, 2003; Neuweiler, 2003) while sitting motionless on perches followed by almost noiseless surprise attacks. Foraging and sleeping in dense vegetation or sleeping in shelters such as nests or tree holes should provide prey with the best protection against both diurnal and nocturnal raptors. Besides, detection of a flying raptor should induce alarm calling accompanied by a sudden flight-to-cover reaction in the detecting animal (e.g., flight to denser vegetation, nest, hole), sky scanning, and similar reactions in nearby conspecifics; detection of

a perched raptor should evoke a mobbing response as described for viverrids. Diurnal and nocturnal raptors are constrained in their hearing capabilities to frequencies below 10 kHz (Fay, 1988), which provides small-bodied lemurs with the possibility of exploiting a range above 10 kHz, for less costly predator advertisement.

4. *Panic cry anti-predator strategy*: If a predator has already seized its prey, the captured prey should use panic, distress calls, or screams as a last-ditch effort to manage the predator that holds it. These calls may startle the predator, bring on mobbing, or attract a larger predator to compete for it (e.g., Driver & Humphries, 1969; Hogstedt, 1983; Owing & Morton, 1998).

   A fifth anti-predator strategy, described for a variety of birds and mammals (e.g., Zuberbühler, 2003; Rainey et al., 2004), is not directly related to perception abilities and hunting styles of predators, but may depend on cognitive abilities of lemurs:

5. *Semantic predator recognition strategy*: Individuals living in dispersed or cohesive groups should benefit if they relate predator alarm calls of sympatric species and calls produced by the predator itself to the same predator category as their own conspecific predator alarm calls irrespective of their acoustic structure. We will explore our hypotheses with regard to the expected anti-predator strategies by reviewing our current knowledge on the behavior of lemurs in the predation context.

Nocturnal Lemurs

Nocturnal lemurs consist of genera with low to high predation risk (Table 5.1 and 5.2). All studied genera forage solitarily during the night (other than *Avahi* (cohesive pairs), Table 5.2) and sleep either solitary (*Mirza coquereli, Daubentonia madagascariensis*) or form sleeping groups of stable composition during the day (e.g., *Cheirogaleus medius, Lepilemur edwardsi, Microcebus murinus*, and *M. ravelobensis, Phaner furcifer*). Anecdotal information suggests that, other than *Cheirogaleus*, all nocturnal lemur genera produce calls in the presence of predators (e.g., Petter & Charles-Dominique, 1979; Stanger, 1995; Zimmermann 1995; Rakotoarison et al., 1996; Table 5.3). In most cases, however, predator-prey interactions were not specified. We will summarize in the following account studies in which this information was documented.

   In four nocturnal species direct snake–lemur interactions were seen in the natural environment. Schmelting (2000) observed a confrontation of a gray mouse lemur male (*Microcebus murinus*) with the Madagascar boa (*Sanzinia madagascariensis)* in the dry deciduous forest of Ankarafantsika in northwestern Madagascar. The mouse lemur detecting the snake jumped around it, and approached and retreated from it to a safe distance producing whistle calls (calls with Fo above 10 kHz, see Zimmermann et al., 2000). Other mouse lemurs in the vicinity are attracted to the sender, themselves producing whistle calls. Whistle calls are not exclusively produced in the predation context but also during various

TABLE 5.3. Alarm calls of different lemur species.

Species	Calls in Response to Predators	Panic Call	Snake	Raptor	Carnivore	Response Toward Heterospecific Alarm Calls	References
				Calls in Response To			
Microcebus murinus	grunt, whistle		whistle[m]			*Microcebus ravelobensis*	Petter & Charles-Dominique, 1979; Stanger, 1995; Zimmermann,1995; Schmelting, 2000; Zietemann, 2000; Braune et al., 2005
Microcebus ravelobensis	grunt, whistle						Zietemann, 2000; Braune et al., 2005
Microcebus rufus	grunt, whistle						Zietemann, 2000
Microcebus myoxinus	grunt, whistle						Zietemann, 2000
Cheirogaleus major	grunt	distress call					Petter & Charles-Dominique, 1979
Cheirogaleus medius	grunt						Petter & Charles-Dominique, 1979; Stanger, 1995; Gilbert, 2001; this paper
Mirza coquereli	ptiak/zek, croak, grunt		zek[m]			*Mirza coquereli*	Petter & Charles-Dominique, 1979; Pages, 1980; Stanger, 1995; Schülke, 2001; this paper
Phaner furcifer	ki, kiu, kea		kiu[m]				Petter & Charles-Dominique, 1979; Charles-Dominique & Petter, 1980; Stange, 1995; Schülke, 2001
Lepilemur leucopus	hein, hee						Petter & Charles-Dominique, 1979
Lepilemur edwardsi	oooai, oui oui oui, grunt, bark, shrill, chatter	scream			bark, shrill, chatter		Petter & Charles-Dominique, 1979; Rasoloharijaona, 2001; this paper
Lepilemur ruficaudatus	"boako-boako", oooai, oui oui oui	distress call					Schülke & Ostner, 2001
Lepilemur septentrionalis							Petter & Charles-Dominique, 1979
Avahi spec.	grunt, "ava hy"						Petter & Charles-Dominique, 1979
Hapalemur aureus	whimpering			whimpering			Goodmann et al., 1993
Hapalemur griseus	grunt	muffled alarm call					Petter & Charles-Dominique, 1979; Rakotondravony et al., 1998
Hapalemur simus	roar						Petter & Charles-Dominique, 1979
Eulemur coronatus	grunt, high pitched call						Petter & Charles-Dominique, 1979
Eulemur fulvus	woofs, huvvs, (grunts), chatter			chatter[r]	woofs[u], huvvs[u]	*Propithecus v. verreauxi*	Sussmann, 1975; Paillette & Petter, 1978; Petter & Charles-Dominique, 1979; Fichtel & Kappeler, 2002; Fichtel, 2004

