Predator Recognition in the Brown Mouse Lemur (*Microcebus rufus*): Experiments in Ranomafana National Park, Madagascar

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Abstract of the Dissertation

Predator Recognition in the Brown Mouse Lemur (*Microcebus rufus*): Experiments in Ranomafana National Park, Madagascar

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It is well established that predator avoidance is an important selective force shaping animal behavior. Much has been written on predation in diurnal primates, but almost nothing is known about predator-prey interactions in nocturnal primates. Even though there has been evidence to the contrary, it is widely accepted that nocturnal primates, in contrast to diurnal species, are limited to indirect anti-predation strategies. To investigate whether nocturnal primates make risk assessments based on direct predator cues, I conducted field and laboratory experiments with wild brown mouse lemurs (*Microcebus rufus*) in the rainforest of Ranomafana National Park, Madagascar, over a four year period. Mouse lemurs are subjected to a wide range of predators and suffer very high predation rates. I presented objects, odors, and sounds representing avian, mammalian and snake predators to mouse lemurs that were captured in live traps und released after the experiments. I documented the behavioral responses as a measure of risk perception. Mouse lemurs demonstrated the capability to differentiate between predator and non-predator objects and odors. I found no evidence that mouse lemurs differentiated among predators. It is possible that predation pressure by a wide range of predator types, does not allow for the selection of predator specific recognition or response mechanisms. There were indications that visual information was perceived as a higher indicator of danger than olfactory information. Individual variation in behavioral responses indicated that learning and experience might affect risk perception. Mouse lemurs did not appear to perceive predator calls as indicators of danger, suggesting that there was little selection for acoustic predator recognition. Mouse lemurs are thought to most closely resemble early ancestral primates. A better understanding of their behavior and adaptations will provide more insight into early primate evolution. My findings indicate that the selection for cognitive mechanisms that lower predation risk might have evolved well before the emergence of diurnal primate species. The importance of visual information to mouse lemurs in my experiments suggests that the need to avoid predation might have facilitated the evolution of the high acuity visual system so typical of primates.

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CHAPTER ONE

Introduction

1.1. Predation and its Consequences to Prey

Animals need to balance three main goals: finding mates, food, and avoiding predators, all of which increase an animals' chance of passing on its genes to healthy offspring. Avoiding predation is possibly the most important task, because a predation event can severely injure or kill an animal, reducing its future fitness to zero [van Schaik and van Hooff 1983]. For many animals, including primates, predation is the major cause of death [Cheney and Wrangham 1987]. Even though actual predation events are relatively rare, especially in large bodied prey, the mere threat of predation is a powerful force [Hart 2007; Terborgh and Janson 1986; van Schaik and van Hooff 1983]. Predation can thus have substantial affects on behavior, including foraging, reproduction, travel and choice of shelter [Gleason and Norconck 2002; Janson 2003; Karpanty and Wright 2007; Lima and Dill 1990; Treves 2000; Wright 1998]. Furthermore, predation has likely also shaped sensory and cognitive systems of prey, as well as predators [Dukas and Ellner 1993; Shettleworth 1998; Zuberbühler 2007].

Considering the impact of predation, it is not surprising that prey animals have evolved behaviors and adaptations that lower predation risk. Such adaptations can be more general or can be very predator specific. Most predators tend to hunt or live in particular habitats and/or use specific hunting techniques. Some predators prefer dense vegetation and rely on ambush tactics (e.g. many species of snake and feline), some are pursuit hunters in open habitats (e.g. cheetahs), and others aerial hunters that pounce on unsuspecting prey from above [Dice 1945; Raxworthy 2003; Vermeij 1982].

Predation risk can be lowered by both indirect and direct measures [Ives and Dobson 1987; Janson and Goldsmith 1995; Lima and Dill 1990; Wright 1998]. Indirect anti-predation measures assume a constant risk of predation and are typically habitual behaviors or adaptations that reduce the likelihood of being detected or attacked by predators. Depending of the types of predators present, these can be 'all purpose" behaviors that take into account several species of predator, or evolved in response to a particular dominant predator. Indirect anti-predation measures do not depend on the prey being aware of the predator's presence. Direct anti-predation adaptations, in contrast, enable prey to detect the presence of a predator, and adjust their behavior accordingly. Very commonly, animals use a combination of both types of strategy.

1.2. Anti-Predation Adaptations and Behaviors

1.2.1. Indirect Anti-Predation Adaptations and Behaviors

Indirect anti-predator behaviors reduce the likelihood of being detected or attacked by a predator. They do not require prey to be aware of predator presence, and assume a constant threat of predation [Enstam 2007; Hill and Weingrill 2007; Thorson et al. 1998]. Indirect anti-predation adaptations can be habitual such as a cryptic appearance (e.g. color or shape camouflage), physical or physiological defenses (e.g. spines or toxins), or living in microhabitats that provide cover or prevent predator access (e.g. dense vegetation, fine branches, rock crevices). Adaptations can also be of a more flexible behavioral nature, such as modifying behavior in response to indirect cues of predation risk, including weather or lunar illumination [Bowers et al. 1993; Orrock et al. 2003; Sauther 2002; Sumner and Mollon 2003; Wright 1989]. For example, nocturnal rodents are subject to predation to predation by mammals, owls, and snakes. They have a cryptic coloration prevents the often much larger predators to reach them, or enables them the escape via one of numerous exits. Oldfield mice (*Peromyscus polionotus*), for example, were furthermore more active in dense vegetation cover than in more open habitat, and they foraged more in nights with rainfall and low lunar illumination [Orrock et al. 2003]. Dense vegetation likely provided cover from detection, and the sound of rain and darkness probably lowers the ability of their predators to hear or see the mice. Even though this is a common pattern in rodents, behavior can depend on the types of predators present. In snake rich habitats, for example, rodents avoided dense vegetation which was the preferred habitat of snakes [Bouliska 1995; Kotler et al. 1991, 1993].

Another common indirect anti-predation measure found in many animals including mammals, birds, and fish, is group living [Janson and Goldsmith 1995; van Schaik and van Hooff 1983; Wright, 1998]. Being a member of a group lowers the likelihood of being targeted by a predator via the dilution effect [Hamilton 1971], and groups can provide confusing, because predators often focus on a single target. Predatory bass, for example, required more time to catch one of two silvery minnows (*Hybognathus nuchalis*) than a single one, and they completely abandoned the hunt when confronted with ten or more minnows [Landeau and Terborgh 1986]. In conjunction with direct predator recognition mechanisms, groups can also potentially detect predators sooner than solitary animals, because there are more ears, noses, and eyes [for a review see Terborgh 1990].

However, although it is obvious that indirect anti-predator behaviors are beneficial, there are also tradeoffs. Indirect (habitual) anti-predation behaviors often incur costs because they can be energetically expensive [Heads 1986; Sih 1988]. For example, the production of armor or toxins can increase energy requirements, and energy-intake can be adversely affected by excluding (food-rich) areas or by having to share food with others [Cowlishaw 1997; Lima 1998; Lima and Dill 1990]. One effective way to lower such costs (i.e. the necessity for habitual anti-predation behaviors) is to make behavioral modifications only in response to immediate and actual threats of predation, rather than in response to potential threats of predation.

1.2. 2. Direct Anti-Predation Adaptations and Behaviors

Direct anti-predation adaptations enable prey to become aware of predator presence via cognitive detection and recognition mechanisms. Recognition can range from very general to highly specific. Some prey animals simply recognize a dangerous situation, whereas others are able to distinguish among different predator types or even predator individuals [Seyfarth et al. 1980]. Predator recognition is beneficial because the early detection of predator enables prey to prevent dangerous, direct encounters, and it can enable prey to respond appropriately to the different types of predators [Colquhoun 2007; Karpanty and Wright 2007; Lima and Dill 1990]. In contrast to indirect anti-predation adaptations where behavior is modified based on the potential threat of predation, direct anti-predation adaptations allow prey to modify behavior in response to *actual* threats of predation (Sih et al. 1998). The extent to which recognition mechanisms are developed in a species, population, or even an individual, will depend on predation rates, types of predators, defense mechanisms and vulnerability of prey (e.g. armor, toxicity, body size/strength), local habitat characteristics, and experience [Caro 2005].

In its most basic form, prey does not take into account the hunting technique of a predator, and respond with the same behavior to all predators. For example, many species of rodent respond to all predator types with flight to cover [e.g. Hendrie et al. 1998; Slobodchikoff 2002. Specific responses take into account the hunting technique of a predator. For example, Diana monkeys (*Cercopithecus diana*) alarm-called in response to leopards that rely on surprise, but became silent in response to chimpanzees, which chase their prey [Zuberbühler 2000]. Vervet monkeys (*Chlorocebus pygerythrus*) and Milne Edwards' sifakas (*Propithecus edwardsi*) distinguished between aerial and terrestrial predators and moved up into the canopy, or dropped to the ground accordingly [Karpanty and Wright 2007; Seyfarth et al. 1980]. Prairie dogs (*Cynomys* spp.) not only distinguished among different predator types, but also adjusted their behavior to the particular hunting strategies of individual coyotes [Slobodchikoff 2002].

There is ample evidence that many animals, including birds, mammals, and fish, recognize predators, and in many cases, respond predator appropriately. What constitutes an appropriate response, however, varies because it depends on the morphological, ecological, and behavioral characteristics of the prey and predator species, as well as the local habitat characteristics.

1.3. Sensory Information and Recognition

The detection and the identification of a predator, as well as that of prey, take place via the perception of sensory information provided by the animals themselves. For prey, sensory information that can be detected from a distance is particularly beneficial. This allows prey to make timely, and usually more subtle and energetically cheaper, behavioral modifications.

Sensory information that is commonly used by animals includes the visual, olfactory, and acoustic detection. Visual information is of high importance for visually oriented animals such as primates and birds. Meaningful visual recognition cues can include shape, color, size or pattern. For example, bonnet macaques (*Macaca radiata*) very more likely to respond fearfully to a model of a right-side-up leopard than to an up-side-down model, and to a spotted model that to a uniformly dark model [Coss and Ramakrishnan 2002; Coss et al. 2005]. Neotropical motmot birds (*Eumomota superciliosa*) avoid coral snake patterns from birth [Smith 1975]. Visual information can be particularly important in the context of predation avoidance, because a visible predator is usually nearby and might have detected its prey. However, visual information is most reliable at optimal illumination levels and in high visibility environments. In low visibility environments such as forests, or for animals with poor visual abilities, chemical and auditory cues can provide useful information. Common chemical cues include body odor, feces, and urine. For example, bank voles (*Clethrionomys glareolus*) avoided pens with the body odor of mammalian predators [Jedrzejewski et al. 1993]. However, compared to visual input, odors can be less specific because they are volatile or can be long-lasting. Consequently they often merely indicate that a predator was present in the area at some point in time, but not necessarily when [Kats and Dill 1998]. Relevant acoustic information includes sounds generated by movement and vocalizations. They too provide indications that a predator, or prey, is in the vicinity. For example, California ground squirrels (*Otospermophilus beecheyi*) respond fearfully to the rattling of rattle snakes, and are able to determine snake size, and thus dangerousness, based on the rattling sound [Swaisgood et al. 1999]. Unlike the visual perception, acoustic information does not necessarily relate an exact location because sound can level long distances. Sound is also subject to distortion by objects such as trees and rocks, and can be obscured by background noise generated by animals, wind or water [Waser and Brown 1986]. Furthermore, since many predators hunt silently, the usefulness of acoustic cues depends on local conditions, as well as on the hearing abilities of animals.

1.4. Recognition and Perception on the Level of the Brain

The process of recognition is a very specialized task because at any given moment there is a tremendous amount of sensory information, both from an animal's internal and external environment [Shettleworth 1998]. In order to be useful, incoming information needs to be integrated and interpreted by the brain [Allman 1999; Dusenbery 1992], and it can thus depend on existing knowledge. The brain is extremely limited in the amount of information it can process simultaneously, and thus discards the great majority of input (possibly > 99% of information) [Dukas 1998; Dusenbery 1992; Shettleworth 1998]. The filtration process takes place in the sensory organs and in the brain itself. Sensory organs are usually limited with respect to the magnitude and range of frequencies that can be perceived. For example, humans are limited to seeing only a fraction of the existing light spectrum. Filtering by the sensory organs still allows a high volume of information to pass on to the brain. Here, incoming information is only meaningful when it can be integrated or matched with existing knowledge (which can be learned or hardwired). Many neural pathways are already in place at birth, but many are expanded upon during an organism's lifetime (learning).

What constitutes as relevant information at any given moment in time largely depends on the organism's intent. For example, a hungry animal will focus its attention on locating food, and as consequence will more easily discard predator relevant information than an animal that is focusing on detecting predator cues. The process of integrating incoming information with existing knowledge is termed “recognition”. How these processes work on the level of the brain is, however, not well understood [Dispenza 2007; Miller 2002; Ramakrishnan et al. 2005; Shettleworth 1998].

1.5. The Acquisition of Predator Recognition

Many prey animals have the ability to detect, and sometimes identify, predators, or the nature of a particular predation threat [Kats and Dill 1998; Lima and Dill 1990]. This ability can innate or might require learning [Gould and Marler 1987; Griffin and Evans 2003; Mathis et al. 1996; Mineka and Cook 1988]. Considering the impact of predation, innate predator recognition mechanisms would seem beneficial. There are many examples: Neotropical motmot birds (*Eumomota superciliosa*) avoid coral snake patterns from birth [Smith 1975], newly hatched salmon (*Salmo* spp.) responded to predator odors [Hawkins et al. 2004], California ground squirrels (*Spermophilus beecheyi*) recognize snakes from birth [Owings 2002] and meadow voles (*Microtus pennsylvanicus*) innately recognize weasel odor [Parsons and Bondrup-Nielsen 1996]. Innate mechanisms have also been observed in primates: captive-born tamarin monkeys (*Saguinus labiatus*) avoided predator odors and discriminated them from non-predator odors [Caine and Weldon 1989], naïve infant vervet monkeys (*Cercopithecus aethiops*) emit alarm calls [Seyfarth and Cheney 2003], bonnet macaques (*Macaca radiata*) innately fear leopard spots [Coss and Ramakrishnan 2000], naïve ring-tailed lemurs (*Lemur catta*) responded to aerial predators [Macedonia and Yount 1991], and infant tarsiers (*Tarsius spectrum*) alarm-called in response to snakes [Gursky 2003].

However, sometimes predator recognition requires learning or is refined with experience [Janson and van Schaik 1993]. For example, different populations of the same species of mice respond differently to predators based on their abundance. When experimentally exposed to snakes, mice from a habitat devoid of snakes where much more likely to be killed by snakes, than those from a snake rich habitat [Dickman 1992]. This suggests that learning might be involved. Having to learn about predators has both disadvantages and advantages. On the downside, learning is costly, because during the initial acquisition or “learning” phase, the behavior is performed sub-optimally [Krakauer and van Schaik 2005; van Schaik and Deaner 2003]. On the positive side, the need to acquire anti-predator behaviors has the advantage that it allows an animal to adapt flexibly to local conditions, including predator species present or predator densities [Anderson 1986; Cheney and Wrangham 1987; Isbell 1994]. This might we particularly beneficial to animals that are likely to encounter environmental change during their life time, such as long-lived animals like primates, or animals that live in volatile environments.

Regardless of whether recognition is innate or learned, there are indications that many animals are able to improve their predator recognition skills with experience or by observing others. Encounters with predators are not necessarily lethal; the average hunting success rate of most predators is below 50% [Vermeij 1982]. Unsuccessful predation events allow for learning by personal experience. Group living species furthermore can potentially learn by observing attacks on conspecifics, or by observing reactions of more experienced individuals. Rock squirrels (*Spermophilus variegatus*) and bonnet macaques, for example, become more sophisticated in their ability to discriminate amongst predators with repeated encounters [Owings et al. 2001; Ramakrishnan and Coss 2000; Ramakrishnan et al. 2005]. Learning from others is less risky. Birds [Curio 1988; Curio 1993], monkeys [Cook et al. 1985; Janson and van Schaik 1993; Seyfarth and Cheney 1980; Struhsaker 1967], marsupials [Griffin and Evans 2003; Griffin et al. 2001] and even fish [Alfieri 2000; Mathis et al. 1996] have demonstrated the ability to learn about predators via observational learning. Learning may act in concert with innate mechanisms. For example, even though naive rhesus monkeys learned to fear both snakes and flowers, snake fear was acquired much faster [Mineka and Cook 1988]. This suggests that animals can have existing specific neural pathways in place that simply need to be activated (predisposition) [Gould and Marler 1987].

1.6. Behavioral Responses to Different Types of Predators

Besides having morphological or physiological defenses that deter predators, prey can also counter a threat of predation by modifying behavior. The most effective behavioral ant-predation response is, however, subject to a number of factors. Just to name a few, variables include the hunting style of a predator, the general vulnerability of prey (e.g. size, age, group size), habitat characteristics, the internal state of the animal (hunger, disease, etc), and even weather [Caro 2005]. In this section, I will, however, focus on responses to the hunting styles and primary sensory modes of predators.

Predators can be broadly grouped into ambush and pursuit hunters, their primary mode of prey detection (visual, olfactory, or acoustic), and by their primary strata use (aerial, arboreal, terrestrial). Ambush predators rely on the element of surprise, and include most snakes and raptors. Many mammals also rely on ambush, but will more often than other predator types engage in the pursuit of their prey. Ambush predators are very difficult to detect, because they stalk or wait under cover very quietly. They therefore provide few visual and acoustic cues. Prey can rely on indirect anti-predation measures such as avoiding microhabitat preferred by such predators, or by being a member of a group. In contrast to a solitary lifestyle, groups provide a dilution effect, can confuse predators, are more likely to detect a predator, and, in case of an attack, can potentially drive off a predator by a counter attack/ mobbing [Gursky 2006; Hamilton 1971; van Schaik and van Hooff 1983]. Solitary prey, on the other hand, has the advantage of being less likely to attract the attention of predators. The best response to a predator that relies on the element of surprise is to advertise that it has been detected [Caro 2005]. If it's a slow predator like a snake, it is also possible to simply move away. Pursuit predators, such as the cheetah, rely on the speed and/or endurance. If prey is unable to outrun a pursuit predator, one solution is to join a group to lower the likelihood of being targeted, or escape into an area where the predator cannot follow (e.g. burrows, fine branches, or rock crevices) [van Schaik and van Hooff 1983].

Aerial predators include birds that hunt from the sky, but here I am also including birds that pounce from perches. Aerial predators tend to rely on the element of surprise and a clear path of attack, because once an attack is initiated only minor adjustments can be made [Karpanty 2006; Rene de Roland and Thorstrom 2003]. Although group living animals might sometimes mob an approaching bird, an effective response is to move out of the dive path quickly and erratically, or to seek cover [Frankenberg 1981]. Terrestrial predators such as canids are limited to the ground. The best response is to move underground or up from the ground to where the predator is unable to follow.

Some largely terrestrial predators such as felids, viverrids and mustelids, are able to climb trees. Some species of snake are also commonly found in trees. In response to arboreal predators, arboreal prey can rely on their often smaller size, that can makes them more agile and faster than their predators, and enables them to escape to smaller branches that cannot carry the weight of a larger predator.

Another factor that needs to be taken into account is the primary sensory mode by which predators locate their prey, although predators might use more than one mode of detection. Visual predators such as birds and felines, rely on the visibility of their, and therefore prefer habitat that is open. Besides a cryptic appearance, an efficient behavioral adaptation of prey is thus to seek out low visibility habitat such as dense vegetation, or to seek cover once a predator has been detected. Diurnal primates, for example, commonly seek cover and move down lower in the canopy once they have detected a raptor [e.g. Macedonia and Polak 1998; Karpanty and Wright 2006]. Some predators, for example many owls, are also able to precisely locate prey solely by sound [Konishi 1973]. An effective behavioral response is to be as quiet as possible to avoid detection, or to become silent once becoming aware of the predators presence [Scheumann et al. 2007]. Some predators, including mammals and fish, are very sensitive to olfactory signals and are able to locate prey by smell [Albone and Shirely 1984, Kats and Dill 1998]. There are few effective behavioral response options other than minimizing body odor and scent marking, and other behavioral options will depend on other characteristics of such predators (e.g. hunting style, size).