Species						Compared with	References
Eulemur macaco	huff-grunts, rasp, scream, whistle, (crouiii), alarm hack			scream, rasp, whistle, alarm hack	huff-grunts[m], rasp[m]		Petter & Charles-Dominique, 1979; Colquhoun, 1993
Eulemur mongoz	grunt, hon						Petter & Charles-Dominique, 1979
Eulemur rubiventer	grunt, high pitched call						Petter & Charles-Dominique, 1979
Daubentonia madagascariensis	ron-tsi/sneeze, grunt						Petter & Charles-Dominique, 1979; Stanger & Macedonia, 1994; this paper
Lemur catta	gulp, click, closed-mouth, click, open-mouth, click, chirp, shriek, rasp, yap			gulp, shriek[r], rasp[r], chirp	gulp, click, closed-mouth click, open-mouth click, yap[r]	*Propithecus v. verreauxi*	Sussmann, 1975; Sauther, 1989; Macedonia, 1993, 1990; Pereira & Macedonia, 1991; Macedonia & Evans, 1993; Oda & Masataka, 1996; this paper
Varecia variegata	abrupt roars with wails, growls, growl snorts, pulsed squaks			abrupt roars with wails[u/m]	growls, growl snorts, pulsed squaks[u/m]		Macedonia, 1990, 1993; Pereira et al., 1988
Propithecus diadema	roar, "simpona"						Petter & Charles-Dominique, 1979
Propithecus verreauxi	growl, alarm barks, roar			growl[u], roar[r]	growl[u]	*Lemur catta, Eulemur fulvus*	Sussmann, 1975; Richard, 1978; Oda, 1998; Fichtel & Kappeler, 2002; Brockman, 2003; Fichtel, 2004
Indri indri	roar, bark, honk	alarm	barks				Pollock, 1975; Petter & Charles-Dominique, 1979

m = mobbing call; u = urgency-based alarm call; r = referential alarm call

social interactions (Stanger, 1995; Zimmermann, 1995; Zimmermann et al., 1995; Zietemann, 2000; Braune et al., 2005). Their high variability in acoustic structure provides the potential for predator specificity. In a sympatric association of fork-marked lemur (*Phaner furcifer)* and Coquerel's dwarf lemur (*Mirza coquereli*) in the dry deciduous forest Kirindy of western Madagascar, Schülke (2001) observed another direct snake–lemur interaction, which provided the first evidence for semantic predator recognition in nocturnal lemurs. The sub-adult male of a dispersed foraging group of fork-marked lemurs detected a snake and gave "kiu" calls while circling around the snake, staring at it, and moving toward and away from it at a safe distance. This vocal reaction induced not only a sudden attraction of and mobbing by other group members, but also the attraction of a sympatrically foraging Coquerel's dwarf lemur, which, after detecting the snake, also started circling around it while giving "zek" calls. There was no indication of mobbing behavior in *Cheirogaleus medius,* but (Fietz & Dausmann, 2003) observed a female fat-tailed dwarf lemur defending its offspring by attacking a snake (*Madagascarophis colobrinus*) next to its sleeping hole. Induced snake–lemur confrontations were investigated in the laboratory. Here, predator-naïve pairs of two nocturnal species–the gray mouse lemur (*Microcebus murinus*; $N = 4$) and the brown mouse lemur (*Microcebus rufus*; $N = 2$)–were visually exposed either to a living python or to a python dummy in front of the enclosure (Zimmermann et al., 2000). In contrast to the situation in the natural environment, there was no significant difference in locomotion and vocal activity before and after stimulus presentation (Bunte, 1998). No information on snake anti-predator strategies exists so far for *Allocebus, Avahi, Lepilemur, Cheirogaleus*, and *Daubentonia*.

To date, direct viverrid interactions with nocturnal lemurs in nature were reported in two genera. Rabesandratana et al. (2005) observed a fossa (*Cryptoprocta ferox*) chasing a Milne-Edwards' sportive lemur through the forest in the Ankarafantsika National Park in northwestern Madagascar. The sportive lemur fled by jumping rapidly from tree to tree into the vicinity of its sleeping site emitting loud bark call sequences (Figure 5.2). As the fossa had almost gripped the lemur, the latter gave much louder shrill and chatter calls. It seemed as if an increase in arousal was encoded in an increasing noisiness and an increasing calling rate, as well as in a change of call types. Sportive lemurs in the vicinity got attracted to the interaction while emitting loud bark calls. The fossa finally gave up and retreated. Schülke (pers. communication) observed an interaction between Phaner and a fossa at the Kirindy research station in central western Madagascar. The lemur sat high in the canopy and produced kiu calls while the fossa was walking over the ground.

Up until now, two direct confrontations between nocturnal lemurs and raptors have been described from the field. Schülke & Ostner (2001) observed a Madagascar harrier-hawk (*Polyboroides radiatus*) attacking a red-tailed sportive lemur (*Lepilemur ruficaudatus)* at its sleeping site in the Kirindy forest in western Madagascar. The Madagascar harrier-hawk seized the lemur with its bill and pulled it out from its hole while the lemur emitted loud distress calls (= panic call). Gilbert & Tingay (2001) saw a Madagascar harrier-hawk preying
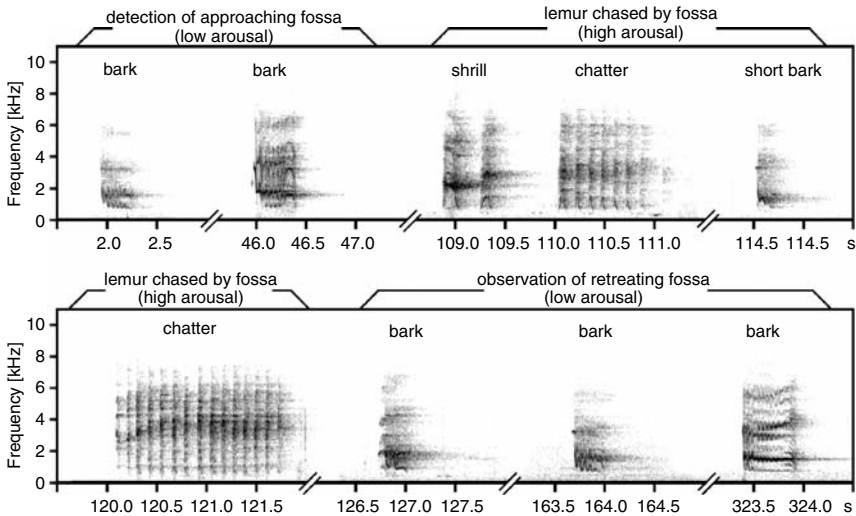
FIGURE 5.2. Sonogram of an alarm calling sequence of a Milne-Edwards' sportive lemur (*Lepilemur edwardsi*) given during a fossa encounter. Differences in call structure and call repetition rate appear to reflect different levels of arousal

on a fat-tailed dwarf lemur (*Cheirogaleus medius*) in the Tsimembo forest in western Madagascar. The lemur emitted a shrill incessant squeaking sound (= panic call) while it was being picked up by the raptor. A playback experiment (Karpanty & Grella, 2001) performed in the Ranomafana National Park with two nocturnal genera, the weasel sportive lemur *(Lepilemur mustelinus)* and the eastern woolly lemur *(Avahi laniger)*, gave first evidence on how nocturnal lemurs reacted toward sounds of sympatric diurnal raptors (Madagascar serpent-eagle (*Eutriorchis astur*), Henst's goshawk (*Accipiter henstii*), and Madagascar harrier-hawk (*Polyboroides radiatus*). The sportive lemur ($N = 1$) did not respond to the playback of a Madagascar serpent-eagle at all, whereas it scanned the sky after playbacks of the Henst's goshawk and the Madagascar harrier-hawk. One group of woolly lemurs looked toward the loudspeaker irrespective of the raptor species diffused whereas the other group reacted only toward the Henst's goshawk. Induced raptor–lemur confrontations were studied in the laboratory. Predator-naïve pairs of gray mouse lemurs (*Microcebus murinus*; $N = 4$) and brown mouse lemurs (*Microcebus rufus*; $N = 2$) were exposed to either a moving barn owl silhouette or a perched barn owl dummy in front of the enclosure (Zimmermann et al., 2000). As in the induced snake–lemur confrontation experiment, no significant difference in vocal activity before and after stimulus presentation was found. *M. murinus* showed, however, a significantly higher locomotion rate afterward (Bunte, 1998). In a confrontation experiment 24 gray mouse lemurs (*Microcebus murinus*) were placed next to a cage containing the predator *Mirza coquereli*, a non-predatory rodent (*Eliurus myoxinus*) or an empty cage (Rakotonirainy, Schülke & Kappeler unpublished data). In response to the predator 17 of 24
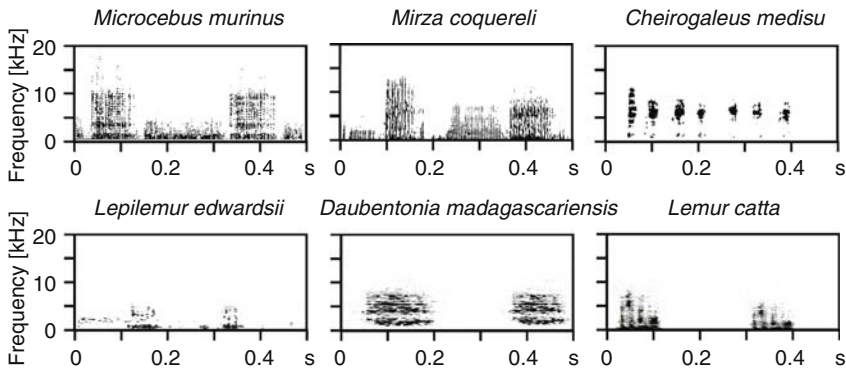
FIGURE 5.3. Sonograms of noisy grunt calls of different lemur genera given as an anti-predator response

mouse lemurs produce vocalisations whereas only 6 of 24 produce vocalisation in response to the non-predatory rodent and none of them to the empty cage.