This brief review of predator types and hunting styles makes clear that anti-predation responses are highly variable among and even within a species. Effective responses depend on the particular characteristics and combined strategies of a predator species, as well as the characteristics of the prey species. For example, anti-predation responses can vary depending on whether animals are aggregated or solitary, and whether it is dark or light. Local conditions also need to be considered, and include habitat characteristics, types of predators present, and the local abundance of predator and prey. Furthermore, the extent of anti-predation behaviors can be affected by an animal’s motivation. For example, a hungry predator or prey individual, might be more willing to take risks, or prey animals might shift their focus during the mating season. For example, during their reproductive season, nocturnal brown mouse lemurs (*Microcebus rufus*) not only put themselves at a higher risk of detection by predators because they emerge in day light, they also often ignored approaching humans while engaged in mating behavior (personal observation).

1.7. Evidence of Predator Recognition in Non-Human Primates

Like many animals, most, if not all primates, use a combined strategy of indirect and direct anti-predation strategies. Many primates live in groups, which benefits them indirectly by providing a dilution and confusion effect, allows for a group defense, and provides many ears, eyes, and noses to directly detect predators [e.g. Janson and Goldsmith 1995; Terborgh 1990; van Schaik 1983]. Solitary primates tend to be small and cryptic [e.g. Bearder et al. 2002], and some solitary species have defenses such as toxic bite (*Nycticebus coucang*) or a scapular shield (*Arctocebus* and *Perodicticus*) [Nekaris et al. 2007]. Many species engage in predator sensitive foraging strategies, for example, by temporally or habitually avoiding areas that increase their vulnerability to predators [e.g. Cowlishaw 1997; Miller 2002; Wright 1989]. In this section, I will however focus on direct anti-predation adaptations of primates.

Primates are able to perceive a wide range of sensory stimuli through several sensory systems including vision, olfaction and audition [Dominy et al. 2001; Fleagle 1999; Martin 1990]. Primates as a group are highly visual animals and are characterized by convergent orbits, depth perception, high visual acuity, and enlarged brains with large visual areas [Allman 1999; Cartmill 1974; Fleagle 1999]. Overall evidence suggests that both diurnal haplorhine and strepsirhine primates are able to utilize a range of direct predator information to lower predation risk. Comparatively little is known about predator-prey interactions in nocturnal primates. Nocturnal primate studies are few, probably because due to their small size, and their nocturnal and often solitary life style, they are much more difficult to locate and observe than diurnal species. The relatively sparse knowledge of nocturnal primate behavior probably led to the long-held belief that they rely largely on indirect cryptic anti-predator strategies [Cheney and Wrangham 1987; Stanford 2002; Terborgh and Janson 1986; van Schaik and van Hooff 1983; Wright, 1998]. Wright [1989, 1998], in her comparison of nocturnal and diurnal primates in the same habitat discovered that the small diurnal primate was cryptic, even when active, but the same-sized nocturnal primate did not show cryptic behavior during its active period. Since that study, good work has been accomplished on understanding the relationship between nocturnal primates and their predators (Bearder, 2007, Gursky, 2005, Nash, 2007, Nekaris et al. 2007]. In the following section, I will provide an overview of what is known about predator recognition abilities, and the associated behavioral responses, in diurnal and nocturnal primates.

1.7.1. Diurnal Primates

Diurnal primates are particularly visually oriented, and there is ample evidence that visual predator information is meaningful to them. Increased vigilance, alarm calling, mobbing, and often predator specific escape behaviors, are commonly observed in both diurnal haplorhine and strepsirhine primates [Caine and Weldon 1989; Chapman 1986; Ferrari and Lopes Ferrari 1990; Gil-da-Costa 2007; Gould and Sauther 2007; Karpanty and Wright 2007; Macedonia 1990; Prescott and Buchanan-Smith 2002; Scheumann et al. 2007; Seyfarth et al. 1980; Struhsaker 1967; Zuberbühler 2007]. Shape, color and patterns can be important warning and recognition cues. Bonnet macaques, for example, are preyed upon by leopards that possess a spotted coat, and, more rarely, a dark coat. Macaques not only displayed a faster flight response to upright than to up-side- down leopard models, but also to the more common spotted coat pattern [Coss and Ramakrishnan 2000; Coss et al. 2005]. Lemurs and monkeys commonly drop in the canopy when exposed to live or model raptors, and also to models vaguely resembling birds, suggesting that shape is an important raptor recognition cue [Brockman 2003; Colquhoun 2007; Karpanty and Wright 2007; Macedonia and Polak 1989; Sauther 1989]. Putty-nosed monkeys (*Cercopithecus nictitans martini*) produced loud alarm calls when they spotted stationary models of leopards and crowned eagles in trees, but they did not necessarily move away [Arnould et al. 2008]. This suggests that they perceived them as dangerous and had some "knowledge" about the ambush hunting tactics. The calls might have served to alert the predators that they had been detected and thus lost the element of surprise. Like many animals, primates commonly display fear in response to snakes. Responses include flight and avoiding the area where the snake had been spotted, but primates are also known to mob snakes [Bayart and Anthouard 1992; Cook et al. 1985; Joslin et al. 1964; Mineka et al. 1980; Ouattara et al. 2009; Vitale et al. 1991] . Snake recognition can very specific. Some monkeys and lemurs are able to distinguish dangerous from nondangerous snakes [*Eulemur macaco*: Colquhoun 1993; *Macaca mulatta*: Mineka and Cook 1988; *Macaca radiata*: Ramakrishnan et al. 2005], or familiar and unknown snakes [Ouattara et al. 2009]. Recognition might have been based on color or scale patterns. Altogether there is ample evidence that diurnal monkeys and lemurs recognize and identify avian, mammalian, and snake predators based on visual features.

Monkeys and lemurs also extract risk relevant information from predator sounds. There are various investigations where predator vocalizations have been presented to wild and captive individuals. Common responses included flight and alarm calling, which were often predator specific [Colquhoun 1993; Hauser and Wrangham 1990; Jolly 1966; Ramakrishnan and Coss 2000; Seyfarth and Cheney 1990]. For example, in response to raptor calls, monkeys and lemurs commonly descend in the canopy, seek cover, emit specific alarm calls and scan the sky [Ferrari and Lopes Ferrari 1990; Fichtel and Kappeler 2002; Karpanty and Grella 2001; Karpanty and Wright 2007; Macedonia and Yount 1991; Sauther 1989; Wright 1998]. When Diana monkeys were presented with leopard or chimpanzee calls, they loudly called in response to the former, but became silent to the latter [Zuberbühler 2000]. This suggests that they differentiate between the calls, and took into account the hunting style of the predators: leopards rely on surprise whereas chimpanzees are pursuit hunters. Campbell's monkeys (*Cercopithecus campbelli*) moved up or down in the canopy to leopard or eagle vocalizations, respectively, but called and approached them when models were visible [Ouattara et al. 2009]. This suggests that the monkeys took into account the hunting technique of the predators.

Comparatively little is known about olfactory predator recognition in diurnal primates, and all studies involved captive callitrichids. Tamarin monkeys (*Saguinus labiatus* and *S. oedipus*) exhibited flight, vigilance, increased sniffing, and general excitement in response to mammalian predator odors while ignoring non-predator odors [Buchanan-Smith et al. 1993; Caine and Weldon 1989]. This suggests that predator odors also potentially convey risk relevant information to primates. Olfactory predator recognition has been most extensively studied in rodents, and evidence suggests that many species of rodent perceive predator odors as dangerous, and that some species are furthermore able to distinguish among predators with different hunting techniques based on odor [e.g. Rosell 2001]. In summary, there is good evidence that many species of diurnal primate recognize visual, acoustic, and olfactory predator cues as indicators of danger. Furthermore, some species have demonstrated the ability to distinguish among predator types and even among species of the same type.

1.7.2. Nocturnal Primates

Compared to diurnal primates, extremely little is known about predator-prey interactions in nocturnal primates. For a long time it has been assumed that nocturnal primates rely largely on indirect anti-predation strategies such as a cryptic appearance and cryptic lifestyle [Cheney and Wrangham 1987; Stanford 2002; Terborgh and Janson 1986; van Schaik and van Hooff 1983; Wright, 1998]. Indeed, nocturnal primates tend to be small, and are solitary or live in very small groups [Bearder et al. 2002; Mittermeier at al. 2010]. Some of the Asian lorises and African pottos are characterized by their slow and silent locomotion, cryptic coloration and often sparse vocalization [Charles-Dominique 1977; Nash 2007; Nekaris et al. 2007], and a slender loris (*Loris* spp.), completely ignored nearby predators, and one individual even climbed over a dangerous snake [Bearder et al. 2002; Nekaris et al. 2007]. Other anecdotal reports suggested that behavioral change occurred only in response to direct face-to-face predator encounters. Responses observed included flight, freezing, dropping to the ground and screaming [Bearder et al. 2002; Charles-Dominique 1977; Nekaris et al. 2007]. However, as more and more knowledge is being gained, it seems that the long-held perception of nocturnal primates is incomplete. For example, it has emerged that not all species are as cryptic as once thought [Wright 1989]. Many species in the genera *Avahi, Lepilemur, Cheirogaleus, Phaner, Microcebus, Aotus* and *Tarsius* live in pairs or small groups, and can at times be very noisy and vocal [Bearder 2007; Mittermeier et al. 2006; Nash 2007; Nekaris et al. 2007; Rowe 1996; Schuelke 2001; Wright 1989; Zimmmermann et al. 2000]. *Aotus*, the nocturnal monkey, is often found in groups of 3-6 individuals, gives loud, long calls, and mobs predators with clicking vocalizations [Wright, 1989]. Even species that are classified as solitary, such as mouse lemurs (*Microcebus* spp.) sometimes aggregate during their activity period, or sleep in groups [personal observation; Braune et al. 2005; Randriamiarisoa et al. 2007]. In spectral tarsiers (*Tarsius spectrum*), individuals from several different family groups have been observed joining together to engage in very noisy and vocal predator mobbing (Gursky 2005).

There have been anecdotal reports suggestive of predator recognition in nocturnal primates [Bearder et al. 2002; Charles-Dominique 1977; Nash 1986], but only more recently have there been empirical investigations involving experiments [Bunkus et al. 2005; Bunte 1998; Deppe 2005, 2006; Görlitz 2004; Gursky 2003, 2005, 2007; Rahlfs et al. 2006; Scheumann et al. 2006; Sündermann et al. 2008]. Even though vision would appear to not be very relevant at night, investigations show that *Galago, Microcebus, Tarsius* and *Aotus* have relatively high acuity vision for a mammal due to a high ganglion cell density [Tetreault et al. 2004], and the presence of a relatively high number of cones in the aye-aye (*Daubentonia madagascariensis*) suggests that some species might have color vision [Perry et al. 2007]. There is evidence from experiments that suggests that both nocturnal haplorhine and strepsirhine species perceive visual predator cues as indicators of danger. A field investigation by Gursky [2003; 2005; 2006; 2007] showed that spectral tarsiers (*T. spectrum*) not only perceived predator models as dangerous, but also responded with different behaviors to the different models. Tarsiers mobbed snake and civet models but froze in response to falcon models. Moreover, tarsiers responded fearfully to models of dangerous snakes but often largely ignored models of harmless snakes. However, since tarsiers also eat snakes, it is possible that there was a strong selection for snake species recognition. African and Asian strepsirhines also demonstrated visual predator recognition. In response to a civet, pottos moved into dense vegetation [Nekaris et al. 2007], whereas a dead snake elicited intense fear and dropping to the ground [Charles-Dominique 1977]. The grey slender loris (*N. lydekkerianus*) has been observed to apparently mimic a cobra by swaying bipedally with arms raised, which can successfully ward of or startle predators [Nekaris et al. 2007]. Nocturnal lemurs changed their behavior upon detecting a snake. Fork-marked lemurs (*Phaner furcifer*) mobbed a boa that was lying on the ground [Schuelke 2001], and a fat-tailed dwarf lemur (*Cheirogaleus medius*) attacked a colubrid snake that was next to its sleeping whole [Fietz and Dausmann 2003]. Several studies have involved mouse lemurs, and those will be reviewed and examined in greater detail in section 1.9. In summary, captive-born mouse lemurs emitted calls in response to snakes and mammalian predator models [Scheumann et al. 2007; Zimmmermann et al. 2000], but wild subjects ignored models of a viverrid predator and diurnal raptors [Rahlfs et al. 2006]. Although there were no audible calls, wild mouse lemurs exhibited avoidance, mobbing, and even attacks of snake models [Deppe 2005; 2006; Görlitz 2004b].

Findings with regards to acoustic predator recognition in nocturnal primates are few and mixed. Mouse lemurs ignored predator calls [see section 1.9.; Bunkus et al. 2005; Scheumann et al. 2006], but other species showed, although comparatively subtle, behavioral change. Karpanty and Grella [2001] presented diurnal raptor to woolly lemurs (*Avahi laniger*) and sportive lemurs (*Lepilemur mustelinus*). In response to calls of the Henst's goshawk (*Accipiter henstii*) and the Madagascar Harrier hawk (*Polyboroides radiatus*) some individuals of sportive lemurs scanned the sky, but all ignored calls of the Madagascar serpent-eagle (*Eutriorchis astur*). Even though recording were played from below the lemurs, lemurs associated the former two raptors with being located in the sky. They appeared to have no knowledge about the eagle. Woolly lemurs appeared to have less knowledge about raptors, because they merely looked toward the speakers. In another experiment, red-tailed sportive lemurs (*L. ruficaudatus*) ignored non-predator sounds, but upon hearing the call of a mammalian predator, the fosa (*Cryptoprocta ferox*), and the

Madagascar harrier hawk, most individuals moved away and scanned the ground or the sky, respectively [Fichtel 2007]. This suggests that the lemurs distinguished between the aerial and terrestrial predator. So even though there is evidence that some species of nocturnal lemur extract predator relevant information from predator calls, behavioral responses were much less dramatic than those of diurnal primates, that often exhibit flight, alarm calling, and predator appropriate strata changes. This, however, might be explained by the fact that the raptors used in the two play-back studies are diurnal. It is known that the diurnal raptors eat sportive and woolly lemurs. The experiments, however, took place during the night when lemurs were active, and it is possible that lemurs did not associate the calls with danger because at night the calls were out of the appropriate context. Lemurs might have been more curious than alarmed which might explain that raptor calls were ignored or merely elicited a looking response rather than flight.

Olfactory recognition has only been examined in mouse lemurs, which distinguished between predator and non-predator odors [see section 1.9.; Scheumann et al. 2006; Sündermann et al. 2005; Sündermann et al. 2008]. Strepsirhine primates would be expected to be more sensitive to olfactory predator cues than haplorhine primates because of they have a more highly developed olfactory system [Evans and Schilling 1995; Martin 1990], and in visually oriented animals such as primates, olfactory cues would be expected to be more important at night than during the day.

1.8. Mouse lemurs

The nocturnal mouse lemurs are the smallest primates, and they are endemic to Madagascar. At a size of 587,000 square kilometers, Madagascar is the fourth-largest island in the world, and is located in the Indian Ocean off the southeast coast of Africa. Mouse lemurs are widely distributed across the island in a variety of habitats. Due to their small size, mouse lemurs are subject to very high predation rates by a wide range of predators.

1.8.1. Distribution, Ecology and Behavior

Mouse lemurs are members of the Family Cheirogalidae, a group of small strepsirhine primates endemic to Madagascar [Garbutt 1999; Martin 1972]. The family Cheirogalidae is comprised of five genera and 30 species: mouse lemurs (*Microcebus*), giant mouse lemurs (*Mirza*), dwarf lemurs (*Cheirogaleus*), forked-marked lemurs (*Phaner*), and the hairy-eared dwarf lemur (*Allocebus*) [Mittermeier et al. 2010]. The number of recognized mouse lemur species has increased dramatically in the past three decades, and particularly in the past five years, to now eighteen different species [Mittermeier et al. 2010]. Mouse lemurs are the smallest primates, and species range in weight from 30 to 87 grams [Louis et al. 2006; Mittermeier et. al. 2010; Yoder et al. 2000]. Mouse lemurs are found in a variety of habitats, including primary and secondary rain, dry, and deciduous forests, in sometimes severely degraded habitats including crop fields and villages [personal observation; Kappeler and Rasoloarison 2003; Yoder et al. 2000]. All mouse lemurs are nocturnal, arboreal, and feed on a variety of fruit, flowers, and flying and crawling insects [Atsalis 1999a; Kappeler and Rasoloarison 2003]. Even though they appear to be largely solitary foragers [Perret 1990; Radespiel 2000], they can aggregated at feeding sites [personal observation]. During the day, mouse lemurs often share sleeping sites with other individuals. Sleeping sites include tree holes, branches, and self constructed spherical leaf nests [Randriamiarisoa et al. 2007; Schmid 1999]. In the dry forest, as many as thirty individuals have been found to share a single tree hole [Fietz 1999; Schmid 1999]. Braune et al. (2005) found that the golden brown mouse lemur (*M. ravelobensis*) has groups that habitually sleep together, and that distinguish themselves from other such groups by group-specific vocalizations. Mouse lemurs often have distinct homer ranges that can persist for many years, and that commonly overlap extensively with those of others [personal observation; Atsalis 2002; Müller and Thalmann 2000; Radespiel et al. 2001]. As a result, mouse lemurs can occur at high densities at one hundred or more individuals per square kilometer [personal observation; Atsalis 2002; 2008; Goodman et al. 1993]. In lean times during the austral winter (June – August), mouse lemurs often undergo a flexible, hibernation type state, called torpor, which can last from a day to possibly several months [Schmid 2001]. Females seem to often undergo longer periods of torpor than males, because males are often captured with live traps during the winter months, whereas females rarely are [Atsalis 1999b; 2008; Schmid 2001]. Mouse lemurs have a high reproduction rate for a primate. Litters of up to three offspring once or twice a year are common [Blanco 2008; Eberle and Kappeler 2004; Radespiel 2002]. Mouse lemurs also have a long life span for a small mammal. In captivity, mouse lemurs are known to live at least thirteen years [Zimmermann, personal communication; Picq 1992], and in Ranomafana National Park, wild brown mouse lemurs (*M. rufus*) have been found to live at least nine years [personal observation; Zohdy et al. submitted].

1.8.2. Mouse Lemur Sensory Systems

Mouse lemurs are well adapted to life in the dark, having large eyes, large mobile ears and a well-developed sense of smell (Martin, 1990; Figure 1.1). Like all primates, mouse lemurs have forward facing eyes, which enable acute close range vision and depth perception [Allman 1999; Kirk and Kay 2004]. Among nocturnal primates, and mammals in general, mouse lemurs have high acuity vision due to a high density of ganglion cells [Kirk and Kay 2004; Tetreault et al. 2004]. Their retina is lined with a light reflective layer, the *tapetum lucidum,* and light and motion sensitive photoreceptors (rods), enabling mouse lemurs to make the most of low light conditions [Dkhissi-Benyahya et al. 2001; Ross 2000]. Due to the presence of some color sensitive cones in the retina, mouse lemurs are dichromatic [Tan and Li 1999]. Dichromatism is thought to enhance the detection of camouflaged objects, such as insects and possibly predators [Morgan et al. 1992].

Mouse lemurs have acute hearing which is facilitated by mobile and large outer ears (pinna). The pinna is tall and narrow, which is thought to enhance high frequency sound perception [Rosowiski 1994]. Their hearing is most acute between 3-40 kHz [Niaussat and Petter 1980; Zimmermann et al. 2000]. Mouse lemurs often vocalize in the ultrasonic frequency range (above 20 kHz), which is thought to be outside the hearing range of many predators [Zimmermann 1995]. Mouse lemurs often use hearing to locate insect prey [Görlitz 2004a; Görlitz and Siemers 2007; Piep et al. 2003], although insects are also detected visually [personal observation]. Sound is also important in social interactions, where vocalizations can be very specific [Braune et al. 2005; Zimmermann 1995; Zimmermann and Hafen 2001; Zimmermann and Lerch 1993; Zimmermann et al. 2000].

Like all strepsirhines, mouse lemurs are characterized by a well-developed olfactory system that includes a rhinarium, vomero-nasal organ and a highly developed olfactory bulb [Evans and Schilling 1995; Martin 1990]. In lemurs, olfaction is important in the context of foraging and social interactions [Estes 1972; Harste 1994; Sündermann et al. 2005].

1.8.3. Mouse Lemur Predators

Being so small, mouse lemurs are preyed upon by aerial, terrestrial and arboreal predators (Figure 1.2). As many as 14 different diurnal and nocturnal predator species prey upon mouse lemurs at any given location [Scheumann et al. 2007]. Predation rates for most primates are low

[Cheney and Wrangham 1987], but almost no information is available for nocturnal primates. In mouse lemurs, predation rates are probably very high.