Observations on how *Allocebus, Cheirogaleus, Microcebus, Mirza, Lepilemur*, and *Daubentonia* reacted against being captured by a human experimenter from a covered sleeping site were also made (see Table 5.3, Zimmermann unpublished data). In all genera, a reflexive lunge toward the disturbing stimulus was observed, accompanied by loud and noisy grunts. These calls show a similar call structure across different lemur genera (Figure 5.3) and may be effective in inducing a startle reflex and escape behaviors in predators. For example, even a human experimenter, who knows that a tiny mouse lemur cannot really hurt him, will show sudden recoil as a reaction toward these calls. Larger-bodied nocturnal lemurs also produce screams (= panic calls) when they are captured and seized by a human experimenter. Thus, for example, some individuals of the Milne-Edward's sportive lemur, which we captured for radio-collaring, produced sequences of these calls under these circumstances of most likely extreme fear (Rasoloharijaona, 2001). Most interesting, these screams sometimes attracted conspecifics from the vicinity. They circled around us giving alarm calls (unpublished data, Rasoloharijaona & Zimmermann) and seemed to mob us, similar to what they did during lemur–snake interactions. Despite the fact that sportive lemurs forage solitarily during the night, it seems as if they are included in a social network of dispersed pairs (families) by long distance vocal communication.

Altogether these findings provide first evidence for the evolution of the expected anti-predator strategies and for semantic predator recognition in nocturnal lemurs. Furthermore, they suggest a possible influence of learning on predator recognition. However, missing are quantitative and experimental studies that address to what extent our hypothesis is supported and whether the emitted calls refer to particular predator categories. There is a strong need for further studies.

Cathemeral and Diurnal Lemurs

Cathemeral and diurnal lemurs face a medium to low predation risk (Table 5.1). All genera forage and sleep either in cohesive pairs or family groups or in cohesive multimale-multifemale groups (Table 5.2). Alarm calls are known from all of them (Table 5.3). In the following discussion we summarize the information of researches in which predator-prey interactions were specified.

Three snake–lemur interactions were reported from the natural environment. Burney (2002) studied Coquerel's sifakas (*Propithecus verreauxi coquereli*) at Anjohibe in northwestern Madagascar. He described that a sifaka group reacted with a roar chorus while observing a boa (*Acrantophis madagariensis*) strangling an adult group member. Another boa-lemur interaction with *Sanzinia madagascariensis* was observed in black lemurs (*Eulemur macaco*) at Ambato Massif (Colquhoun, 1993). They produced mobbing calls and showed mobbing behavior. An eastern lesser bamboo lemur (*Hapalemur griseus griseus*) seized by a boa of the same species at the littoral forest of the Forestiére de Tampolo Station in eastern Madagascar emitted panic calls (Rakotondravony, 1998).

Direct lemur–viverrid interactions in nature were reported only rarely. Sussman (1975) described that a red-fronted brown lemur (*Eulemur fulvus rufus*) reacted toward ground predators similar to their reaction toward humans by producing grunts and wagging their tails. Black lemurs (*Eulemur macaco*) at Ambato Massif responded to dogs and endemic viverrids by producing huff-grunts and by tail wagging (Colquhoun, 1993). These calls may integrate into rasping loud calls while mobbing.

To date, three field observations describe direct lemur interactions with raptors. Colquhoun (1993) observed that black lemurs (*Eulemur macaco*) produced alarm hacks and rasping loud calls in response to raptors (*Accipiter madagascariensis*, *Buteo brachypterus*, and *Milyus migrans*) circling at the sky. If lemurs detected a Madagascar harrier-hawk (*Polyboroides radiatus*) there, they emitted alarm hacks and rasping loud calls with a sharply ascending and descending scream whistle while they climbed down and searched for cover in the inner trunk of the tree. In Beza Mahafaly Special Reserve, southwest Madagascar, a harrier-hawk attacking from the air a group of *Propithecus verreauxi* immediately elicited roars and climbing into the dense canopy (Brockmann, 2003). In the same forest, Sauther (1989) observed that troops of ring-tailed lemurs (*Lemur catta*), travelling on the ground, responded to the presence of Madagascar harrier hawk (*Polyboroides radiatus*) and Madagascar buzzard (*Buteo brachtypterus*) by approaching the tree and produced chirp and moaning vocalisations which could escalate into shriek vocalisations. In contrast, in the presence of Black kite (*Milvus migrans*) they produced no vocalisations and moved silently into the bush. A playback experiment (Karpanty & Grella, 2001) performed in the Ranomafana National Park with four cathemeral and two diurnal lemur species provided some insight into how these species reacted toward sounds of sympatric diurnal raptors Madagascar serpent-eagle (*Eutriorchis astur*), Henst's goshawk (*Accipiter henstii*), and Madagascar harrier-hawk (*Polyboroides radiatus*). In contrast to the tested nocturnal lemurs,

all of these species responded to the playbacks of all three diurnal raptors. The eastern lesser bamboo lemur (*Hapalemur griseus griseus*; $N = 3$) and the golden bamboo lemur (*Hapalemur aureu*; $N = 2$) gave alarm calls in response to the calls of Madagascar serpent-eagle and Henst's goshawk while dropping into the canopy, whereas they looked toward the sound source in response to the Madagascar harrier-hawk (*Polyboroides radiatus*). The red-fronted brown lemur (*Eulemur fulvus rufus*; $N = 4$) and the red-bellied lemur (*Eulemur rubriventer*; $N = 2$) produced alarm calls to all three diurnal raptors but fled more often in response to Madagascar serpent-eagle and Henst's goshawk. The diurnal red ruffed lemur (*Varecia variegata rubra*; $N = 2$) emitted aerial alarm calls in response to the Madagascar serpent and Henst's goshawk but dropped into the canopy only in response to Henst's goshawk. The Milne-Edwards' sifaka (*Propithecus diadema edwardsi*; $N = 2$) showed a stronger response to *A. henstii* by producing alarm calls and fleeing from the sound source. In summary, the lemurs in this study showed significantly stronger responses to playbacks of Henst's goshawk than to the two other raptor species. In an experimental study with semi-free-living ring-tailed lemurs at the Duke Primate Center, the visual assessment of avian threat was investigated (Macedonia & Polak, 1989). Five different moving silhouettes were used as visual stimuli: (1) a naturalistic silhouette of a hawk (*Buteo jamaicensis*), (2) a stylized hawk, (3) a stylized goose, (4) a diamond, and (5) a square control. Besides the hawk silhouette, all were presented in two different sizes, large and small. Individuals responded with a higher calling rate (rasps and shrieks) to the large naturalistic hawk silhouette than to the large stylized goose, diamond, or square silhouette. Furthermore they responded with a higher calling rate and longer calls to the large stylized hawk silhouette than to the small one. Furthermore, the large naturalistic and stylized hawk silhouettes led to significantly longer calls than the large goose and the large square, but not the large diamond silhouette. Regarding the small silhouettes it was found that individuals produced significantly longer calls in response to small hawk and goose silhouettes compared to the small square but not to the diamond silhouette. In summary, it seems that a stylized hawk shape was perceived as equally threatening as a realistic hawk shape. Likewise, the shapes of the stylized hawk were perceived as more threatening than the goose and the square shape but not more than the diamond shape. This suggests that features of size and proportions of silhouettes could trigger visual avian predator recognition.

Quantitative playback experiments studying the responses of cathemeral and diurnal genera toward ground and aerial predators to illuminate how they are perceives and categorized are available for only four different species of four genera, one of which is cathemeral and the three others, diurnal. All of these lemurs belong to the medium predation risk class, are relatively large-bodied (between 2 kg and 4 kg), but differ in their degree of arboreality and in the used habitat. The cathemeral red-fronted brown lemurs and the diurnal Verreaux's sifakas as well as the black and white ruffed lemurs are primarily arboreal. Whereas the two former species live in the dry deciduous forest, the latter is distributed in the evergreen

rainforest. The diurnal ring-tailed lemur is semi-terrestrial and occurs in dry deciduous forests. Major results are outlined as follows.

Red-Fronted Brown Lemurs (*Eulemur fulvus rufus*)

Red-fronted brown lemurs were investigated at the Kirindy research station in central western Madagascar (Fichtel & Kappeler, 2002; $N = 8$–9). They emitted three different call types in the context of predation, tentatively described according to their acoustic structure as "chutters," "woofs," and "huvvs." Chutters were given to raptors (*Polyboroides radiatus*) circling at the sky, woofs and huvvs to ground predators (*Cryptoprocta ferox*, *Canis familaris*). Woofs were not given exclusively in the predation context, but in other social contexts such as group encounters, also. Chutters were only produced in response to aerial predators. An acoustic analysis of alarm calls given to the different predator species was not performed. In playback experiments, woofs were diffused as the terrestrial alarm call and chutters as the aerial alarm call. The subjects responded to the terrestrial alarm call by woofs and to the aerial alarm call by chutters and woofs. After playbacks of calls of the aerial predator and of the aerial alarm call, lemurs looked up more often and climbed down, whereas they looked down and climbed up more often in response to terrestrial alarm calls and terrestrial predator calls.

   Red-fronted brown lemurs respond to heterospecific alarm calls of Verreaux's sifakas. They emitted woofs (general alarm call) in response to sifakas' aerial and terrestrial alarm calls, but showed an appropriate escape strategy with regard to the type of alarm call (Fichtel, 2004; $N = 8$).

   The authors conclude that red-fronted brown lemurs recognize their conspecific aerial alarm calls semantically, whereas they produce and recognize ground alarm calls based on the urgency of a response. Furthermore, they showed heterospecific alarm call recognition.

Verreaux's Sifakas (*Propithecus v. verreauxi*)

Verreauxi sifakas were observed at the same study site as red-fronted brown lemurs (Fichtel & Kappeler, 2001; $N = 8$). In the context of predation two call types were produced. According to their acoustic structure they were tentatively classified as "growl" and "roars." Growls were emitted in response to aerial (*Polyboroides radiatus*) and terrestrial predators (*Cryptoprocta ferox, Canis familaris*), but also in non-predator social situations such as group encounters, whereas roars were given exclusively toward the aerial predator. An acoustic analysis of alarm calls given to the different predator species is lacking. Playback experiments were performed with growls as the terrestrial alarm call and roars as the aerial alarm call. When growls were played back, none of the subjects responded vocally, whereas five of eight individuals produced roars in response to roars. Like red-fronted brown lemurs, sifakas looked down more often and climbed up in response to terrestrial predators and terrestrial alarm calls, whereas they looked up and climbed down in response to aerial alarm calls and aerial predator calls.