Owls, including the large Madagascar long-eared owl (*Asio madagascariensis*) and the Madagascar red owl (*Tyto soumagnei*), are thought to be the biggest threat to mouse lemurs [Goodman 2003c; Goodman et al. 1991; Hart 2007]. Goodman et al. (1993) estimated that owls alone killed 25% of mouse lemurs annually in the dry deciduous forest of Beza Mahafaly. Diurnal raptors including the Henst's goshawk (*Accipiter henstii*), the Madagascar buzzard (*Buteo brachypterus*), and the Madagascar harrier hawk (*Polyboroides radiates*) are also known to prey on mouse lemurs [Alcock 1989; Goodman 2003c; Karpanty 2006; Karpanty and Wright 2007; Thurow and Black 1981; Wright and Martin, 1995] which they might take from their sleeping sites, or in instances where mouse lemurs become active before dusk. Karpanty (2003) estimated that in the rainforest of Ranomafana National Park, diurnal raptors kill around 4.5% of mouse lemurs annually.

Historically, the only mammalian carnivores present on Madagascar were viverrids. Predation rate estimates are not available. At an average weight of 6.75 kilos, the fosa (*Cryptoprocta ferox*) is the largest extant mammalian predator [Hawkins 2003]. Due to retractable claws, the fosa is both terrestrial and arboreal [Hawkins 2003]. The fosa is a solitary, very quiet, animal with large territories and is very rarely seen [Dollar 1997; Dollar et al. 2007; Hawkins 2003]. However, during the mating season that occurs between October – December, fosa can be very conspicuous because they congregate and are very vocal [Hawkins 2003]. Even though the fosa is known to target nocturnal and diurnal lemurs, and can sometimes kill entire groups [Goodman 2003; Wright personal communication], it probably preys on the tiny mouse lemurs only opportunistically. There are several species of smaller, partially arboreal, endemic diurnal and nocturnal viverrids (*Galidia* spp. and *Galidictis* spp.), as well as the introduced small Indian civet (*Viverricula indica*), which likely prey on mouse lemurs [Goodman 2003a; Goodman 2003b; Goodman 2003c]. The ring-tailed mongoose (*Galidia elegans*, Figure 1.2) has been observed to prey on brown mouse lemurs during the day [Deppe et al. 2008].

Snakes are likely also a threat. Boas in particular are thought to eat mouse lemurs [Cadle 2003; Raxworthy 2003; Wright and Martin 1995]. However, due to their slowness, snakes might be most dangerous to sleeping mouse lemurs.

1.9. A Review of Anti-Predation Adaptations and Behaviors in Mouse Lemurs

Mouse lemurs are very small, nocturnal, arboreal, and tend to forage alone. Mouse lemurs are also often found in dense vegetation, and they tend to sleep in groups of two or more in concealed places, such as leaf nests or tree holes. Mouse lemurs often occur at high densities, have a high reproduction rate for a primate, and like in the majority of lemurs, reproduction is somewhat synchronized and seasonal. Due to their small size, both young and adults are subject to predation by a wide range of predators, including diurnal and nocturnal birds, mammals, and snake.

It has been proposed that characteristics typical of many nocturnal primates, such as small size, a nocturnal lifestyle, and a solitary or small group size, lower predation risk via crypsis [e.g. Cheney and Wrangham 1987]. In the following section I will provide a review and discussion of this viewpoint.

1.9.1. Indirect Anti-Predation Responses

Nocturnality is not necessarily a means to reduce exposure to predators, because often there are as many nocturnal predators as there are diurnal ones [Caro 2005; Lima and Dill 1998]. All predator types (birds, mammals, and snakes) have both diurnal and nocturnal species that prey on mouse lemurs [Goodman 2003; Scheumann et al. 2007]. If nocturnality is an ancestral state [Fleagle 1998], it might have been maintained to avoid competition with diurnal species [Wright 1989], or because insects, an important food source of mouse lemurs [Atsalis 1999], are more active at night.

Being solitary during one's activity period likely reduces conspicuousness to predators, and might also lower the likelihood of encountering predators [Caro 2005; Terborgh 1990]. While living in a group can provide protection from predation via the dilution and predator confusion, as well as enable group defense strategies and potentially an early detection of predators [e.g. Janson and Goldsmith 1995; Terborgh 1990], staying in contact with group members can pose a problem at night. Under such conditions, vocal communication would be a preferred means of staying in touch, but sound can attract the attention of predators. Even though mouse lemurs often use ultrasonic vocalizations that is thought to be outside the hearing range of many predators [Harste 1994; Scheumann et al. 2007], the increased noise or motion of the locomotor activity that several lemurs would generate might increase conspicuousness. Moreover, the very dense microhabitat often utilized my mouse lemurs [Musto et al. 2005] can severely diminish the anti-predation advantages of groups, because even if group members are nearby, predators might only perceive an individual. So in mouse lemurs, a solitary life style might be more advantageous because it reduces overall conspicuousness. Solitary foraging in mouse lemurs might also reflect their reliance on insects. Insects are often dispersed, and foraging alone would reduce feeding competition. Nocturnal lemurs with a high reliance on usually dispersed insect or vertebrate food, tend to be solitary foragers (*Microcebus*, *Mirza*, *Daubentonia*, and *Allocebus*), whereas those with relying on more clumped foods like leaves or fruit tend to live in pairs or family groups (*Avahi*, *Lepilemur*, and *Cheirogaleus*). So even though solitary foraging at night might lower conspicuousness to predators, it might also be an adaptation to an insect diet.

Even though mouse lemurs are solitary at night, they often sleep in groups during the day.   It has been proposed that this behavior is a thermoregulatory adaptation to their small body size [e.g. Schmid 2001]. However, it might also lower predation risk because it provides a dilution and confusion effect. For example, when a ring-tailed mongoose attacked two mouse lemurs sleeping in a leaf nest, mouse lemurs shot out in different directions and one escaped unharmed [Deppe et al. 2008]. The fine branch niche that mouse lemurs often utilize likely also lowers predation risk. The much heavier arboreal predators, including snakes and viverrids, are unable to go there, and it provides cover from owls. Brown mouse lemurs often construct leaf nests in very fine and dense branches [Randiamiarisoa et al. 2007; Wright and Martin 1995], which excludes access by arboreal predators and provides concealment from diurnal aerial predators.

Even though it has been suggested that small body size lowers conspicuousness to predators, small animals typically suffer much higher predation rates than large ones [Cheney and Wrangham 1987; Kotler et al. 1998; Lima and Dill 1990; Caro 2005]. Mouse lemurs are known to suffer by far the highest predation rates in primates [Goodman et al. 1993], so small size by itself is not an effective anti-predation adaptation. However, their size allows their insect diet, because locating and handling dispersed insects is time consuming, and thus only energy efficient for small animals [Kay 1972]. The pelage of mouse lemurs might provide some protection from predators. Mouse lemurs tend to be grey or brown with a darker dorsal stripe, which likely provide good camouflage in the forest. When seen from above, mouse lemurs have the appearance of a dry leaf. Brown mouse lemurs, for example, sometimes become active late afternoon when it is still light [personal observation], and based on my personal experience, from a distance it can be very difficult to distinguish them from their leaf nests and from surrounding vegetation. Their cryptic pelage might provide protection from diurnal, visually oriented predators such as raptors.

There is also evidence that many nocturnal primates increase activity during moonlit nights, and it has been proposed that this is due to the better detection of predators compared to dark nights [Bearder et al. 2002; Gursky 2003; Nash 2007; Wright 1989]. It is not known whether mouse lemurs change their activity in response to ambient light.

In summary, mouse lemurs appear to have indirect anti-predation adaptations. Their cryptic pelage, preference for dense vegetation and fine branches, and social sleeping are very likely to lower predation risk. Solitary foraging might lower predation risk, but might be an adaptation to diet. Their nocturnal activity period and small body size are likely not anti-predation adaptations.

1.9.2. Direct Anti-Predation Responses

Almost nothing is known about predator recognition in nocturnal primates, but among nocturnal species, most is known about mouse lemurs. Anecdotal reports about predator-prey interactions are very few and included one instance of a mouse lemur mobbing a boa, and mouse lemurs observing predators from a distance [Scheumann et a. 2007]. I have many times witness the reaction of the brown mouse lemur to humans, a potentially dangerous predator. Mouse lemurs often approach humans in the forest and observe them from a distance of two or more meters, often from above. If a human moves towards a mouse lemur, it leaps away, but will often stop and observe from a distance. When previously captured mouse lemurs are released from a trap back into the forest, they usually leap away from the human, and then stop to observe, but sometimes mouse lemurs will also leap to the ground and then climb up branches. Dropping to the ground, presumably an evasion tactic, has also been observed in infant *Galago* [Charles-Dominique 1977]. I have made several other observations while handling wild brown mouse lemurs. When they are grabbed by a human, they sometimes utter loud and fast paced calls. Such calls might serve to startle the predator, or to alert other mouse lemurs in the vicinity. For example, when spectral tarsiers encounter a predator, especially snakes, they often emit loud calls, which attract family group members, and sometimes other groups of tarsiers, which then engage in collective predator mobbing [Gursky 2005, 2006]. It is not known if group mobbing occurs in mouse lemurs. Before being grabbed by the approaching hand of a human, brown mouse lemurs often raise their arms, expose their teeth by opening their mouths wide, and often even leap at the approaching hand to bite it [see also Scheumann et al. 2007]. These behaviors probably serve to make a mouse lemur look larger and more threatening, although this probably does not deter the usually much larger predators. Charging, biting, and calling might, however, startle a predator long enough for the mouse lemur to make a quick escape.

There are several experimental studies that investigated how mouse lemurs react to visual, olfactory, and acoustic predator cues. Visual experiments involved snakes, mammals, and raptors. Thirteen captive-born mouse lemurs (*M. murinus and M. lehilahytsara*) were exposed in their cages to a stuffed owl, a moving owl silhouette, an immobile model of a large snake, and a moving live boa [Bunte 1998]. Overall, *Microcebus murinus* tended to move away from the snake stimuli, but ignored other stimuli, and *M. lehilahytsara* largely ignored all stimuli. Neither species distinguished between predator and non-predator stimuli, between predator types, or still or moving stimuli. However, *Microcebus murinus* exhibited more locomotor activity in response to a still snake than to the live boa, and *M. lehilahytsara* sometimes hid in response to the moving owl silhouette. Scanning (vigilance) rates were not affected by any stimuli in *M. murinus*, but rates increased in *M. lehilahytsara* after exposure to the snake stimuli. Both species vocalized during stimuli encounter, largely in high frequency ranges outside of human hearing. However, vocalizations did not significantly differ with respect to the predatory type, but overall, *M. murinus* vocalized significantly more often than *M. lehilahytsara*. Bearder [2007] likewise found that calls in galagos did not seem to be predator specific. Overall, it does not appear that the mouse lemurs perceived any of the stimuli as highly dangerous, but instead behaviors suggest an alert state, at most. In another experiment, captive-born mouse lemurs were exposed to a live non-predator (rodent) and to a live predatory lemur (*Mirza coquereli*). Mouse lemur vocalized more often to the predator, but other behavioral responses were not reported [Schuelke and Kappeler in Scheumann et al. 2007]. Rahlfs et al. [2006] presented wild grey mouse lemurs with a model of a large viverrid (fosa) and of a diurnal raptor. Mouse lemurs completely ignored both models. In contrast, wild grey and brown mouse lemurs avoided or mobbed a snake model. Mouse lemurs were hesitant to leave a nest box in the presence of a snake [Görlitz 2004b], and sometimes singly mobbed and even attacked and bit a rubber snake [Deppe 2005, 2006].

Even though experiments have shown that mouse lemurs are highly sensitive to acoustic cues in the context of foraging [Görlitz and Siemers 2007], there is no evidence that mouse lemurs perceive predator calls as dangerous. There are no anecdotal reports available, but play-back studies with captive-born grey mouse lemurs found no behavioral change to calls of known avian and mammalian predators, nor did mouse lemurs distinguish between predator and non-predator vocalizations [Bunkus et al. 2005; Scheumann et al. 2006].

There is one study that tested olfactory recognition in mouse lemurs. Captive-born grey mouse lemurs were presented with the feces of historical (owl and fosa) and introduced carnivores (cat and dog), as well as non-predator controls [Sündermann et al. 2008]. Mouse lemurs spent a significant shorter time feeding next to the odors of predators than to those of non-predators. They also exhibited more locomotor activity in trials with predator odors than in those with control odors. Five of the twenty-two subjects produced high frequency calls during trials, but they did not distinguish between predator and non-predator trials. Since these were predator naïve subjects, this suggests that olfactory predator recognition is innate in grey mouse lemurs. The finding that mouse lemurs failed to distinguish between historical and introduced carnivores further suggests that recognition might have been based on general metabolic byproducts of meat digestion. Similar finding and conclusions have been reached in studies with rodents [Nolte et al. 1994].

In summary, evidence suggests that mouse lemurs recognize snakes as dangerous, but there is no evidence that they recognize other predators visually. There is evidence that mouse lemurs perceive predator odors as indicators of danger, but not predator calls. It is important to keep in mind that the studies had relatively small sample sizes, and that in several cases, mouse lemurs were predator naïve. Behavioral differences observed between species further suggest that predator recognition abilities might vary among mouse lemur species or populations.

1.10. Goals of this Study

The broader goal of this study was to gain a better understanding of how a small nocturnal primate avoids predation. The specific aim was to examine whether mouse lemurs perceive sensory information provided by predators as indicators of danger. Furthermore, this was the first comprehensive study that tested three sensory modalities (vision, hearing, and smell) in one species and population.

Mouse lemurs suffer very high predation rates, at least in the dry forests [Goodman et al. 1993], which might have resulted in a selection for direct recognition mechanism that lower predation risk. Being subject to a wide range of predator types with different hunting techniques, mouse lemurs would further benefit from the ability to differentiate among predators. It has been proposed that the high acuity visual system in primates could have evolved, or been accelerated, in early (diurnal) anthropoid primates in the context of predation avoidance [Isbell 2006]. However, the high acuity vision found in some nocturnal primates, particularly owl monkeys, galagos and mouse lemurs [Tetreault et al. 2004], raises the question whether selection for visual processing might have occurred before the emergence of diurnal primates, or at least independent of activity mode.

I chose wild individuals as my study subjects, because in order to learn about behavior, it is useful to look at animals that live in their natural surroundings. Mouse lemurs are ideal among nocturnal primates because they occur at high densities and are easily captured using live traps [Atsalis 2008; Blanco 2008]. Moreover, I found that mouse lemurs quickly habituate to novel environments, which allows for experiments in a controlled environment away from the forest. Because many mouse lemur individuals are repeatedly and reliably captured, sometimes every night, I could limit their time in captivity and was able to release mouse lemurs back into the forest within a few hours of capture.

I used live trapping and laboratory experiments to investigate whether mouse lemurs recognize predator cues. The measure of risk perception was behavioral change. I presented mammalian, avian, and snake stimuli, as well as a wide range of non-predator controls to mouse lemurs. Experiments addressed three sensory systems (vision, hearing, and smell). I conducted two types of experiment: one took place under relatively natural conditions in the forest, and one under more controlled conditions in a laboratory. In the forest, I predicted that mouse lemurs would be less likely to be captured in a trap next to predator stimulus, than in a trap next to a non-predator or no stimulus. For the laboratory trials I predicted that mouse lemurs would display fear behaviors in response to predator stimuli, but not non-predator stimuli. This is the first comprehensive experimental study of predator recognition in a nocturnal primate, using a wide range of predators and addressing three sensory systems.

1.11. Study Site and Subjects

This study took place in Ranomafana National Park (RNP), southeastern Madagascar (Figure 1.3). The region of the park where our study site was located had been selectively logged in the 1980s, and is now characterized by endemic trees with patches of invasive species such as strawberry guava (*Psidium cattlynium*), rose apple (*Syzygium jambo*) and soapbush (*Clidemia hirta*). The park, established in 1991, is 43,500 ha of continuous rain forest located in southeastern Madagascar at 21^{o} 16'S latitude and 47^{o} 20'E longitude [Wright 1992; Wright and Andriamihaja 2004]. The park is located 25 km from Madagascar's second largest city, Fianarantsoa, and 60 km from the Indian Ocean. Elevations range from 500 – 1500 m, and annual rainfall is, on average, 3400 mm (range 1748-4230mm) (RNP records), most of which falls during the months from December to March. Temperatures range from lows in June-September (4-12 C) to highs in December – February (30-32 C). Brown mouse lemurs were captured in area of approximately 1 square kilometer that was within the Talatakely trail system (Figure 1.4). On the edge of the park, near the main park entrance, is the Centre ValBio research station (Figure 1.5). This "state of the art" research facility, inaugurated in 2003, was my home base during my field research, and many components of this study took place there.

The study species, the brown mouse lemur (*Microcebus rufus*), is the only known mouse lemur species in the study area (Figure 1.1) [Mittermeier et al. 2009]. The Talatakely brown mouse lemur population was first briefly assessed by Harcourt [1987] and Wright and Martin [1995] using live trapping, and their distribution, abundance and diet was later more extensively studied by Atsalis [2008; 1998; 1999a,b]. At 45 grams, the brown mouse lemur is one of the smallest species of mouse lemur [Atsalis et al. 1996]. Like all mouse lemurs, its diet consists mainly of fruits and insect such as moths and beetles [Atsalis 1999a]. Individuals have home ranges of varying sizes, and that overlap, often extensively, with those of others [Atsalis 2000; Deppe, unpublished data]. In Talatakely, brown mouse lemurs occur at densities of around 100 individuals per square kilometer [Atsalis 2000]. I began studying the brown mouse lemurs in Talatakely in 2003, and have since conducted live trapping for 3 months each year until 2008 [Blanco 2008]. Since 2003, over 400 individuals have been fitted with micro-chips in Talatakely an dthe surroundings areas, which allow for identification and enable the long-term study of individuals [Durden at al. 2010; Zohdy et al. submitted]. The long-term study revealed that between 25-40% of mouse lemurs disappear from the population each year, but repeated capture has also revealed that some individuals maintain stable home ranges for at least 4 years [Deppe, unpublished data]. A brief study using radio telemetry revealed that during the day, brown mouse lemurs sleep in self constructed leaf nests, branches, tree ferns and tree holes [Randriamiarisoa et al. 2007]. Mouse lemurs were found sleeping singly, in pairs, or in groups of 3 individuals. There is also evidence that the brown mouse lemurs are more abundant in areas with dense vegetation such as strawberry guava and bamboo [Musto et al. 2005]. An absence of females, but not males, in traps during the months of June- late Sept suggest that females might undergo long periods of torpor, whereas males are often active [Atsalis 1999b; personal observation]. Their reproductive season begins in October and usually has a duration of two weeks, although there is evidence of a second estrus in January-February [Blanco 2008]. Female brown mouse lemurs most often have one litter of up to three offspring per year although there has been one case of a possible second litter [Blanco, 2008].

1.11.1. Mouse Lemur Capture Methods

Live trapping was the basis for this study; a method commonly employed to study the elusive mouse lemurs (Figure 1.6) [Atsalis 2000; Harcourt 1987]. Across the study area, there were 30 fixed trap locations in 25-50 meter intervals along the trails. Two traps were allocated to each location; one on each side of the trail, approximately 5-15 meters deep into the forest. Because mouse lemurs commonly return to traps each night, I oftentimes used only half of the trap locations to minimize the time mouse lemurs were removed from the forest. Traps were placed into the forest, and baited with fresh banana, starting at 17:00 hours. They were removed from the forest at 21:00 hours. Captured mouse lemurs were either processed at the laboratory at the Centre ValBio research station, or in the forest. First lemurs were placed in small cotton bags so they could be weighed and scanned for a preexisting micro-chip. Unknown individuals were sexed and micro-chipped. Some individuals were released immediately thereafter (by 23:00 hours), and others were kept for several more hours to participate in the experiments reported in this dissertation. Those subjects were usually released at their capture site by 03:00 hours. Trapping took place 4-5 nights a week, for three consecutive months each year from 2004-2008. Trapping took place between the months of September – December, because this is the only time period where both males and females are abundantly captured [Atsalis, 2008].