Verreaux's sifakas showed also evidence for heterospecific alarm call recognition. Thus, they responded to the aerial alarm call of red-fronted brown lemurs by aerial alarm calls (roar) at the Kirindy field site. They looked up more often in response to the aerial than to the terrestrial alarm call, whereas they looked down more often in response to terrestrial than to aerial alarm calls of red-fronted lemurs (Fichtel, 2004; $N = 8$). At the Berenty field site, where Verreaux's sifakas live sympatrically with ring-tailed lemurs, they showed a predator-specific escape response to aerial and terrestrial alarm calls of ring-tailed lemurs. More individuals looked up in response to ring-tailed aerial alarm calls and more individuals moved up in response to the terrestrial alarm call (Oda, 1998; $N = 11$).

In summary, Fichtel & Kappeler (2001) emphasized that Verreaux's sifakas use aerial predator calls referentially and terrestrial alarm calls according to the urgency of predator threat. Furthermore, Verreaux's sifakas demonstrate heterospecific alarm call recognition.

Black and White Ruffed Lemurs (*Varecia variegata variegata*)

One group of ruffed lemurs was studied under semi-free conditions in a large outdoor enclosure at the Duke Primate Center, USA (Macedonia, 1990, 1993). Predator–lemur interaction was observed toward naturally occurring predators as well as in experimental confrontations of lemurs with two aerial and a terrestrial predator (aerial predators: stuffed museum specimen of a perched red-shouldered hawk (*Buteo lineatus*) or a great-horned owl (*Bubo viginianus*); terrestrial predator: living dog; Macedonia, 1993). Four different call types were evoked by these predators, tentatively classified as "abrupt roars," "growls," "growl snorts," and "pulsed squawk" according to their acoustic structure. Abrupt roars were used as mobbing calls to aerial predators. They were continued after the potential threat visually disappeared. With increasing arousal abrupt roars were combined with wails. Ruffed lemurs on the ground, detecting an aerial predator, assumed a threatening posture and emitted roars that induced "scan and roar" behavior in nearby group members. When they were in the tree, they climbed toward the treetop and emitted roars in the direction of the predator. Growls, growl snorts, and pulsed squawks were produced in response to the dog as a potential terrestrial predator while lemurs showed mobbing behavior. Calls may integrate into each other with increasing arousal. In a playback study, abrupt roars were diffused as the aerial alarm call and pulsed squawks as the terrestrial alarm call. Ruffed lemurs responded to playbacks of the aerial alarm call by producing roars and to playbacks of terrestrial alarm calls by producing pulsed squawks. Growls and growl snorts were produced in response to both call types, but significantly more often to terrestrial than aerial alarm calls. Lemurs showed more sky scanning and roaring behavior in response to the aerial alarm call than to the terrestrial alarm call. In response to terrestrial alarm calls, adults on the ground ran up into trees more often. Adults in the tree did not show a specific escape response, whereas immatures in the trees climbed higher more often in response to terrestrial than to aerial alarm calls. In summary, ruffed lemurs did mob both aerial and terrestrial

predators, and consequently did not show a strong predator-specific response. Macedonia (1993) argued furthermore that the pulse squawk (terrestrial alarm call) lies at one end of a structurally graded acoustic continuum and the wail of the abrupt roars (aerial alarm call) at its other end. This acoustic continuum coincides with predictions for an urgency-based alarm call system.

Ring-Tailed Lemurs (*Lemur catta*)

Ring-tailed lemurs were studied under the same conditions as ruffed lemurs at the Duke Primate Center (Macedonia, 1990, 1993) under similar semi-free conditions in the Izu Cactus Park in Shizuoka, Japan, and additionally in the field in the Berenty Reserve in southern Madagascar (Oda & Masataka, 1996). Direct interactions with naturally occurring predators as well as experimental confrontations of lemurs with two aerial predators and a terrestrial predator (aerial predators: stuffed museum specimen of a perched red-shouldered hawk (*Buteo lineatus*), or a great-horned owl (*Bubo viginianus*); terrestrial predators: living dog; Macedonia, 1993) were observed. Ring-tailed lemurs produced seven acoustically different call types, which were tentatively classified, based on their acoustic structure, as "gulps," "rasps," "shrieks," "chirps," "clicks," "closed mouth click," "open mouth click," and "yaps." In response to aerial and terrestrial predators subjects first emitted gulps. When a large moving bird approached a lemur group subjects emitted rasps grading into a shriek chorus when all group members detected it. During aerial predator detection subjects looked skyward and tracked the flight of the predator or ran into cover. Group relocation was accompanied by chirp calls. In response to terrestrial predators ring-tailed lemurs produced clicks, closed mouth clicks, open mouth clicks, and yaps and usually jumped immediately into the trees. Rasps, shrieks, open mouth clicks, and yaps were only observed in alarm contexts in contrast to gulps, chirps, clicks, and closed mouth clicks. In a playback experiment rasps and shrieks were used as aerial alarm calls, whereas yaps were used as the terrestrial alarm call. In response to aerial alarm calls subjects emitted significantly more chirp calls than in response to the terrestrial alarm calls, whereas subjects emitted significantly more clicks in response to terrestrial than to aerial alarm calls. Furthermore ring-tailed lemurs showed different escape responses to aerial and terrestrial alarm calls. Ring-tailed lemurs on the ground looked up and stood up bipedally in response to aerial alarm calls, subjects in trees climbed lower to dense vegetation. In response to terrestrial alarm calls subjects on the ground ran up into the trees or climbed higher into the dense canopy.

Oda & Masataka (1996) provided evidence for heterospecific alarm call recognition in ring-tailed lemurs at Berenty, where they live sympatrically with Verreaux's sifakas. Ring-tailed lemurs on the ground ($N = 26$) looked skyward in response to playbacks of sifakas' aerial alarm calls and ran up into the trees in response to playbacks of sifakas' terrestrial alarm calls. Ring-tailed lemurs in the trees ($N = 26$) responded also by looking skyward in response to the aerial alarm call and climbed down in response to the terrestrial alarm call. These results coincide well with their reactions to the respective conspecific alarm calls. Experience

seems to influence the recognition of heterospecific alarm calls since subjects in captivity did not show such a predator-specific escape response.

An experiment illustrating the effect of learning on acoustic recognition of raptor calls was performed by Macedonia & Yount (1991). They conducted a playback experiment with two ring-tailed lemur groups at the Duke Primate Center. Calls of three avian species–red-tailed hawk (*Buteo jamaicensis*), Madagascar harrier-hawk (*Polyboroides radiatus*), wood thrush (*Hylocicla mustelina*)–and one mammal species–the eastern gray squirrel (*Sciurus carolinensis*)–were used as acoustic stimuli. All subjects were familiar with all acoustic stimuli besides the Madagascar harrier-hawk. Results of this experiment were mixed. No significant difference in bipedal scanning was found after the presentation of the familiar red-tailed hawk and the unfamiliar Madagascar harrier-hawk. However, one of the two tested groups jumped significantly more often onto tree trunks in response to playbacks of the familiar red-tailed hawk than the unfamiliar Madagascar harrier-hawk. Furthermore, more individuals of this group leapt more often onto trees in response to playbacks of red-tailed hawks and of gray squirrels than to playbacks of wood thrushes.

In summary, ringtail lemurs show evidence for predator-specific alarm calls and semantic conspecific alarm call recognition. Furthermore, experience appears to shape heterospecific alarm call recognition as well as acoustic predator recognition.

Discussion

In this paper we have estimated predation risk of lemurs based on a review of current data on the number of predator species. We have related this information to the variation of particular life history traits and ecology to explore whether these traits are shaped by predation. According to our study foraging group size and female maximum reproductive output per year were not related to predation risk for the whole lemur sample, whereas body mass was significantly correlated and could be best illustrated by a logarithmic model. This contradicts findings in anthropoid primates where predation is an important selective force shaping group size and female fecundity (e.g., Anderson, 1986; Hill & Lee, 1998; Hill & Dunbar, 1998; Janson, 2003). Predation risk in our study was estimated solely by the number of predatory species per genus based on direct predator–lemur interactions and indirect cues such as owl pellets, feces, and dietary analyses, and should therefore be treated cautiously. Accordingly, the intensity with which predation and anti-predator strategies were studied differs among the different genera. However, the described anecdotal observations and experimental data on lemurs indicate that not only hunting styles of predators (as suggested by current theory, see Seyfarth & Cheney, 2003), but also predation risk linked to body mass seem to have an impact on the evolution of their anti-predator strategies.

Reviewing the lemur literature we found that lemurs, including the nocturnal ones, do not only rely on crypsis to avoid predators as often is suggested by

the anthropoid literature (Stanford, 2002; Janson, 1998), but they do show as highly sophisticated anti-predator strategies as anthropoid primates. We found information about anti-predator behaviors for 11 out of 13 genera (no information is available yet for *Daubentonia* and *Indri*) based on direct predator–prey interactions as well as visual and acoustical confrontation experiments. Snake anti-predation behaviors during direct snake–lemur interactions were observed in six lemur genera of the medium to high predation risk class (Table 5.3). In one genus (*Cheirogaleus*) it was observed that a female attacked a snake defending her offspring. Five out of six lemur genera showed mobbing responses toward the snake, supporting the prediction of snake anti-predator strategy outlined at the beginning of this chapter. Mobbing seems to be a universal snake anti-predator strategy, similar to the strategy shown by anthropoid primates. Terrestrial carnivore anti-predator behaviors were observed in five lemur genera belonging exclusively to the medium and low predation risk class. All of them showed a universal escape response by climbing up into the canopy. Furthermore, three of them also displayed mobbing behavior. In these cases the animals were directly confronted with the predator. These findings support the prediction of the terrestrial carnivore anti-predator strategy concerning medium and large bodied lemurs, whereas data for small-bodied lemurs are lacking so far and require further studies. Furthermore, playback experiments with predator calls were conducted for four lemur genera. They indicated that three out of four lemur genera perceived predator calls semantically, as is known for anthropoid primates (e.g., Seyfarth & Cheney, 2003; Zuberbühler, 2003). Aerial anti-predation behaviors were noted in seven lemur genera belonging to the medium to low predation risk class, confirming the predictions of aerial anti-predator strategy. Observations of direct raptor–lemur interactions occurred in two lemur genera. In both cases the animals searched for cover by climbing into the dense canopy. Anti-predator behaviors were experimentally induced in seven lemur genera by playback studies using predator calls and in two by confrontation experiments with potential predators. One genus (*Varecia*) responded with mobbing behavior ("scan and roar behavior"; Macedonia, 1990, 1993). Six out of seven lemur genera showed a universal anti-predator response of scanning the sky and five of them also responded by searching for cover. Results of playback experiments imply that calls of raptors are perceived semantically, as is shown for anthropoid primates. A panic cry anti-predator strategy was observed in three lemur species belonging to the high and medium predation risk class. In all cases the lemurs were already gripped by the predator and emitted panic cries. Panic crying seemed also to be universal across lemur genera. But to date there is no evidence that these calls may startle the predator, lead to mobbing, or attract a larger predator to compete for the prey. Evidence for the presence of the semantic predator recognition strategy as outlined in this paper currently seems to exist for three lemur genera. Two of them responded specifically to the alarm calls of one sympatric lemur genera, whereas one genus, *Propithecus*, showed heterospecific alarm call recognition of two sympatric lemur genera. It is not clear, however, to what extent these heterospecific alarm calls differ in acoustic structure. *Microcebus murinus* also responded to alarm calls of sympatric *M. ravelobensis*.