1.12. Mouse Lemurs Predators in Ranomafana National Park

Brown mouse lemurs in Ranomafana National Park (RNP) are subject to a variety of avian, mammalian, and snake predators. Diurnal avian predators are the Henst's goshawk (*Accipiter henstii*), the Madagascar buzzard (*Buteo brachypterus*), and the Madagascar Harrier hawk (*Polyboroides radiates*). These raptors rely heavily on lemurs, but predation rates on mouse lemurs are estimated to be relatively low at around 4.5% annually [Karpanty 2003]. Owls present in RNP include the large Madagascar long-eared owl (*Asio madagascariensis*), the small Madagascar Scops owl (*Otus rutilus*), and the Madagascar Red owl (*Tyto sumagnei*). Predation rates are unknown, and according to Patricia Wright, owls are relatively rare in RNP. I myself have only ever seen a Madagascar Scops owl on one occasion. Mammalian predators include several species of viverrid. The large cathemeral fosa (*Cryptoprocta ferox*) is probably the rarest viverrid, but it is known to prey on diurnal lemurs in RNP. The much smaller diurnal ring-tailed mongoose (*Galidia elegans*) is occasionally seen singly or in groups of two during the day. Also present is the nocturnal broad-striped mongoose (*Galidictis fasciata*), and the nocturnal Malagasy civet (*Fossa fossana*). Predation rates are not available for any of the viverrids, but both the fosa and the ring-tailed mongoose are thought to prey on mouse lemurs, whereas the broad-striped mongoose and the exclusively terrestrial civet are not thought to be a threat. Even though there are many dogs in the area, I have never seen or heard one in the forest, and since they cannot climb trees, dogs probably do not pose a threat to mouse lemurs. Cats are very rare in Ranomafana, and are usually kept as pets in the village. Cats have never been observed in the rainforest of Ranomafana National Park [Wright personal communication]. Although due to their agility cats could be a threat to mouse lemurs, cats are unlikely to be a significant threat in the study area.

There are several species of boas and smaller colubrid snakes present in RNP [Raxworthy 2003], but predation rates are unknown. The nocturnal tree boa (*Sanzinia madagascariensis*) can be found on the ground, in trees, or in scrub. The cathemeral ground boa (*Arcanthrophis dumerili*) is not found above ground and therefore does not pose a threat to mouse lemurs. There are also many diurnal and nocturnal colubrid snakes smaller in size than the boas [Cadle 2003].

1.13. Predicted Behavioral Responses by Brown Mouse Lemurs to Predators

a) Diurnal raptors hunt when mouse lemurs sleep. Since mouse lemurs usually have concealed sleeping sites, the only early warning cue would be raptor vocalizations. In this case, the best anti-predation strategy would be to remain inside the sleeping site as to not attract attention. At times brown mouse lemurs are active in the late afternoon when it is still light. In this case, both calls and visual features might serve as early warning cues. Since raptors rely on vision and a clear dive path, the best response would be to quickly move to cover. There are indications that diurnal raptors recognize mouse lemur sleeping sites. Wright [Wright and Martin, 1995] has observed a *Polyboroides radiatus* (Madagascar harrier hawk) reach into a leaf nest, extract a mouse lemur in its talons, and fly to a perch, squeezing it until it died (eyes extruded). Karpanty [Karpanty and Wright, 2007] observed 14 mouse lemurs (the highest number of primates in the observation) of prey transport to the nest of *Polyboroides radiatus* and 8 mouse lemurs (fourth most common primate prey) observed to be brought to the nest of *Accipiter henstii* (Henst's goshawk) in a three year study of seven nests of each species. *Buteo madagascariensis* (the Malagasy buzzard) was, in contrast, never observed carrying a primate to its nest [Karpanty and Wright, 2007].

b) Owls prey on mouse lemurs during their activity period. In the forest, owls hunt from perches. Their primary mode of prey detection is visual, but some species can also precisely locate prey based on sound [e.g. Konishi 1973]. The best response to an owl might depend on the microhabitat. In dense vegetation where visual detection is difficult, it might be best to freeze in order to avoid noise. In more open areas it might be better to immediately run to cover, or to leap away erratically.

c) The large fosa (8 – 12 kgs) is active during the day and at night [Hawkins 2003]. At night, it might not pose a great threat because it is much heavier and less agile in the trees than the tiny mouse lemurs. An approaching fosa is probably easily detected, and easily evaded by seeking out fine branches or by simply leaping away. Mouse lemurs should first try and locate the fosa before moving in any direction. During the day, sleeping mouse lemurs are more vulnerable.

Early warning cues include sound, vibration, or body odor. Unless in places that cannot carry the weight of a fosa, it would be most effective to first locate the fosa before running away.

d) The diurnal ring-tailed mongoose is known to attack sleeping mouse lemurs [Deppe et al. 2008; Wright and Martin 1995]. Since mouse lemurs are often in an enclosed sleeping environment, there are few early warning cues besides vibration, locomotor noise and odor. Since the ring-tailed mongoose is very agile in the trees, immediate flight or dropping to lower strata would be expected.

e) Diurnal snakes prey on sleeping mouse lemurs and give away few early detection cues other than vibration of branches. However, snakes are relatively slow, so responses could include flight, but also mobbing to drive it away from the sleeping site. The nocturnal tree boa is an ambush hunter, which provides few early detection cues. Upon detecting a snake at night, mouse lemurs would be expected to move away, since the boa is much less agile than a mouse lemur.

1.14. Chapter Introduction

Chapters 2 to 4 are organized as independent articles, and Chapter 5 provides the conclusions of this study and suggestions for further research. In Chapter 2 I analyze four years of trapping data to test whether the lunar cycle, daily rainfall, or daily temperatures affect the likelihood of capturing mouse lemurs. I predicted that mouse lemurs would be more active, and thus more likely to enter traps, during times of a fuller moon, because higher night time illumination allows for the better detection of predators. I predicted that mouse lemurs would be less active, and thus captured less often, during cold or wet nights because of the higher energy demands required to upkeep an optimal body temperature. In Chapter 3 I report on a play-back experiment that tested whether mouse lemurs distinguish predator from non-predator calls. I predicted that mouse lemurs would fear predator calls, but not other sounds. Using a cage setting, I predicted mouse lemurs would change their behavior and spatial preferences after hearing a predator call, and that they would display fear behaviors upon hearing a predator call. In Chapter 4 I report findings from two experiments that tested visual and olfactory predator recognition. Testing took place in a controlled laboratory setting, where single subjects were presented with mammalian, avian, snake, and non-predator models, objects, and odors. Risk perception was measured by the presence or absence of distinct, pre-defined fear and non-fear behaviors occurring during short trials. A second experiment took place under more natural conditions in the forest using live traps. A trap was presented with a single predator or non-predator stimulus, or without any stimulus. Average capture rates were calculated for each condition and stimulus, to determine whether capture likelihood differed. In the final Chapter 5 I discuss the implications of my findings in the context of the selective pressures affecting the evolution of primate sensory and cognitive systems and anti-predation strategies.

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Figure 1.1. The brown mouse lemur *Microcebus rufus*. (photo by David Haring).

Figure 1.2. Mouse lemur predators. Clockwise starting top left: Madagascar ground boa (*Boa madagascariensis*), an endemic viverrid the ring-tailed mongoose (*Galidia elegans*), the long-eared owl (*Asio* spp), and the endemic viverrid the fosa (*Cryptoprocta ferox*).

Figure 1.3. A map of Madagascar and the location of Ranomafana National Park. (Figure courtesy of ICTE).

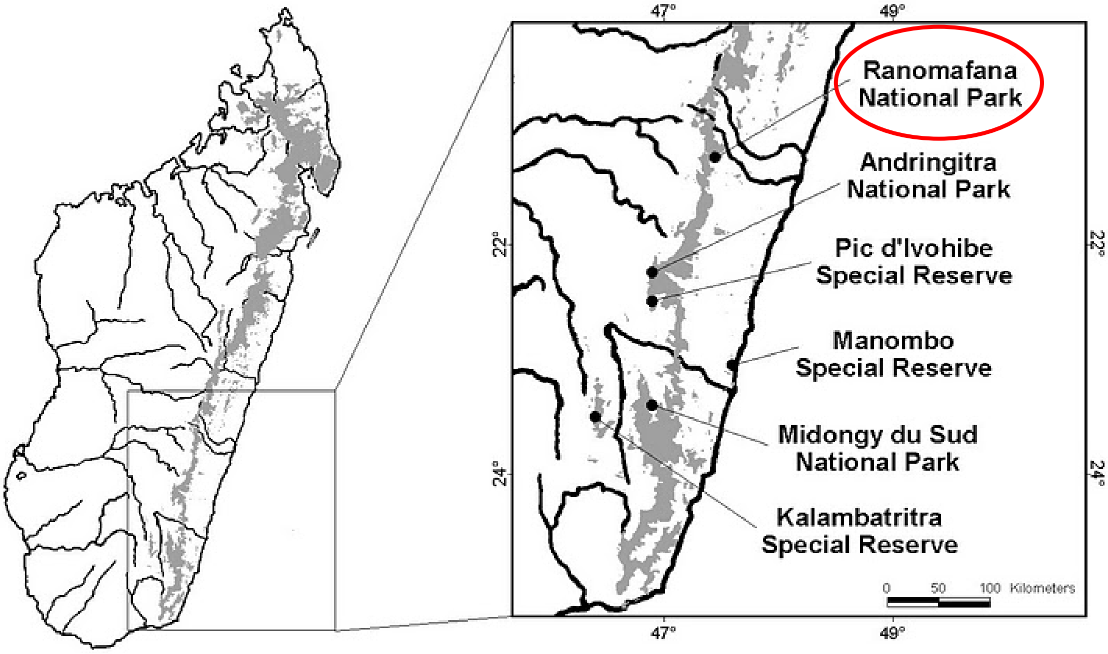

Figure 1.4. The Talatakely trail system in RNP. The area where trapping took place is encircled.

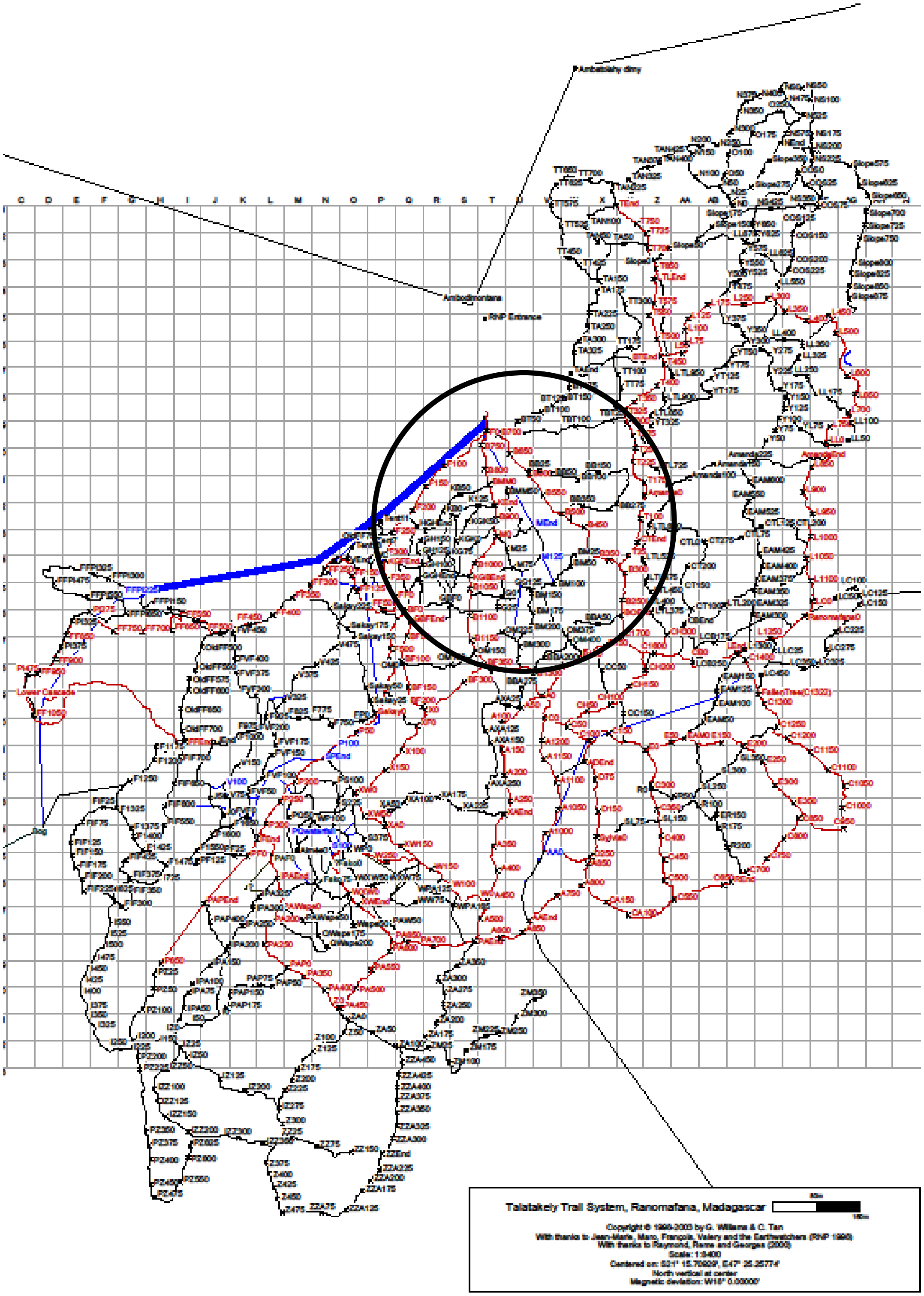

Figure 1.5. Centre ValBio research station on the edge of Ranomafana National Park, Madagaser. (top photos courtesy of ICTE).

Figure 1.6. Sherman live trap (30 x 8 x 10 cm) in the forest, with a brown mouse lemur at the trap entrance.

CHAPTER TWO

The Influence of the Lunar Cycle, Temperature and Rainfall on Trapping Brown Mouse Lemurs (*Microcebus rufus*)

2.1. Introduction

Micromammals are notoriously difficult to observe because of their small size, and their cryptic and often nocturnal lifestyle [Halle and Stenseth 2001]. Live trapping methods are thus often employed to determine distribution, estimate population densities and infer animal behavior and activity [Atsalis 2000; Caro et al. 2001; Gentry et al. 1965; Halle 2006; Radespiel et al. 2001; Schwab and Ganzhorn 2004; Vickery and Rivest 1991]. Since trapping is an indirect method of studying animal behavior, results must be interpreted cautiously, and various factors should be considered. For example, activity patterns may be affected by external influences such as predator behavior and the temporal and spatial availability of food and shelter [Caro et al. 2001; Davidson and Morris 2001; Kelt et al. 2004; Kotler et al. 1993]. Season, temperature, rainfall and the lunar cycle may also lead to behavioral modifications [Daly et al. 1992; Kotler et al. 1991; Stokes et al. 2001; Sutherland and Predavec 1999; Wright 1989]. For example, small mammals may reduce activity during extreme temperatures (either hot or cold) due to thermoregulatory demands [Gentry and Odum 1957; Vickery and Bider 1981]. Old-field rodents (*Peromyscus polionotus*) were less frequently captured during cold nights than warm nights [Gentry and Odum 1957] and common voles (*Microtus arvalis*) reduced activity with decreasing temperature, where activity ceased completely when cold temperatures coincided with rain [Lehmann and Sommersberg 1980]. Rain, in some instances can cause an increase in activity because insect prey may become more active or predation risk is reduced [Doucet and Bider 1974; Gentry et al. 1965; Jahoda 1973; Stokes et al. 2001; Vickery and Bider 1981]. Insectivorous mice and shrews were found to be more active during rainy nights [Doucet and Bider 1974; Jahoda 1970; Vickery and Rivest 1991], whereas badgers on the other hand became less active [Cresswell and Harris 1988]. Rain may also lower predation risk by eliminating odor trails, decreasing visibility and increasing background noise [Vickery and Rivest 1991]. Moonlight is also known to affect behavior. Many small animals reduce foraging, travel and vocalizations during moonlit nights [Bowers et al. 1993; Cresswell and Harris 1988; Fenton et al.

1977; Hughes et al. 1994; Kotler 1984; Kotler et al. 1991; Lockard and Owings 1974; Plesner Jensen and Honess 1995; Price et al. 1984]. ‘Lunar phobia’ may likely serve to reduce predation by visual predators such as owls [Bowers et al. 1993; Clarke 1983; Dice 1945; Kotler et al. 1991; Morrison 1978; Yunger et al. 2002] and is most commonly found in rodents, particularly in open habitat species, but has also been observed in bats [Daly et al. 1992; Erkert 1974; Lang et al. 2006; Lima and Dill 1990; Morrison 1978; Wolfe and Summerlin 1989]. In some instances, reduction of activity may simply be an adaptation to lunar phobic behavior of (insect) prey. For example, because insects where less active during dark nights, bats appeared to reduce hunting activity [Erkert 1974]. Even though lunar-neutrality has been observed in some species of marsupials [Caro et al. 2001; Sutherland and Predavec 1999], rodents [Caro et al. 2001; Erkert 1974; Kotler 1984; Owings and Lockard 1971; Stokes et al. 2001] and bats, this might have been due to local conditions of a low predator density, dense vegetation cover or prey abundance [Kotler 1984; Sutherland and Predavec 1999]. Other species appear benefit from illumination, because they are more active during bright, moonlit, than dark nights. Such ‘Lunar philic’ behavior has been most commonly observed in nocturnal primates [Bearder et al. 2006; Donati et al. 2001; Erkert 1974; Gursky 2003; Nash 1986; Wright 1989]. Primates, including some nocturnal species, are very visual animals [Kirk and Kay 2004; Tetreault et al. 2004] and thus might benefit from enhanced visual acuity during higher illumination. Benefits can include more efficient foraging of live prey [Bearder et al. 2006; Charles-Dominique 1977; Gursky 2003; Sutherland and Predavec 1999] and possibly enhanced predator detection [Bearder et al. 2002; Bearder et al. 2006; Blumstein et al. 2000; Erkert 1974; Erkert 1976; Erkert 1989; Erkert and Gröber 1986; Fernandez-Duque and Erkert 2006; Gursky 2003; Nash 1986; Nash 2007; Wright 1989]. Curiously, two primate species contradict the primate typical pattern. Both slow lorises (*Nycticebus coucang*) and grey mouse lemurs (*Microcebus murinus*) reduced activity during high-illumination. However, in both cases the subjects were in captivity where there is no need to search for food or dodge predators [Erkert 1989; Trent et al. 1977].

The purpose of this study was to test the hypotheses that abiotic factors, specifically temperature, rainfall and lunar cycle influence activity patterns and behavior in the brown mouse lemur (*Microcebus rufus*), a small-bodied (45g), nocturnal primate found only in the southeastern rainforests of Madagascar [Atsalis et al. 1996; Kappeler and Rasoloarison 2003; Wright and Martin 1995]. Brown mouse lemurs are arboreal and forage mostly alone for fruit and insects [Atsalis 1999a]. They typically occur at high densities [Atsalis 2000] and although predation rates for this species are unknown, they are probably subject to intense predation by a wide range of nocturnal predators including owls, mammals and snakes [Goodman 2003; Goodman et al. 1993]. Owls in particular have been found to be by far the greatest threat to grey mouse lemurs (*M. murinus*) with predation rates estimated at 30 percent [Goodman et al. 1993]. Owls are highly visual hunters, and subsequently mouse lemurs may be less active during bright, full moon nights. On the other hand, mouse lemurs may benefit from enhanced predator detection during bright nights [Bearder et al. 2002]. Due to their small size, mouse lemurs are sensitive to low temperatures and frequently undergo a light hibernation-type state (torpor) during cold winter nights where temperatures may reach lows of 4 Celsius [Kobbe and Dausmann 2009; Schmid 2001; Schmid and Ganzhorn 2009; Wright and Martin 1995]. For the same reason mouse lemurs may reduce activity during heavy rain as wet fur may result in higher energy demands due to increased heat loss. We investigated how weather (daily total rainfall and minimum night temperature) and light levels (moon phase) are associated with activity in wild mouse lemurs. We applied an indirect measure, live-trap rates, assuming that a higher capture rate reflects higher general activity.

2.2. Methods

I present data generated over a 4-year period (2004-2007) collected mostly during Madagascar's austral spring (September – December), and resulting in a total of 247 trap nights and 1668 captures of 130 individuals (Table 3.1). Data collection was limited to the spring because mouse lemurs were generally absent from traps during the austral winter (Jun-Aug) and fall (Mar-May) possibly because of inactive torpor periods or high food availability, respectively (data not presented). During January and February frequent storms and cyclones limit research.

Fieldwork was conducted in Talatakely, a well-established trail system, [~9ha, Blanco 2008] in Ranomafana National Park (RNP). The park, established in 1991, comprises 43,500 ha of continuous rain forest located in southeastern Madagascar at 21^{o} 16'S latitude and 47^{o} 20'E longitude [Wright 1992; Wright and Andriamihaja 2004]. Elevations range from 500 – 1500m, and the mean annual rainfall is 3000 mm (RNP/Centre ValBio, unpublished data), most of which falls during the summer months from December to March. Based on RNP/Centre ValBio research station records, temperatures range from lows in June-September (4-12 C) to highs in December – February (30-32 C).

Capture-mark-recapture techniques were employed as part of a long-term collaborative project (established in 2003) to monitor the behavioral ecology of brown mouse lemur populations within the study site. Lemurs were captured up to 5 nights per week using Sherman live traps (30 x 8 x 10 cm). Following standard protocol [Atsalis 1999a; Blanco 2008; Harcourt 1987; Wright and Martin 1995], traps were set at 25-50m intervals in pairs (approx 30m apart) along opposing sides of pre-existing trails. Each trap was situated at least 5 m off-trail and fixed to a sturdy, horizontal substrate at ~ 1.5 m above the ground. At 1700 hours traps were baited with a piece of fresh banana and were checked and re-collected at 2100 hours. Experience has shown that at this site mouse lemurs are most likely to enter the traps within the first 2 hours of darkness. Captured lemurs were brought in their traps to the Centre ValBio research station laboratory where they were sexed and identified, or if unknown, marked with AVID microchips for later re-identification. Subjects were then released between 2300 and 0100 hours at the site of their original capture. Because many subjects were often recaptured, 30 traps were rotated amongst 60 fixed locations to minimize dependence on provisioning. All methods and procedures complied with protocols approved by the Stony Brook University Institutional Animal Care Committee, adhered to ASM guidelines and the legal requirements of Madagascar.

Nightly capture success was calculated by dividing the number of captured individuals by the number of total traps opened each night. Abiotic conditions were divided into three main categories: 1) Rainfall (mm), 2) Minimum daily temperature (Celsius), and 3) Moon phase. Rainfall was further divided into three sub-levels: No (0 mm, N=92), Medium (0.10-5.6 mm, N=79) and High (6.0-60 mm, N=76) rainfall. Minimum temperature was similarly subdivided into Low (0-14C, N=84), Medium (15-17C, N=103) and High (18-22C, N=60). We excluded daily maximum temperatures measured for each day because low (night) temperatures were most relevant to the nocturnal mouse lemurs and because there was a strong correlation between daily maximum and minimum temperatures. Said sub-level ranges were chosen so to yield comparable sample sizes in each category. Moon phase was subdivided into four states: full moon (defined as the night of full moon, plus two days prior to and following full moon, i.e., 5 days total, N=44), new moon (defined as the night of new moon, plus two days prior to and following i.e., 5 days, N=45), waning (the 10 days between full and new moon state, N=85), and waxing (the 10 days between new and full moon state, N=73). Rainfall and temperature data were extracted from the CVB database and moon phases were determined using a moon calendar (e.g. www.paulcarlisle.net/mooncalendar/). Statistical analysis was conducted using SPSS 15.0. A univariate analysis of variance (ANOVA) was applied to the total number of animals captured, as well as separately for both males and females. The alpha level was set *a priori* at 0.05.

2.3. Results

A total of N = 130 individuals were captured 1668 times, approximately 28% (467 captures) of which were females and 72% (1201 captures) were males. Minimum temperatures were variable, ranging from 9 C to 22 C (average 15.45 C for the entire study period). Rainfall ranged from 0 – 60 mm per day (daily average 6.30 mm) (Table 3.2). An initial analysis of the correlations among the three variables revealed only a weak correlation (*r's* between -0.21 and + 0.18). A one-way analysis of variance was conducted to evaluate the relationship between the capture rates (dependent variable) and the lunar cycle, nightly minimum temperature and rainfall (independent variables). The first independent variable, the lunar cycle, did not significantly affect total capture rate (both sexes combined; F = 1.66, $P = 0.18$), nor female (F = 0.183, $P = 0.91$) or male (F = 0.16, $P = 0.92$) capture rate. Minimum temperature also did not significantly influence total capture rates (F = 1.67, $P = 0.19$), it did however significantly affect rates when sexes were considered separately. Females were more likely to be captured during warmer nights (F = 17.86, $P < 0.001$), and males were more likely to be captured during colder nights (F = 17.93, $P < 0.001$). Rainfall on the other hand only significantly affected capture rate (F = 10.76, $P < 0.001$) when sexes were combined, with the ‘No Rain’ category yielding the highest capture rates. Rainfall did not have a significant effect when sexes were considered separately (females, F = 3.44, $P = 0.07$; F = 17.93, $P = 0.07$). In summary, males were more likely to be captured during cold nights and females during warm nights. The absence of rain slightly increased the likelihood of capture, whereas the phase of the moon had no effect.

2.4. Discussion

2.4.1. Moonlight

In contrast to rodents that often became less active with increasing illumination [e.g. Kotler et al. 1991; Lockard and Owings 1974], and in contrast to tarsiers, bushbabies, and owl monkeys that are more active during full moon nights [Bearder et al. 2002; Erkert 1974; Gursky 2003; Nash 2007; Wright 1989], mouse lemurs did not appear to change their behavior in response to the lunar cycle. Sensitivity to nightly illumination has been linked to predation risk, so animals with low visual acuity such as rodents, might reduce activity to minimize exposure during bright nights. Visually oriented animals such as primates might in contrast benefit from enhanced vision during bright nights. Lunar neutrality could be a result of living in a forest or dense vegetation. Rainforests in particular are characterized by dense canopy cover and overcast skies. This will greatly reduce nightly light fluctuations below the canopy, which greatly diminishes the effect of the moon. This view is supported by findings that night time activity of rodents that live in open habitats correlates much stronger with the lunar cycle than in rodents that live in forest or brush habitat [Kotler 1984; Sutherland and Predavec 1999].

2.4.2. Temperature

Temperatures have not been measured in activity patterns of other nocturnal primates, but Wright [1989] found that owl monkeys seem to forage during the day rather than at night when temperatures are low. The findings of this study show that temperature affected the capture rates of brown mouse lemurs. Males were more likely to be captured when temperature were low, and females when they were high. This is partly the result of females being absent from traps between the months of June-September. This absence might be due to differences in torpor duration in males and females. Mouse lemurs undergo periods of torpor during the cold winter months [Schmid 2001; Wright and Martin 1995]. The absence of females suggests that females might undergo much longer periods of torpor than males [Atsalis 1999b; Blanco 2008; Harcourt 1987]. Why relatively fewer males are captured when temperatures are higher is more difficult to explain. The reproductive season of brown mouse lemurs lasts from October-January, and it is possible that during that time, males are more focused on establishing home ranges and locating females than locating food (i.e. traps).

2.4.3. Rainfall

Rainfall significantly affected the likelihood of capture. Night with no rain yielded most captures. Reduced or no activity during (heavy) rain might help conserve energy. Mouse lemurs are very small and thus vulnerable to hypothermia. Rainy nights are relatively colder than dry nights and wet fur may facilitate loss of body heat. In addition, insect prey, such as beetles and moths may be less active during rainfall or may be more difficult to detect. Mouse lemurs greatly rely on hearing to locate insects [Görlitz and Siemers 2007; Martin 1972] and the noise generated by rain may decrease their ability to locate insect prey. For this same reason, acoustic predator detection may be impaired during rainy nights. Thus, overall, it may be safer and more energy efficient to be more active during dry nights or nights with little rain.

In summary, between August – December brown mouse lemurs were most commonly captured during dry nights, and males were more commonly captured during colder nights and females during warmer nights. However, since data collection was limited to one season and I used an indirect measure of activity, trapping success, it is possible the findings of this study to not accurately reflect activity patterns. Future investigations should aim to include additional seasons and radio telemetry techniques to obtain more direct information about mouse lemur activity.

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Table 2.1. Details of the annual and total trapping effort during the study period.

Month and Year	# of Trap Nights	# of Traps	# of Captures
Sep-Dec 2004	55	2112	395
Oct-Dec 2005	68	1605	294
Sep-Nov 2006	52	1249	416
Sep-Dec 2007	72	1728	563
TOTAL	247	5988	1668

Table 2.2. Monthly and total average (ranges) minimum temperatures and rainfall.

Month	Min. Temp (Celsius)	Rainfall (mm)
Aug (N=10)	11.2 (9-13)	1.88 (0-12)
Sep (N=42)	13.6 (10-17)	7.01 (0-42)
Oct (N=97)	14.67 (9-19)	4.66 (0-54)
Nov (N=73)	16.89 (10-21)	6.11 (0-58)
Dec (N=25)	19.28 (11-22)	13.74 (0-60)
Average (N=247)	15.47 (9-22)	6.30 (0-60)

CHAPTER THREE

Acoustic predator recognition experiments with wild brown mouse lemurs (*Microcebus rufus*) in Ranomafana National Park, Madagascar

3.1. Introduction

Predation is thought to be a major selective force shaping the evolution of primates and for many species, predation is the major cause of death [Anderson 1986; Cheney and Wrangham 1987; Janson and Goldsmith 1995; van Schaik 1983]. Recognizing predator presence can greatly improve survival rates because it allows prey to reduce dangerous direct encounters. Even though predator efficiencies vary, post-prey detection capture success can be as high as 50% in mammals and might exceed 75% in birds of prey [Vermeij 1982]. For prey it is thus of primary importance to avoid detection and natural selection is likely to have acted on mechanisms that enable prey to detect predator presence and on behaviors that lower the likelihood of capture [Lima and Dill 1990; Miller and Treves 2007; Stanford 2002]. Many species are confronted with multiple predators, including aerial, terrestrial and arboreal species, which differ in their prey detection and capture techniques. For example, diurnal raptors hunt visually on the wing [Karpanty 2006; Rene de Roland and Thorstrom 2003], owls are visual and acoustic hunters that often ambush prey from perches [Dice 1945; Konishi 1973; Payne 1971], mammals can detect prey via vision and olfaction and may rely on speed or surprise tactics [Albone and Shirely 1984; Kats and Dill 1998; Powell 1978; Wright, 1989], and snakes wait in ambush for vibration or heat cues [Cadle 2003; Cock Buning 1983]. In addition to sensing predator presence, an ability to differentiate amongst the different classes of predators can greatly lower predation risk because prey may respond with predator appropriate evasion behaviors [Lima and Dill 1990; Stanford 2002]. For example, freezing may prevent detection by owls [Hendrie et al. 1998; Payne 1971] but may mean certain death when confronted with a mammalian predator [King 1985; Powell 1978].

Prey may recognize predators via sensory information provided by the predators themselves. Prey animals that live in low visibility environments such as forests or are active at night should benefit from the ability to utilize non-visual predator signals. Predator vocalizations in particular can provide useful information with respect to predator presence and identity. It is well establish that many diurnal primate species are able to recognize, and discriminate amongst, predators based on their calls because they commonly respond with predator-specific evasion behaviors. For example, in response to aerial predator calls monkeys and lemurs commonly descend in the canopy, seek cover, and scan the sky [Ferrari and Lopes Ferrari 1990; Fichtel and Kappeler 2002; Hauser and Wrangham 1990; Karpanty and Grella 2001; Karpanty and Wright 2007; Macedonia and Yount 1991; Sauther 1989; Searcy and Caine 2003; Wright 1998; Zuberbühler 2000]. In response to terrestrial predator calls in contrast they often ascend and scan the ground [Bshary and Noe 1997; Fichtel and Kappeler 2002; Ouattara et al. 2009; Schel and Zuberbühler 2009; Zuberbühler 2000].

Even though there is ample anecdotal and empirical evidence of predator vocalization recognition in diurnal species, very little is known about predator recognition abilities in nocturnal primates. It is has long been thought that nocturnal species largely rely on cryptic, indirect anti-predator strategies such as small size and a solitary life style [Janson 2003; Miller and Treves 2007; Stanford 2002; Terborgh and Janson 1986; van Schaik 1983]. There is however increasing evidence that nocturnal primates, including galagos (*Galago*), mouse lemurs (*Microcebus*), owl monkeys (*Aotus*) and tarsiers (*Tarsius*) utilize predator cues, in particular visual information, to lower predation risk [Bearder et al. 2002; Bunte 1998; Charles-Dominique 1977; Deppe 2005; 2006; Deppe and Wright 2006; Görlitz 2004b; Gursky 2003; 2007; Karpanty 2003; Nash 2007; Nekaris et al. 2007; Scheumann et al. 2007; Schuelke 2001; Wright 1989; 1996]. Living in dark forest environments, nocturnal primates would be expected to benefit from recognizing predators by the calls. Very few studies have tested this assumption and all published reports are limited to lemurs [Bunkus et al. 2005; Fichtel 2007; Karpanty and Grella 2001; Scheumann et al. 2006]. Findings show that nocturnal lemurs overall responded less dramatic to predator calls than diurnal lemurs (Table 3.1). However, there is variation amongst the different nocturnal species. Woolly lemurs (*Avahi laniger*) showed no evidence of recognizing diurnal raptor calls, whereas weasel sportive lemurs (*Lepilemur mustelinus*) and red-tailed sportive lemurs (*L. ruficaudatus*) seemed to associate such calls with the sky, even though they did not flee [Fichtel 2007; Karpanty and Grella 2001]. Only one study used calls of a mammal, and red-tailed sportive lemurs responded similar to diurnal species, in that they looked down and escaped [Fichtel 2007]. When captive-born grey mouse lemurs (*Microcebus murinus*) were presented with predator and non-predator calls, they avoided predator calls and novel sounds, but not familiar sounds [Bunkus et al. 2005; Scheumann et al. 2006]. Details of the experimental procedure were however not provided by the authors. This study suggests that acoustic predator recognition may not be innate in mouse lemurs and thus due to their predator-devoid environment, subjects may have simply perceived predator calls as unfamiliar sounds.

To learn more about how nocturnal primates perceive and respond to predator information, I conducted play-back experiments with wild brown mouse lemurs (*Microcebus rufus*). This species is endemic to the rainforests of Madagascar and, at 45 grams, is one of the smallest primates [Atsalis 2008; Atsalis et al. 1996; Kappeler and Rasoloarison 2003]. Mouse lemurs are arboreal and even though they may forage solitarily for fruit and insects [Atsalis 1999], several individuals may sleep together in tree holes, leaf-nests or dense vegetation [Braune et al. 2005; Radespiel et al. 2003; Randriamiarisoa et al. 2007]. Individuals have distinct but overlapping home ranges that may persist for many years [Atsalis 2000] and they have litters of up to three offspring once or twice per year [Blanco 2008; Eberle and Kappeler 2004; Radespiel et al. 2002]. Mouse lemurs posses a well-developed olfactory system typical of strepsirhines [Martin 1990; Perret 1995; Schilling 1979] and high visual acuity [Tetreault et al. 2004]. Both senses are utilized in the detection of predators and prey [Bunte 1998; Deppe 2005; Deppe 2006; Deppe and Wright 2006; Görlitz 2004b; Piep et al. 2003; Sündermann et al. 2008]. Mouse lemurs also possess highly mobile outer ears and sensitive hearing which is most acute between 3-40 kHz [Niaussat and Petter 1980; Zimmermann et al. 2000]. Hearing is used to locate insect prey [Görlitz 2004a; Görlitz and Siemers 2007; Piep et al. 2003] and is important in social interactions, where vocalizations can be very specific [Braune et al. 2005; Zimmermann 1995; Zimmermann and Hafen 2001; Zimmermann and Lerch 1993; Zimmermann et al. 2000]. Due to their tiny size mouse lemurs are preyed upon by a wide range of predators including birds, viverrids and snakes [Karpanty and Wright 2007; Scheumann et al. 2007; Wright and Martin 1995]. As many as 14 diurnal and nocturnal predator species may prey on any given population, and the annual predation rate may exceed 30 % [Goodman et al. 1993; Scheumann et al. 2007].

Since mouse lemurs rely on hearing in social and foraging contexts, hearing may also play an important role in detecting and identifying predators. I hypothesized that wild, and thus presumably predator experienced, brown mouse lemurs are able to differentiate between acoustic predator and non-predator stimuli. I furthermore predicted that they would adjust their behavior predator appropriately, moving lower, looking up and seeking cover when hearing a diurnal raptor call, but moving higher and looking down in response to a terrestrial predator. In response to owl calls I predicted flight and freezing, behavioral responses commonly observed in rodents [Hendrie et al. 1998; Kotler et al. 1991]. I also expected activity levels and spatial preferences to change after hearing predator calls but not in response to non-predator stimuli.

3.2. Methods

3.2.1. Study Site, Subjects, and Capture

This study took place April through May 2008 in Ranomafana National Park (RNP) and at the associated Centre ValBio research station in southeastern Madagascar. Detailed geographical, climatological and ecological data are found in Wright [1992] and Wright and Andriamihaja [2004]. The brown mouse lemur population has been studied here continuously since 2003, and over 130 individuals have been marked with micro-chips for long-term identification. In this study, I included only known individuals that had been repeatedly captured in the weeks preceding the experiments because we wanted to present as many different stimuli to each subject as possible. Mouse lemurs were captured using a standard procedure employing Sherman live traps (30x8x10cm) that were placed along the Talatakely trail system 5 nights per week [Atsalis 2002; Blanco 2008; Harcourt 1987; Wright and Martin 1995]. For a total of 39 nights, 30 traps were rotated each night among 60 fixed trap sites. Traps were set in pairs, one trap on each side of the trail. A trap was between 5-15 meters off trail and fixed horizontally to vegetation about 1.5 meters above the ground. The distance between pairs was 25-50 meters. Traps were baited with banana at 17:00 hours and re-collected at 21:00 hours. Captured mouse lemurs were taken inside their traps to the research station where they were weighed, sexed, identified using a chip-scanner, and if unknown, marked with an AVID micro-chip. Lemurs were released back into the forest at their capture site the same night, usually by 02:00 hours. All methods and procedures were approved by the Stony Brook University Institutional Animal Care Committee (IACUC), adhered to the American Society of Primatologists principles for the ethical treatment of nonhuman primates and to the legal requirements of the government of Madagascar.

3.2.2. Stimuli

A total of ten different acoustic stimuli, including vocalizations of three sympatric predators and five non-predators, and two novel controls were presented to 29 adult subjects in 77 trials. Predators were the 1) Henst's Goshawk (*Accipiter henstii*), a medium sized diurnal raptor [Goodman 2003; Rene de Roland and Thorstrom 2003], 2) fosa (*Cryptoprocta ferox*), a large (7-10 kilos) viverrid that is active at night and during the day [Dollar 1997; Dollar et al. 2007; Hawkins 2003], and 3) the Madagascar long-eared owl (*Asio madagascariensis*) [Goodman et al. 1991; Rene de Roland and Goodman 2003]. Predation rate estimates at the study site are only available for the Henst's goshawk, which may kill between 1-3 % of the mouse lemurs annually [Karpanty 2006; Karpanty and Wright 2007]. Owls may be the most serious threat, and are estimated to kill up to 25% of mouse lemurs annually at other locations [Goodman et al. 1991; Goodman et al. 1993]. Non-predator vocalizations were from 2 sympatric nocturnal lemurs, the aye-aye (*Daubentonia madagascariensis*) and the weasel sportive lemur (*Lepilemur mustelinus*), the vasa parrot (*Caracopsis nigra*), a dog (dogs sometimes can be heard from the park edge) and human conversation. Novel controls were country music and a cat meowing (there is only one known pet cat at our site and we have never encountered or heard it in the forest). Recordings were provided by M. Scheumann and E. Zimmermann at the Technische Hochschule in Hannover, Germany, except for *A. henstii* and *D. madagascariensis*, which were obtained from the Macauly Library of Sounds, and the human voices which we produced ourselves.

3.2.3. Experimental Procedure

Experiments took place at night between 22:00 – 02:00 hours in a wire mesh cage (1.2x1x1 meters) fitted with bare branches (Figure 3.1). The cage had one large door (50x50 centimeters) for general access, and a small door (10x12 centimeters) through which a Sherman trap could be pushed to release or recapture a mouse lemur. The cage was located just outside the research lab near the forest edge. A black curtain with viewing slits was placed between the cage and 2 experimenters that sat 1.5 meters away from the cage. Stimuli were broadcast via two small Hama speakers (10x5 centimeters, frequency output range between 20 Hz – 20 kHz) from a laptop computer (HP z4114). The speakers were attached next to each other, one on a top corner and one on the top of the cage and sound files were played at full volume. Stimuli were clearly audible 5 meters away but not 25 meters away and in our opinion adequately represented a nearby source. Trials took place under natural night time illumination except for some residual light from the research station and a red-light placed above the cage, which increased our ability to observe. Subjects were captured in the hours preceding trials and they remained in their traps inside the lab for up to 4 hours before participating in a trial (average 2.82 hours, range 2–4 hrs, SD 0.68). While waiting, subjects were provided with fresh fruit to ensure that they were well hydrated and not hungry during trials. Preceding experimental nights, each subject received a 1-hour habituation trial in the cage. Before each experimental trial, a subject was allowed to habituate to the cage for 15 minutes. A trial lasted a total of 12 ¼ minutes and consisted of a 15-second stimulus presentation preceded and followed by six stimulus-free minutes. Each subject was tested separately, received only one trial per night and stimuli were presented only once to each subject to avoid habituation.