TABLE 5.3. Overview of anti-predation behavior in response to direct confrontations with predators (marked bold) and predator calls.

Genus	Terrestrial	Snake	Aerial	References
Microcebus		**mobbing**		Schmelting, 2000
Cheirogaleus		**attacking**		Fietz & Dausmann, 2003
Mirza		**mobbing**		Schuelke, 2001
Phaner		**mobbing**		Schuelke, 2001
Lepilemur	**mobbing from conspecifics**[1] **victim fleeing in canopy**[2]		scanning sky[3]	[1]Zimmermann, unpubl. data; [2]Rabesandratana et al., 2005; [3]Karpanty & Grella, 2001
Avahi			looked to sound source scanning sky climbed into cover	Karpanty & Grella, 2001
Hapalemur				Karpanty & Grella, 2001
Eulemur	**mobbing**[4,5] looked down[7] climbed up[7]	**mobbing**[4]	**scanning sky**[6,7] **climbed into cover**[4,6] climbed down[7]	[4]Colquhoun, 1993; [5]Sussman, 1975; [6]Karpanty & Grella, 2001; [7]Fichtel & Kappeler, 2001
Lemur	climbed up		scanning sky climbed into cover	Macedonia 1990, 1993; Oda & Masataka 1994
Varecia	**mobbing**[9] climbed up[9]		scanning sky[8] climbed into cover[8,9] **mobbing**[9] scan and roar[9]	[8]Karanty & Grella, 2001; [9]Macedonia, 1993
Propithecus	looked down[13] climbed up[13]	**mobbing**[10]	**climbing up into dense canopy**[11] scanning sky[12,13] climbed into cover[12] climbed down[13]	[10]Burney, 2002; [11]Brockmann, 2003; [12]Karpanty & Grella, 2001; [13]Fichtel & Kappeler, 2001

However, in this case calls did not differ statistically in their acoustic structure (Zietemann, 2000).

So far, for most genera, sophisticated quantitative and experimental approaches aimed toward gaining insight into sensory and cognitive abilities of lemurs are lacking. Our overview of our current knowledge nevertheless provides some evidence for the expected anti-predator strategies outlined at the beginning of this paper. Thus, it seems as if all lemur species studied to date, irrespective of their activities and social patterns, have evolved particular anti-predator strategies that minimize the risk of being eaten. Behavior strategies shown under these circumstances appear to be adapted to the perception abilities and hunting styles of three different predator categories as well as to body mass and location of the respective lemur itself. Further direct observations on natural predator–lemur interactions, comparative studies on induced predator–lemur confrontations and playback experiments with lemur alarm and predator calls using the same experimental paradigm and exploring all sensory domains for predator detection are necessary to assess the extent to which signaling and recognition mechanisms in lemurs correspond to those of anthropoid primates or show lineage-specific constraints. They may also shed light on potential universal principles governing communication and cognition.

First research on anti-predator behaviors of predator-naïve lemurs in comparison to experienced ones (see also Oda, 1996; Bunte, 1998; Bunkus et al., 2005; Sündermann et al., 2005) provided some evidence for the influence of experience on predator perception and recognition, a rather neglected area of research in the strepsirrhines. The question on why and how lemurs learn about predators is, however, highly important from an applied perspective. Almost all extant lemurs bear a high risk of extinction (e.g., Mittermeier et al., 2003). Conservation and reintroduction programs are therefore urgently needed, and some are partly established, for the most threatened species. From a variety of bird and mammalian species it is known that reintroduced and translocated individuals are highly vulnerable to predation after release, unfortunately reducing the success of the respective conservation programs (e.g., MacMillon, 1990; Beck, 1994; Wolf et al., 1996). To improve their anti-predator skills and to enhance the efficiency of these programs, pre-release anti-predator training was used in which individuals learned to associate particular predator categories with an unpleasant experience (e.g., Ellis et al., 1977; Miller et al., 1990; Richards, 1998; Griffin et al., 2000; McLean et al., 2000; Griffin et al., 2001). Research on predator learning in lemurs is therefore required not only to get a better understanding on the origin and evolution of primate communication and cognition, but also to deliver appropriate tools for effective management and conservation.

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