3.2.4. Variables Measured

During the 6 minutes preceding and following the presentation of the stimulus, a subject's location and behavior was recorded every 15 seconds. During the 15-second stimulus presentation behavior was recorded *ad libitum*. Three spatial and 1 behavioral category were recorded: 1) Height within the cage (Top, Middle, Bottom), 2) Front (speaker side) or Back of the cage, 3) Left or Right of the cage as viewed from the speaker side, and 4) subject is Motionless or Moving. A pilot study two years prior had shown that behaviors such as eating, bipedality, grooming etc. were very rare and potentially difficult to discern, so we did not include them in this study. Subtle behaviors like gaze and monitoring (head turning) were extremely difficult to discern due to the tiny size of the subjects, the characteristics of the cage and the low light conditions. Even filming trails with an infra-red handycam (SONY) did not help because the light mostly accentuated the branches and the cage mesh, making it sometimes even more difficult to see the lemurs. However, *during* stimulus presentation all observable behaviors were recorded continuously because this is when we expected the most dramatic responses.

3.2.6. Data Analysis

To determine whether a stimulus induced a lasting and significant change in behavior or spatial preferences I compared their frequencies Before and After the 15-second stimulus presentation within each trial. For each trial the 4 categories were separated. Within each category there were two states, (for example Front/Back) except for Height, which had three (Top, Middle, or Bottom). Within each of the three categories with two states, the number of occurrences for each state was calculated for the Before period of a trial. Since there were 25 data points (6 min/15seconds = 25), the state that occurred a minimum of 13 times (>50%) was declared the dominant state. The dominant state Before was compared to the same state's occurrence in the period After, and the absolute number of change for that state was calculated. For example, if Front occurred 14 times Before and 1 time After, the Absolute Change Score (ACS) was 13 (14 – 1), and it was irrelevant whether the ACS was positive or negative. I found that this score adequately quantified both very drastic and very little change in behavior but not intermediate changes (moderately active subjects). For example, an overall motionless subject that changed its location form the front to the back of the cage right after the playback and stays there would receive the maximum ACS of 25 (e.g. [Front Before=25] – [Front After=0]=25). An overall very active animal that became and remained motionless right after hearing the stimulus would on the other hand receive a much lower ACS (e.g. [Front Before=14]-[Front After 1]=13), even though the behavioral change is equivalent to the former if not more drastic. To equalize the sometimes misleading ASC, I converted them into Percent Change Scores (PCS) by calculating the highest possible change available to the subject in that trial: in the first example the maximum change possible would be 25 (going from 25 occurrences of Front to 0 = 100% change) and in the second example it would be 14 (going from 14 occurrences to 0 = 100% change). The PCS was calculated by dividing the ACS by the maximum change possible, so in the latter example the percent change was (ACS=13)/14 x 100 = 92.9%. The PCS allowed quantifying the change within each trial taking into account a subject's overall activity and location preferences. With this method it made no difference where a subject was or what it did; it only mattered if a given pattern *changed* after the stimulus presentation. The above calculations were applied to each trial in all three 2-state categories, and it was slightly modified to accommodate the 3-state Height category: instead of calculating the dominant state we calculated a general change score. Each height change a subject made was scored as 1 change. The more a subject moved up and down, the higher the change score. Again, the change score Before was compared to After within each trial, and using the same above equations, the ASC and the PCS were calculated. One-way (factor) ANOVAs followed by Fisher's PLSD posthoc tests were applied to compare both the ACS and the PCS separately amongst the ten stimuli. The alpha level was set at *a priori* at 0.05.

3.3. Results

A total of 77 trials were conducted with 29 subjects. Each subject was presented with at least 1 predator and 1 non-predator stimulus (average number of trials 2.59, range 2-6). During stimuli presentation subjects overall did not exhibit escape or startle responses indicative of predator recognition and I listed all responses observed in table 3.2. When I compared the change scores the ANOVA results were uniformly non-significant, for both the ACS: Height ($F(9,67) = 0.47$, $P = 0.89$), Front/Back ($F(9,67) = 0.93$, $P = 0.50$), Left/Right ($F(9,67) = 0.29$, $P = 0.97$), and Behavior ($F(9,67) = 0.72$, $P = 0.68$) the PCS: Height ($F(9,67) = 0.47$, $P = 0.89$), Front/Back ($F(9,67) = 0.88$, $P = 0.54$), Left/Right ($F(9,67) = 0.51$, $P = 0.86$) and Behavior ($F(9,67) = 0.59$, $P = 0.80$). Subjects did not significantly change their activity or spatial preference patterns *after* hearing any of the stimuli indicating they did not perceive an increase in danger.

3.4. Discussion

This study suggests that brown mouse lemurs may not generally recognize predators by their vocalizations nor do they perceive predator calls as indicators of danger. Our findings are in agreement with play-back studies conducted with captive-born mouse lemurs where subjects failed to discriminate between predator and control stimuli [Bunkus et al. 2005; Scheumann et al. 2006]. A number of explanations may account for this observation: the failure to respond may mean that the predators used were not perceived as dangerous, that mouse lemurs respond differently to predator calls than most other primates, or that predator vocalization recognition in general may not be present in mouse lemurs. One of the most commonly used stimulus in play-back studies is the diurnal raptor call, which diurnal primates generally perceive as acute danger from above, as indicated by escape, decent in the canopy and looking towards the sky [e.g. Karpanty and Wright, 2007]. My subjects did not move nor did they seem to associate the hawk call with the sky. However, nocturnal primates may not have many opportunities to learn about diurnal predators. Diurnal primates may learn to associate raptor calls with images of overhead birds, and they may learn to associate those cues with danger via personal experience or by observing attacks on conspecifics. Amongst nocturnal primate species tested, only sportive lemurs associated raptor calls with the sky [Fichtel 2007; Karpanty and Grella 2001]. Sportive lemurs are known to take sun baths during the day [Fichtel 2007] which not only makes them vulnerable to diurnal raptors but also provides them with opportunities to learn about them. Mouse lemurs on the other hand sleep under cover in leaf nests, tree holes or dense vegetation which prohibits them from observing birds. Nocturnal woolly lemurs also failed to recognize raptor calls and they too tend to sleep low and sheltered within the canopy [Karpanty and Grella 2001]. Furthermore, the well camouflaged sleeping sites of mouse lemurs may largely prevent detection by aerial predators. If mouse lemurs escaped from their shelters upon hearing a raptor call they would probably be much more conspicuous and thus vulnerable to aerial predators. The very low predation rate by the Henst's goshawk [Karpanty 2006] suggests that ignoring diurnal raptor calls may be a highly effective strategy for mouse lemurs and possibly other nocturnal primates.

The fossa is a solitary predator with very large territories, and is naturally rare in RNP (Gerber et al. 2010). My subjects did not appear to perceive fossa calls as indicators of danger but they may have some understanding about this predator because nearly 40% of our subjects looked down. At night mouse lemurs have a great advantage over this relatively large predator due to their agility and small size. Rather than immediately escaping, it might be more beneficial for brown mouse lemurs to make visual contact with this predator first, and in absence of any additional cues indicating predator proximity, they may perceive themselves safe. Mouse lemurs may be more vulnerable to the fossa during the day while they are sleeping. However, at my study site mouse lemurs seem to prefer sleeping sites in the fine branches which provides protection from the much heavier carnivores [Randriamiarisoa et al. 2007]. Nocturnal red tailed sportive lemurs in contrast responded like diurnal lemurs with flight to the call of the fossa [Fichtel 2007] but due to their larger size and their habit of sleeping in tree holes they may be much more vulnerable to the fossa than the tiny mouse lemurs. My subjects may not perceive the fossa as dangerous because they are rarely confronted with it, but mouse lemurs at other sites, for example in the deciduous forests in northeastern Madagascar, might behave differently [e.g. Radespiel et al. 2003].

Much more curious was the lack of owl call recognition because owls are probably by far the greatest threat to mouse lemurs [Goodman et al. 1991; Goodman et al. 1993], even though predation rates are unknown at our site. Based on owl hunting techniques, freezing, or escape followed by freezing, would be highly effective and expected anti-predator strategies [Hendrie et al. 1998; Payne 1971]. Only 3 of my subjects responded appropriately by freezing or moving lower but since they almost immediately resumed “normal” activity it is very possible that these responses were unrelated to the owl. It is possible that due to the high hunting success of many owl species [Konishi 1973; Payne 1971; Vermeij 1982], mouse lemurs may not often survive attacks to learn about owls. Interestingly, rodents commonly respond to owl calls with appropriate behaviors but this might be explained by their use of open habitat [Hendrie et al. 1998; Konishi 1973; Kotler et al. 1991]. Open habitat owl species often hunt on the wing which may make them more conspicuous to prey thereby providing opportunities to form associations between the owl overhead and its call. Forest owls on the other hand hunt from perches within the canopy and are thus very well camouflaged and elusive, providing few or no cues that could allow learning. This is supported by evidence suggesting that brown mouse lemurs also fail to recognize owls visually and olfactorily [unpublished data].

It is also worth considering that even though it is obvious how predator recognition and associated behaviors can benefit prey, there are also potential disadvantages and costs in terms of energy and time [Lima and Dill 1990; Miller and Treves 2007; Stanford 2002]. Immediate responses like flight or mobbing require energy. Even though they can benefit group-living animals via dilution and predator confusion effects [Hamilton 1971], they may make solitary animals more conspicuous. Post-detection behavioral alterations such as increased vigilance, reduced activity and the avoidance of the potentially dangerous location can persist for as long as 30 minutes or even hours [e.g. Bshary and Noe 1997; Hauser and Wrangham 1990; Karpanty and Grella 2001; Searcy and Caine 2003; Treves 1999; Zuberbühler 2000]. Depending on how frequently animals perceive danger, such behavioral alterations can affect the quantity and quality of food intake, resting and social interactions [Cowlishaw 1997; Lima 1998; Lima and Dill 1990]. Furthermore, responding to one particular species or class of predator can make animals more susceptible to another because they are focused on a particular type of threat [Sih et al. 1998]. Due to their small size, mouse lemurs are preyed upon by a multitude of predator species both during the day and night. If they responded strongly to every predator cue encounter, including acoustic, visual and olfactory, their life may be dominated by anti-predator behaviors. In order to balance the costs and benefits of such behaviors mouse lemurs may only recognize, or respond to, cues most useful. Predator calls may be of a low priority because they do not allow to accurately pinpointing the predator’s location nor is a hunting predator likely to be vocalizing. To a visual animal like a mouse lemur, visual predator cues may for example be more important than acoustic cues. A predator that is visual to prey may have in turn detected its prey, so this may be a situation likely to become dangerous. There is evidence that mouse lemurs recognize predators visually [Bunte 1998; Deppe 2005; 2006; Deppe and Wright 2006; Görlitz 2004b] and in the context of foraging, visual cue were preferred to acoustic cues [Piep et al. 2003].

How animals perceive or respond to predators, or particular predator cues, may vary between species and even populations, depending on factors such as predation rates, predator densities, and the number and classes of predator species present. Studies with captive-born mouse lemurs suggest that acoustic predator recognition is not innate in mouse lemurs and thus would require learning [Scheumann et al. 2006]. Solitary animals must largely learn by experience. In order to form associations between predator cues and danger, they would need to survive dangerous encounters. In order to associate predator cues with a particular predator they require opportunities to observe predators. So it is possible that mouse lemurs, and other nocturnal primates, may not know much about diurnal predators or about highly efficient predators. Due to a high predation pressure by multiple predators and the need to balance costs and benefits, mouse lemurs may benefit from paying attention only to select predator cues. Furthermore, mouse lemurs compensate for high predation rates by high reproduction rates. Anti-predation strategies, including predator detection mechanisms and associated behavioral responses likely reflect an optimal trade-off based on the characteristics of a species and its environment.

Even though it is very possible that brown mouse lemurs ignore or fail to recognize predator calls, we would like to address some methodological factors that could have affected the findings of this study. It is possible that being inside a walled space may have increased the mouse lemurs' perception of safety. Especially the cage top may have been perceived as adequate protection from overhead raptors [see also Seary and Caine 2003], although there was no tendency for subjects to prefer this area. Alternatively it is possible that the capture procedure preceding the trials or being inside the cage resulted in a heightened state of fear that could have taken precedence over fear potentially elicited by the predator stimuli [see also Caine 1989]. We however find this unlikely because subjects were familiar with the capture procedure because they had been repeatedly captured across the weeks, and sometimes years, preceding the play-back experiments and habituation trials allowed familiarization with the cage. Moreover, none of the subjects appeared fearful because they moved around, groomed themselves and capture insects while in the cage. Mouse lemurs in a high state of fear are easily distinguished from unafraid because the fearful ones freeze up for long periods of time [see also Picq 1998; 1993]. Various other experiments we conducted in previous years have also shown that mouse lemurs are very curious and readily explore novel environments. Lastly it is possible that the recordings we used omitted crucial sound recognition features or that the sound volume did not realistically reflect a nearby predator. Based on our experiences in the forest, we however perceived the volume as adequate. To control for predator proximity and potential effects of capture and artificial environments future experiments might include a variety of sound volumes and qualities and could be conducted under more natural conditions, for example by using feeding platforms in the forest [Joly et al. 2008].

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Table 3.1. Common behavioral responses by lemurs to predator calls during play-back studies. The letters in brackets behind a genus refer to the predators class presented (A = aerial, T = terrestrial) with the associated references in superscript. Within the diurnal lemur group, responses listed for each predator class apply to all genera tested. Within the nocturnal lemur group, responses are listed by genus.

Group/ Genus	Aerial threat (A) Responses	Terrestrial threat (T) Responses	References
Diurnal			
Eulemur (A[1,2], T[1,3])	climb down	climb up	[1]Fichtel and Kappeler 2002
Propithecus (A[1,2], T[1,3])	escape	escape	[2]Karpanty and Grella 2001
Lemur (A[4])	look up	look down	[3]Karpanty 2003
Varecia (A[2])	scan	alarm call	[4]Macedonia and Yount 1991
Hapalemur (A[2], T[3])	look at sound source		[5]Fichtel 2007
	alarm call		[6]Bunkus et al. 2005
			[7]Scheumann at al. 2006
Nocturnal			
Lepilemur (A[2,5], T[5])	look up look at sound source scan	climb up look down scan	
Avahi (A[2])	look at sound source	N/A	
Microcebus (A[6,7], T[6,7])	avoidance	avoidance	

Table 3.2. All immediate responses that occurred during the 15-second stimulus presentation are listed by stimulus. The number of trials in which a response occurred is in brackets.

Stimuli	Total # of Trials	Movement	Gaze
PREDATORS			
Hawk	13	move down (1) approach speaker (2) look at speaker (2)	look up (1) look down (2)
Owl	12	move down (2) Freeze (1)	look at speaker (1) scan (2)
Fossa	13	move up (1) look up (1)	look down (5)
NON-PREDATORS			
Aye-aye	10	jump sideways (1)	look at speaker (3) scan (5)
Sportive lemur	4	move up (1)	look at speaker (1) scan (1)
Parrot	5	------	look at speaker (1)
Dog	4	freeze (1)	None
Human	3	-----	look at speaker (1)
NOVEL			
Cat	3	-----	None
Music	10	-----	look at speaker (3) scan (2)

Figure 3.1. Cage used in play-back experiment (1.20 m x 1 m x 1 m).

CHAPTER FOUR

Visual and Olfactory Predator Recognition Experiments with wild brown mouse lemurs (*Microcebus rufus*) in Ranomafana National Park, Madagascar

4.1. Introduction

For many primates, predation is the major cause of death [Cheney and Wrangham 1987]. Behaviors and mechanisms that lower predation risk have, therefore, likely been subject to intense selection [Janson 2003; Zuberbühler 2007]. Nocturnal primates have long been thought to rely on indirect, cryptic anti-predation measures such as being active at night, small body size, and a solitary lifestyle [Cheney and Wrangham 1987; Stanford 2002]. While such attributes might well serve to lower predation risk, there is now increasing evidence that nocturnal primates, like diurnal species, also utilize direct predator cues. An ability to recognize predator presence is of great benefit because it allows appropriate behavioral modifications only in response to immediate danger, whereas prey can focus on other fitness enhancing behaviors such as foraging when danger levels are low.

Predators can be detected and, potentially identified, by sensory information provided by the predators themselves, including odors, vocalizations, and visual features. Primates are highly visual animals [Allman 1999] and when confronted with live or model predators, diurnal monkeys and lemurs commonly react with increased vigilance, alarm calling, and predator specific escape behaviors, such as seeking cover or descending in the canopy in response to aerial threats [Ferrari and Lopes Ferrari 1990; Karpanty and Wright 2006; Macedonia and Polak 1989], ascending in response to terrestrials predators [Karpanty and Wright, 2007; Ouattara et al. 2009], and mobbing or avoiding snakes [Gleason and Norconck 2002; Mineka et al. 1980; Ramakrishnan et al. 2005]. Comparatively little is known about nocturnal primate species, but both anecdotal observations and empirical investigations have shown that many species, including mouse lemurs (*Microcebus*), galagos (*Galago*), fork-marked lemurs (*Phaner furcifer*), dwarf lemurs (*Cheirogaleus medius*), and spectral tarsiers (*Tarsius spectrum*) respond to snakes just like diurnal primates [Deppe and Wright 2006; Fietz and Dausmann 2003; Görlitz 2004; Gursky 2006; Nash 2007; Schuelke 2001]. Information regarding other predators is sparse. Spectral tarsiers froze in response to raptor models, whereas mouse lemurs ignored them, and both slender lorises (*Loris tardigradus tardigradus*) and mouse lemurs ignored mammalian predator models, whereas pottos (*Perodicticus potto edwardsi*) and spectral tarsiers sometimes exhibited alarm calling, flight, or mobbing [Deppe et al. 2007; Gursky 2007; Nekaris et al. 2007; Rahlfs et al. 2006]. In addition to vision, olfaction might provide potentially useful information, especially in low visibility environments like forests and at night. Olfactory predator recognition has been most extensively studied in rodents, which were often found to avoid areas or traps laced with predator urine or feces [e.g. Dickman and Doncaster 1984; Jedrzejewski et al. 1993; Stoddart 1976]. Primate studies are few, but tamarin monkeys (*Saguinus labiatus* and *S. oedipus*) and mouse lemurs (*M. murinus* and *M. rufus*) exhibited flight, vigilance, and increased sniffing in response to mammalian predator odors while ignoring non-predator odors [Buchanan-Smith et al. 1993; Caine and Weldon 1989; Deppe et al. 2007; Sündermann et al. 2008].

Since so little is known about how nocturnal primates perceive and respond to predator information, we presented a wide range of objects and odors to wild mouse lemurs. Mouse lemurs are ideal subjects because they are abundant, easily captured, and readily participate in experiments. Our study subject, the brown mouse lemur (*M. rufus*), is endemic to the rainforests of Madagascar and, at 45 grams, is one of the smallest primates. It is nocturnal, arboreal, and foragers solitarily for fruit and insects [Atsalis 2008]. Males and females have distinct but overlapping home ranges [Atsalis 2000]. Mouse lemurs have high visual acuity [Tetreault et al. 2004] and a sensitive olfactory system [Schilling 1979]. Due to their tiny size, mouse lemurs are preyed upon by a wide range and a high number of predators, including diurnal and nocturnal snakes, birds, and mammals; annual predation rates might well exceed 30% [Goodman 2003; Goodman et al. 1993; Scheumann et al. 2007]. My preliminary investigations indicated that the brown mouse lemur has the capability to recognize at least some predators [Deppe 2006, 2007; Deppe and Wright 2006; 2007]. The purpose of this study was to test a much wider range of stimuli, as well as expand sample sizes. I furthermore conducted two types of experiment, where one took place in the laboratory under controlled conditions, and another in the forest under more natural conditions. I hypothesized that mouse lemurs would differentiate between predator and non-predator stimuli, and predicted that predator stimuli would elicit fear behaviors or avoidance, whereas non-predator would be ignored.

4.2. Methods

4.2.1. Study Site, Subjects, and Capture Procedure

This study took place in Ranomafana National Park (RNP) and at the associated Centre ValBio research station in Southeastern Madagascar, and covered a period of 4 years (2005-2008). Detailed geographical, climatological, and ecological data are found in Wright and Andriamihaja [2004]. A total of 108 (66 males, 42 females) known, micro-chipped, adult individuals were involved in this study. Of those, 25 participated in both the laboratory and forest experiment, but only 14 were involved in the same sensory category across experiments. Mouse lemurs were captured using Sherman live traps (30x8x10cm) that were placed along the Talatakely trail system [Atsalis 2008; Blanco 2008]. There were a total of 30 fixed trap locations in 25-50 meter intervals along the trail. Each location consisted of 2 trap sites, one on each side of the trail, about 5-10 meters into the forest. At 17:00 hours, traps were fixed horizontally to vegetation about 1.50 meters above ground and baited with fresh banana. Traps were checked and removed from the forest at 21:00 hours. Captured lemurs were weighed and identified with a chip-scanner, and unknown individuals were fitted with an AVID micro-chip under the neck-skin. Lemurs were released back into the forest at their capture site as soon as possible, usually by 02:00 hours. Since many individuals consistently return to the same traps, we limited trapping to 4-5 nights per week, and rotated 15 trap pairs among the 30 trap locations to minimize the time mouse lemurs were removed from the forest. All methods and procedures were approved by the Stony Brook University Institutional Animal Care Committee (IACUC), adhered to the American Society of Primatologists principles for the ethical treatment of nonhuman primates, and to the legal requirements of Madagascar.

4.2.2. Predators and Stimuli

Across all experiments, I used a total of 36 different stimuli, 18 of which were predator (Table 4.1, Figure 4.1) and 16 non-predator stimuli. Predators included large and small snakes [Cadle 2003; Raxworthy 2003], owls [Rene de Roland and Goodman 2003], and viverrids [Deppe et al. 2008; Dollar 1997; Hawkins 2003]. Due to the large quantities of predator odors required in the olfactory trials, and the limited availability of fresh predator urine and feces, I also used commercially available urine from mammalian predators not found on Madagascar (Figure 4.2). In preliminary investigations brown mouse lemurs did not differentiate among carnivore odors [Deppe et al. 2007]. Non-predator odor stimuli were perfume, coffee, rubbing alcohol and water, and visual control stimuli included objects in various sizes, colors and textures, such as aluminum foil, latex gloves, rope, toys, and fabrics. Fresh stimuli such as urine, feces, and feathers, were collected at the Tzimbazaza Zoo in Antananarivo, Madagascar, and canine and feline urine was purchased from Lexington Outdoors, Inc. ME, USA. Visual stimuli were purchased at various stores.

4.2.3. Laboratory Experiments

Experiments took place between September and December in 2005 and 2006 in the laboratory at the Centre ValBio research station. The purpose was to minimize the sensory information available. The experimental design was based on my preliminary studies conducted in previous years with subjects not involved in this study [Deppe 2005; 2006; Deppe et al. 2007; Deppe and Wright 2006]. Testing took place in an acrylic box (1.2 m x .45 m x .40 m) consisting of two equal-sized chambers that were separated by an opaque divider with a small doorway, allowing free movement between chambers (Figure 4.3). The box was placed on a table and sectioned off from the rest of the room and the experimenter, with a black curtain with a viewing slit. Initially, each mouse lemur received a 30 minute habituation trial, where the box was empty, except for 3 small pieces of banana to encouraged exploration. Only individuals that actively explored the box were included in subsequent experiments (approximately 90% of mouse lemurs). During experimental trials, a single stimulus was placed in the center of one of the chambers (experimental chamber), while the other remained empty. Visual stimuli were placed directly on the floor of the box, with the exception of the viverrid and the owl model, which due to their large size were placed just outside the transparent side of the box. Objects were presented still or were briefly moved by pulling an attached fishing line. In odor trials, owl feathers and snake shed were placed into an opaque, perforated plastic container. All other odor stimuli were placed in a small shallow dish, which by itself had no effect. All trials took place at night after 22:00 hours under low light conditions. For a trial, a subject was placed into the empty chamber after a stimulus had been placed into the box. A trial lasted 4 min because behavioral responses always occur immediately upon stimulus encounter, and habituation can take place quickly. At the end of a trial, the subject was captured with a baited trap and box wiped clean. Up to 5 trials were conducted each night, but each subject received only 1 trial per night. There was no predetermined order to stimulus presentation, but to avoid potential effects of lingering odors on other trials, we had nights devoted exclusively to a single type of odor stimulus.

My aim was to conduct as many trials per predator stimulus, and exposing each subject to as many different stimuli. I conducted a total of 291 trials, 172 of which involved visual stimuli (147 predator and 25 non-predator), and 119 olfactory stimuli (89 predator and 30 non-predator). Of the 55 total subjects tested, 26 participated in both visual and olfactory trials. Forty-five subjects (26 males, 19 females) participated in an average of 3.82 visual trials (range 1-10), and in at least 1 predator trial (average 3.0). Thirty-nine subjects (24 males, 15 females) participated in an average of 3.05 olfactory trials (range 1-8), and in at least 1 predator trial (average 2.0). During trials I recorded the occurrence of distinct fear and non-fear behaviors (Table 4.2) that were defined and categorized based on our prior observations and descriptions in the literature [e.g. Charles-Dominique 1977; Görlitz 2004; Picq, 1998; Scheumann et al. 2007]. A trial was scored as either 1) Fear (when fear behaviors occurred), or 2) No Fear (when fear behaviors were absent). A motion condition trial was only scored as a Fear trial if fear behaviors persisted beyond a common initial startle response (longer than 5 seconds). Visual and olfactory trials were analyzed separately. First, a chi-square test was applied to test for a significant difference in the frequency of Fear trials between the combined predator and non-predator stimuli. Thereafter, chi-square tests were applied to determine whether there were differences among predator stimuli. The alpha level was set a priori at 0.05.

4.2.4. Forest Experiments

This experiment was conducted in the forest, using the trapping methods outlined above. The purpose was to determine if the presence of a stimulus affected capture likelihood. Both olfactory and visual trials were conducted on alternating nights between September and December of 2007, and additional olfactory trials took place between September and November of 2008. Before experimental trials began, 2 weeks of capture took place without stimuli to habituate the lemurs to the trap locations. During the experimental phase, traps were always set in pairs (one on each side of the trail), where one was the experimental trap (next to a stimulus), and the other was the control trap (no stimulus). Depending on size, visual stimuli were placed in front of, on top of, or within 1 meter of the trap, but always in clear view of an approaching lemur (Figure 4.4). Olfactory stimuli were dripped onto a cotton ball directly at the trap entrance

(Figure 4.5). Stimulus assignment to a trap was arbitrary, but the same stimulus was never placed at the same trap location within one week.

Visual trials involved a total of 1160 traps, of which 580 were experimental (255 predator and 325 non-predator), and 580 were control traps. Olfactory trials involved 366 traps in 2007 (179 experimental and 187 controls) and 466 traps in 2008 (232 experimental and 234 controls. A total of 76 individuals were involved, 31 of which participated in both visual and olfactory trials. Visual trials yielded 318 captures of 67 individuals (42 male, 25 female), which were each captured on average 4.75 times (range 1-16). Olfactory trials yielded 182 captures (92 in 2007 and 90 in 2008) of 40 subjects (26 male, 14 female) in both years combined, 15 of which were captured in both years. In the 2007 odor trials, subjects were captured on average 3.0 times (range 1-6), and 3.6 times (range 1-6) in 2008. To correct for a possible habituation effect, I first removed all captures from the data set where an individual was captured more than once in a trap with the same stimulus (20 captures for visual and 7 for olfactory trials). To avoid inflation of the control condition, the same number of captures was removed. Next capture rates (number of lemurs captured/ number of traps) were calculated for each condition (predator, non-predator, and control) and for each stimulus. Olfactory data was analyzed separately for 2007 and 2008, because the capture rates of the base-line control condition (No stimulus) were very different. Chi-square tests were applied to determine whether there were significant differences among capture rates. The alpha level was set a priori at 0.05.

4.3. Results

4.3.1. Visual Stimuli

In the laboratory, the combined predator stimuli resulted in Fear trials significantly more often than the combined non-predator stimuli (Table 4.3). However, when looking at individual stimuli, only the snake shed, and the small snake and ring-tailed mongoose in the motion condition, had a significant effect. Feared objects always triggered a set or sequence of fear behaviors; an initial Flight response was followed by quadrupedal or bipedal Monitoring and repeated Cautious approaches. Mobbing, attack, and freezing were not observed. Non-predator stimuli never resulted in Fear trials, but they commonly elicited a startle response when moved.

Fifty-six percent of all subjects (N = 43) that were involved in 1 or more predator trials expressed fear in at least 1 trial. Subjects were, however, not universally fearful or fearless, but discriminated among predator stimuli. Subjects (N = 33) that were exposed to 2 or more predator stimuli (range 2-9), never expressed fear in response to all, but only to between 22-57% of them. Sex differences were not found. Of the 91 predator trials involving males, 26 % were Fear trials, and of the 56 trials involving females, 27 % were Fear trials. In the forest, mouse lemurs were significantly less likely to be captured in traps next to predator stimuli (X^2 [1] = 15.57, P <0.0001) and non-predator stimuli (X^2 [1] = 4.63, P <0.04) than in traps without stimuli (Table 4.4). However, mouse lemurs did not differentiate between predator and non-predator stimuli (X^2[1] = 3.51, P=0.06).

4.3.2. Olfactory Stimuli

In the laboratory, all predator odors, with exception of the owl, were feared significantly more often than non-predator odors (Table 4.5). Feared odors always produced the same set or sequence of behaviors; an initial Flight response was followed by Monitoring and repeated Cautious approaches involving Long Sniffs. Thirty-nine percent of all subjects (N = 38) that were involved in 1 or more predator trials expressed fear in at least 1 trial. Subjects were, however, not universally fearful or fearless, but discriminated among predator stimuli. Subjects (N = 18) that were exposed to 2 or more predator stimuli (range 2-7), never expressed fear in response to all, but only to between 29-67% of them. Sex differences were not detectable. Of the 61 predator trials involving males, 26 % were Fear trials, and of the 28 predator trials involving females, 29 % were Fear trials. In the forest, odor stimuli did not affect the likelihood of capture (Table 4.4). A 3-way comparison among conditions (predator, non-predator, and control) revealed no significant differences for 2007 (X^2 [2] = 1.13, P=0.57) nor for 2008 (X^2 [2] = 0.43, P=0.81).

4.4. Discussion

Brown mouse lemurs demonstrated the capacity to differentiate between predator and non-predator stimuli, but only under laboratory conditions. Here, predator models were most effective in the motion condition. Motion likely directs attention and might indicate that an object is alive and therefore potentially dangerous. Since non-predator objects never resulted in fear trials, regardless if they were still or moving, it is likely that stimulus specific visual features were perceived as dangerous. For example, unlike the small snake, the boa was ignored in the lab. However, unlike the small snake, the boa was only partially visible due to its large size, suggesting that shape recognition might have been important. Pattern might have also provided important cues. For example, even though lacking the distinctive snake shape, the small flat pieces of snake shed elicited fear. The shed did, however, have very visible scale patterns. Other primate studies also suggest that the perception of danger is affected by visual features, including shape, size, pattern or color [Coss and Ramakrishnan 2000; Coss et al. 2005; Gursky 2007; Ramakrishnan et al. 2005]. It should be noted though, that while yielding clear broad patterns of responses, our decision to employ a wide range of test stimulus conditions, and subsequent dichotimization of the dependent variable, limits the ability to reliably comment on the character of the fear responses. Clearly, additional future work, based upon our preliminary data and using a stimulus set limited to the effective models shown presently and in a controlled repeated-measures design, will be able to better determine the precise stimulus features eliciting fear responses and characterize the nature of the fear responses in more detail.

Like New World monkeys and grey mouse lemurs [Buchanan-Smith et al. 1993; Caine and Weldon 1989; Sündermann et al. 2008], our subjects perceived mammalian carnivore odors as dangerous, and like grey mouse lemurs, they did not differentiate between local historic and other predators. This suggests that mouse lemurs, as has been proposed for other prey species, might respond to chemical byproducts of general meat digestion rather than to predator specific compounds [Kats and Dill 1998; Nolte et al. 1994; Russell 2007]. The reason why some odors triggered fear more often than others might have been due to stimulus quality. For example, the commercially purchased urine (i.e. bobcat) might have been concentrated, and even though both fossa and ring-tailed mongoose feces were collected at the same time at the same zoo, there might have been differences with respect to freshness or composition. It is, for example, possible that volatile compounds, which dissipate over time, provide information with respect to how recently the predator was present.

The finding that owl stimuli never elicited fear was surprising, because owls are thought to pose the greatest threat to mouse lemurs [Goodman et al. 1993]. Although unlikely, it is possible that at our site, owls are not a noteworthy threat, or alternatively, our owl stimuli might have not been of an adequate quality. However, other nocturnal primates, such as grey mouse lemurs and Asian lorises, also ignored owls [Nekaris et al. 2007; Zimmermann et al. 2000], so there might also be owl specific reasons why they were ignored. Owls are swift and silent ambush hunters, so they might provide comparatively few cues that would allow for an early detection or identification [Wright 1989]. This might explain why owls are one of the most successful predators [Vermeij 1982]. The high (estimated) predation rates by owls indicate that owl recognition might be poorly developed or even absent in mouse lemurs.

Even though brown mouse lemurs have the capacity to differentiate between predator and non-predator stimuli, this was not evident in the forest experiment. One might argue that in the laboratory, the unusual environment or the spatial restrictions could have enhanced the overall perception of danger. This could explain why predator odors were perceived as less, but not why non-predator objects were seemingly perceived as more dangerous in the forest. One major difference between the two experimental conditions was the availability of sensory information, which was much more limited in the laboratory that in the forest. Risk assessment in the laboratory was probably largely based on the experimental stimulus, whereas in the forest a multitude of, naturally present, information needed to be integrated. When exposed to a wide range of information, visual input might take precedence, not only because primates are highly visual animals, but also because a visible predator is close and thus an immediate threat. Odors, in contrast, can persist for a long time and therefore provide less reliable information about a predator’s whereabouts. Therefore in the forest, mouse lemurs might have applied a simple rule such as “when uncertain, avoid all unusual objects”, whereas in the absence of more immediate danger signals, they might have eventually habituated to the predator odors [see also Little 1985; Parsons and Bondrup-Nielsen 1996]. However, it is also possible that since stimuli were present for several hours in the forest, odors might have dissipated or became diluted by moisture, which could have resulted in their being perceived as less dangerous than in the laboratory, where subjects were presented with “fresher” samples in an enclosed box. Future investigations that include observations of mouse lemur-stimuli interaction in the forest by, for example, using feeding platforms and/or recording equipment, might provide more insight into how stimuli are initially perceived and if habituation takes place. Altogether, the differences between the two experimental conditions suggest that risk perception is dependent on the integration of all the relevant information available at any given time and place [see also Lima and Dill 1990; Thorson et al. 1998].

I also found that, overall, predator stimuli were more often ignored than feared. One explanation could be that our subjects were comprised of largely fearless, or bold, individuals because those might be more likely to enter, or repeatedly return, to traps than fearful, or shy, individuals. Even though I cannot rule out an effect of personality, we think frequently captured individuals likely had established home ranges, whereas less frequently captured ones were dispersing individuals. The observation that subjects did not respond to all predator stimuli in the same way, but differentiated among them, suggests that factors other than personality traits contributed to their behavior. It is possible that recognition was dependent on genetic factors, learning or both. I think it is unlikely that fearlessness was solely due to genetic factors, because considering the high predation pressure, individuals lacking predator recognition abilities would have not likely lived to adulthood. In monkeys and ground squirrels it was found that predator recognition becomes increasingly refined with exposure and age [Joslin et al. 1964; Mineka et al. 1980; Ramakrishnan et al. 2005; Swaisgood et al. 1999], so it is possible that differences in experience might explain our subject's behavior. I do not think that learning due to our experiments affected our results, because there were little stimuli and subject overlaps between the two experiments, and they took place in different years. The great majority of individuals was exposed only once to each stimulus. It is difficult to say why a predator stimulus was ignored. Since a complete lack of recognition would likely lead to an early death, it is more likely that fearless individuals had some experience. My predator stimuli might have not fooled an experienced mouse lemur. A potentially major limitation of our and similar studies is that predators were reduced to a single sensory category. Under natural conditions, prey probably often receives a wider range of information, for example, the sight *and* odor of a predator. As a result, our stimuli might have provided incomplete or limited information, which could have caused uncertainty, or a lack of fear. Uncertainty might explain why feared stimuli were not necessarily avoided, but instead re-approached repeatedly. When Temple Grandin [Grandin and Johnson 2005] noticed repeated approaches in cows, she fittingly described it as being "curiously afraid" [see also Hennessey and Owings 1978]. Re-approaches might serve to obtain additional information for more accurate risk assessments.

The main finding of this study is that our subjects differentiated between predator and non-predator stimuli, perceiving only the former as dangerous. This suggests that the ability to recognize predators based on visual and olfactory sensory information is within the capacity of the brown mouse lemur. My conclusion is in agreement with other empirical studies and anecdotal observations, which suggest that nocturnal primates, do not solely rely on indirect anti-predation measures, but like diurnal species, are able to use information provided by predators. Future investigations could include a more varied range of predator stimuli to investigate how specific visual (i.e. color, shape, size) or odor (i.e. quantity, concentration) characteristics affect perception. The use of real predators, or multi-sensory stimuli, would furthermore create more realistic predator-prey interactions.

4.5. Literature Cited

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Table 4.1. All predators (11) and associated stimuli (18) used in this study. The table further shows the main stimulus characteristics, as well as stimuli inclusion in the laboratory (L) and forest (F) experiments.

Predator	**Visual Stimuli**				**Olfactory Stimuli**		
	Size	**Color**	**Material**	**Experiment**	**Type**	**Size/Quantity**	**Experiment**
Snake							
1a+b. Tree Boa (large) (*Sanzinia madagascariensis*)	100 x 6 cm	Grey	Inflatable	L, F	Shed	15 x 8 cm	L
2. Hognose (large) (*Leioheterodon* spp.)	---				Shed	15 x 8 cm	L
3 a-d. Colubridae (small)	35 x 3 cm	Brown	Rubber	L, F	-----------------------------		
	35 x 3 cm	Green	Rubber	F			
	35 x 3 cm	Grey	Rubber	F			
	35 x 3 cm	Striped	Rubber	F			
Avian							
3 a+b. Madagascar long-eared owl	55 cm tall	Brown	Plastic	L	Feathers	3	L
(*Asio madagascariensis*)	55 cm tall	Brown	Inflatable	F			
Mammal							
4 a+b. Ring-tailed mongoose (*Galidia elegans*)	60 x 16 cm	Brown	Wood	L	Feces	20 g	L
5. Fossa (*Cryptoprocta ferox*)	---				Feces	20 g	L
6. Broad-striped mongoose (*Galidictis fasciata*)	---				Urine	50+ drops	L
7. Bobcat (*Lynx rufus*)	---				Urine	15 drops	L, F
8. Mountain lion (*Puma concolor*)	---				Urine	15 drops	F
9. Fox (*Vulpes vulpes*)	---				Urine	15 drops	L, F
10. Wolf (*Canis lupus*)	---				Urine	15 drops	F
11. Coyote (*Canis latrans*)	---				Urine	15 drops	F

Table 4.2. Behaviors recorded during olfactory and visual laboratory experiments.

Behavior	**Definition**	**Category**
1. Flight	Running or leaping away from stimulus.	Fear
2. Bipedal Monitor	Standing erect on hind feet, moving head left-right	Fear
3. Monitor	Subject is motionless, only turning head left-right	Fear
4. Cautious approach	Subject elongates body, sliding slowly on its stomach towards stimulus, then leaps backwards.	Fear
5. Mob	Fast, repeated approach-retreat of stimulus.	Fear
6. Lunge/ bite	Subject leaps towards stimulus, may involve biting.	Fear
7. Freeze	Subject becomes motionless for 1+ minute.	Fear
8. Long Sniff	Sniffing stimulus for 3+ seconds.	Curiosity
9. Casual approach	Swift, quadrupedal stimulus approach.	Curiosity
10. Short Sniff	Sniffing stimulus once (1 second), no re-approach.	Curiosity
11. No interest	Stimulus is never directly approached, but might be used as substrate.	Ignore

Table 4.3. Results of the visual laboratory tests are shown in percent for the two main behavioral categories (Fear and No-Fear). Although not considered statistically, the No-Fear category is further broken down into trials where subjects displayed curiosity versus trials where they did not.

Stimulus	**Fear**	**No–Fear**		**Significance**
		Curiosity	**Ignore**	
Non-predator (N = 25)	0%	12%	88%	
All Predator (N = 147)	27%	7%	66%	X^2 [9] = 49.3, *P* <0.01
Snake small move (n = 21)	67%	15%	18%	X^2 [1] = 21.0, *P* <0.001
Mongoose move (n = 9)	67%	0%	33%	X^2 [1] = 17.5, *P* <0.001
Boa shed (n = 21)	33%	10%	56%	X^2 [1] = 8.4, *P* <0.001
Hognose shed (n = 23)	26%	4%	70%	X^2 [1] = 6.3, *P* <0.01
Boa move (n = 7)	14%	0%	86%	No
Galidia still (n = 11)	10%	18%	72%	No
Small snake still (n = 33)	10%	0%	90%	No
Owl still (n = 12)	0%	0%	100%	No
Boa still (n = 10)	0%	0%	90%	No

Table 4.4. Forest experiment capture rates in percent by stimulus and conditions.

Stimulus	Capture Rates	
	2007	2008
Visual		
Control traps (N = 606)	38 %	---
All stimuli (N = 575)	27 %	---
All non-predator (N = 315)	29 %	---
All predator (N = 260)	25 %	---
Large snake (boa) (N = 59)	22 %	---
Small snakes (N = 144)	25 %	---
Owl (N = 57)	28 %	---
Olfactory		
Control traps (N = 421)	23 %	19 %
All stimuli (N = 411)	27 %	20 %
All non-predator (N = 97)	36 %	24 %
All predator (N = 314)	26 %	19 %

Table 4.5. Results for the visual laboratory tests by stimulus and condition. Results are shown in percent of the total trials for the two main behavioral categories (Fear and No-Fear). Although not considered statistically the No-Fear category is further broken down into trials where subjects displayed curiosity versus trials where they did not. Due to the small sample sizes, the broad-striped mongoose (*Galidictis*) and fox trials were excluded from the statistical analysis.

Stimulus	**Fear**	**No–Fear**		**Significant**
		Curiosity	**Ignore**	
Non-predator (N = 30)	0%	13%	87%	
All Predators (N = 89)	27%	12%	61%	X^2 [5] =27.1, $P < 0.0001$
Bobcat urine (n = 13)	54%	15%	31%	X^2 [1] = 19.2, $P < 0.0001$
Galidia feces (n = 23)	43%	14%	43%	X^2 [1] = 16.0, $P < 0.0001$
Fossa feces (n = 15)	13%	40%	47%	X^2 [1] = 4.1, $P < 0.04$
Snake shed (n = 19)	16%	0%	84%	X^2 [1] = 5.3, $P < 0.02$
Owl feathers (n = 9)	0%	0%	100%	No
Galidictis urine (n = 6)	17%	0%	83%	Excluded (small N)
Fox urine (n = 4)	25%	0%	75%	Excluded (small N)

Figure 4.1. A selection visual predator stimuli used in this study. Clockwise from top left: snake shed, a plastic owl, a wood carved ring-tailed mongoose, and a small rubber snake.

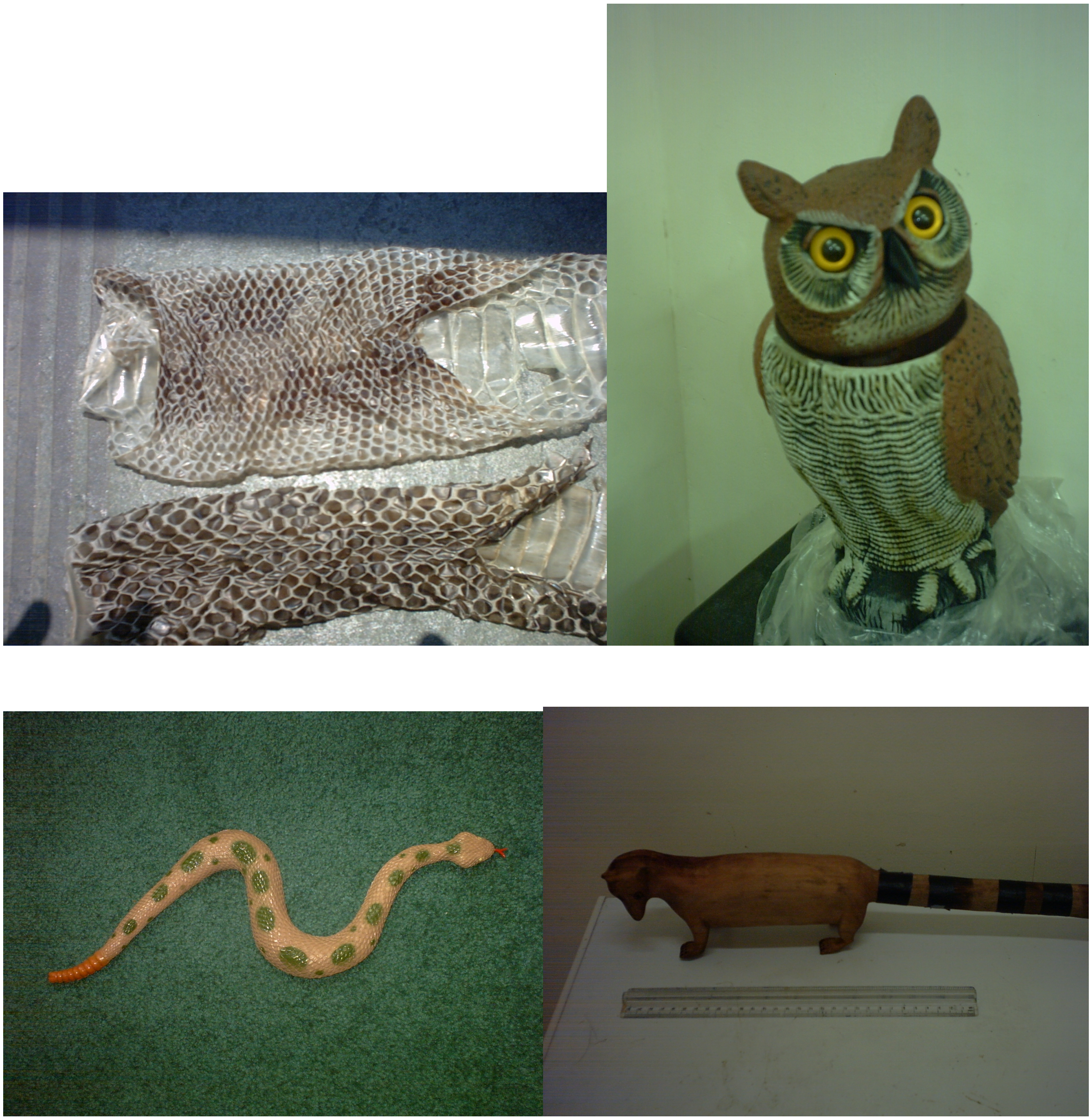

Figure 4.2. Olfactory non-local predator stimuli used in this study.

Figure 4.3. The testing apparatus consisted of a box with lid built of transparent acrylic. An opaque divider with a doorway separated the box into two equal sized chambers. Testing took place at night under low-light conditions, and a black curtain with a viewing slit separated the box from the experimenter and the rest of the room.

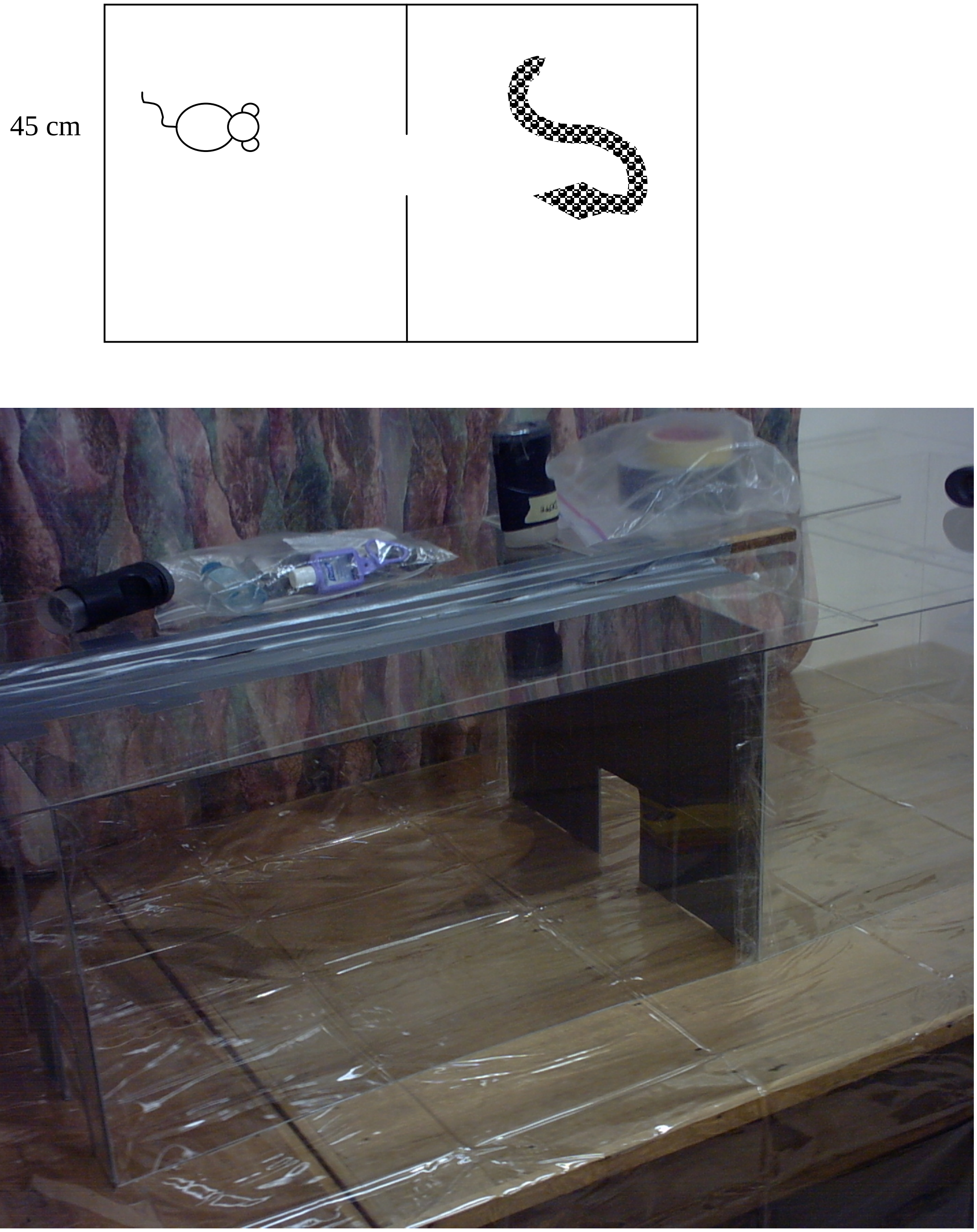

Figure 4.4. Examples of visual predator stimuli placement in the forest experiments.

Figure 4.5. Olfactory stimuli were dripped onto a cotton ball placed at the trap entrance.

CHAPTER FIVE

Conclusions and Future Research

5.1. Conclusions

Every animal needs to obtain food, find mates, and avoid predators, and an animal's traits reflects a balance of those needs [Janson 1992]. Anti-predation strategies can vary greatly among prey species and even populations, because they depend on the type of predators present, the type of habitat used by prey, and the morphological, ecological and behavioral characteristics of prey. Broadly put, animals can lower predation risk indirectly or directly, and combinations of strategies are common. Indirect anti- predation avoidance includes avoiding habitat frequented by predators, micro habitats that are difficult to access for predators, and crypsis [Caro 2005]. Animals can lower the risk of being targeted by a predator by evolving physical or chemical defenses, or by forming groups that provide a dilution and predator confusion effect [Janson 1992, 1998; Stanford 2002; Terborgh and Janson 1986]. Some characteristics of mouse lemurs are likely to lower predation risk indirectly, including solitary foraging and their preference for dense vegetation, their pelage, and their cryptic sleeping habitats.

Mouse lemurs, like all nocturnal primates, are arboreal forest dwellers that live in a low-visibility environment. Dense vegetation in particular can offset the anti-predation advantages that group living provides [Terborgh 1990]. For example, the dilution and predator confusion effect can be severely reduced, because a predator might not detect other group members. Moreover, since visual cues are often not available due to an obstructed line of sight or darkness, animals in such environments would need to rely on other means of staying in touch with group members, such as vocal communication. This can, however, attract the attention of predators, that have probably likewise evolved to be more sensitive to non-visual cues. The anti-predation benefit of being quiet at night might at least partially explain why nocturnal primates are solitary or live in smaller groups than most diurnal primates. Nocturnal primates tend to be smaller than diurnal primates. Smaller animals generally suffer higher predation rates than larger ones [Lima and Dill 1990], and the tiny mouse lemurs are thought to suffer the highest predation rates of all primates [Cheney and Wrangham 1987; Goodman et al. 1993]. Thus a small size in itself is not an anti-predation adaptation in mouse lemurs. Being solitary and small might, however, reduces conspicuousness, and among nocturnal lemurs, the smallest species are also solitary foragers (*Microcebus, Mirza, and Allocebus*). Solitary foraging might also be the consequence of a dispersed diet. Mouse lemurs rely heavily on highly dispersed insects for food [e.g. Atsalis 1999]. Nocturnal lemurs with a reliance on highly dispersed foods such as insects or gums tend to be solitary foragers (*Microcebus, Mirza, Allocebus, Daubentonia*), whereas species more reliant on fruits or leaves tend to occur in pairs or small family groups (*Cheirogaleus, Avahi, Phaner, and possibly Lepilemur*). Even though an insect diet is only sustainable with a small body size, it is difficult to say whether the small size of mouse lemurs is an adaptation to an insect diet, or whether if their size allows such a heavy dependency on insects.

It has also been suggested that nocturnal primates increase activity during moonlit nights, because it allows them to better detect predators [Bearder et al. 2002; Gursky 2003; Nash 2007; Wright 1989]. However, light might also benefit predators in detecting prey. Alternatively, lunarphilia in primates might be an adaptation to diet. Lorises, for example, appear to eat more insects during bright nights, possibly because they are able to detect them better than in dark nights [Bearder et al. 2002; Bearder et al. 2006]. I found no evidence that brown mouse lemurs changed their activity according to the lunar cycle. However, I used trapping success as an indirect measure, which might not accurately reflect activity or ranging. It is, however, possible that nocturnal primates that live in dense canopy forests, frequent dense vegetation, or that live in areas with a frequent dense cloud cover (e.g. rainforests) do not experience significant fluctuations of illumination.

Mouse lemurs frequently utilize the fine branch niche, and there is evidence that brown mouse lemurs are more abundant in dense vegetation [Musto et al. 2005]. This preference very likely lowers predation risk. Dense vegetation lowers the likelihood of being detected by predators and provides cover from predators that need a open dive or pounce path (e.g. raptors). Rodents that had access to ample cover suffered lower predation rates by owls than those with little or no access to cover [e.g. Brown et al. 1988; Kotler et al. 1990]. The fine branch niche further excludes many predators because fine branches cannot bear the weight of many arboreal predators. Mouse lemurs in fine branches are safe from the majority of their arboreal predators such as large snakes and viverrids. Brown mouse lemurs furthermore often sleep in self constructed leaf nests built in fine branches, which provides safety from diurnal viverrids and snakes. Nocturnal lemurs tend to sleep in tree holes or nests which provide concealment from (visual) predators in the day. The only exceptions are the woolly lemurs, which are the largest nocturnal lemurs. Due to their body and group size, nests or tree holes are not usually sleeping site options. Maybe as a result of their greater visibility, they can suffer heavy predation by raptors. Raptor predation rates on woolly lemurs in RNP were estimated to be as high as 20%, whereas raptor predation was estimated to be no higher than around 7% in *Microcebus* and *Cheirogaleus* [Karpanty and Wright 2006]. Even though mouse lemurs tend to be solitary during their activity period, they commonly sleep in groups. This might have thermoregulatory benefits [Schmid 2001], but is probably also lowers predation risk via the anti-predation benefits of group living. The likelihood of being killed in an attack is reduced with larger group size, and predator confusion enhances the odds of survival [Hamilton 1971]. For example, upon disturbance by a diurnal viverrid, mouse lemurs shot out in all directions from their leaf nest, which allowed some to escape unharmed while one was killed by the *Galidia elegans* [Deppe et al. 2008]. Other nocturnal lemur species habitually benefit from the same effects, including *Avahi, Cheirogaleus, Phaner,* and possibly *Allocebus* and *Mirza*).

Other adaptations might also lower predation risk in mouse lemurs. For example, mouse lemurs are well camouflaged. Their pelage is grey or brown, and many species have a dark dorsal stripe, which gives them the appearance of a dry leaf. While observing mouse lemur nests during the late afternoon, I found it very difficult to distinguish mouse lemurs emerging from their nests from the surrounding vegetation. Their pelage might lower the likelihood of being detected from aerial predators during day light hours. Mouse lemurs commonly use vocalizations in high frequency ranges inaudible to humans and owls [Knudsen and Konishi 1980], and it has been suggested that high frequency sounds are outside the hearing range of most predators, which would greatly lower conspicuousness [Zimmermann 1995; Zimmermann et al. 2000], and thus lower the likelihood of being detected. Mouse lemurs are also highly sensitive to detecting motion which allows them to detect of moving insect prey easily, and might assist in the detection of moving predators. In my experiments, mouse lemurs were more likely to display fear and vigilance behaviors in response to moving than immobile objects.

Although indirect anti-predation adaptations are beneficial, they often incur costs to prey because they assume a constant and unchanging risk of predation [Lime and Dill 1990]. Indirect adaptations and behaviors can lower energy intake because certain habitats and the associated food sources might be off-limits, or food must be shared with group mates. They can also increase energy output, because, for example, growing and maintain armor or toxins requires energy, or prey must travel longer distances to find food or shelter. However, predation risk is not constant because predator abundance can vary with season, and predators move around [Lima and Dill 1990]. Predation risk is the highest when a predator is in close range. Having the ability to detect actual predator presence is thus highly beneficial. Predator recognition mechanisms lower the need for potentially costly indirect anti-predation behaviors, can reduce predator encounter rates, and potentially enable prey to respond with behaviors appropriate to the prey detection and hunting style of the different predators.

Many animals including birds, fish, and a variety of mammals respond to sensory cues of predators [for reviews see Caro 2005, Kats and Dill 1998, Lima and Dill 1990]. In primates it has been shown that many diurnal monkeys and lemurs respond to visual, olfactory, and acoustic predator cues with flight, and other, often predator appropriate, defense and escape behaviors [e.g. Karpanty and Wright 2007; Karpanty and Grella 2001; Macedonia and Polak 1989; Seyfarth et al. 1980; Zuberbühler 2000]. Nocturnal primates, in contrast, have long been thought to rely on indirect anti-predation measures only [e.g. Cheney and Wrangham 1987; Terborgh and Janson 1986], although there is more and more evidence that they too have access to direct predator recognition mechanisms.

Nocturnal primates tend to be smaller than diurnal primate species and are thus often subject to more species of predators as well as a wider range of predator types. Any given mouse lemur population is subject to fourteen or more species of predator, that include diurnal and nocturnal aerial and arboreal predators such as raptors, snakes and viverrids [Scheumann et al. 2007]. Many other species of nocturnal primate will likewise find themselves confronted with a similar assembly of predators, and predation rate estimates by raptors are found in Karpanty and Wright [2007]. Nocturnal lemurs, like all forest dwelling primates, are often confronted with ambush predators that take advantage of the concealment that vegetation provides. Because small primates can easily escape their often much larger predators by seeking refuge in fine branches and vegetation tangles, even a moments advanced notice can greatly increase survival. My study shows that brown mouse lemurs perceive both visual and olfactory predator cues as dangerous. This was especially true for snake models, motion, and mammalian odors. Motion in particular is a highly useful warning cue in low visibility environments, where other visual features such as color, shape, or size might be difficult to perceive. However, mouse lemurs did not display a range of behavioral response like often observed in diurnal primates, but, in contrast, always responded with the same behavior. The behavioral response was flight/retreat, followed by monitoring the environment (vigilance), which was often followed by a careful reapproach of the feared stimulus. It is possible that because mouse lemurs were restricted to the horizontal plane in the lab, strata changes often observed in diurnal primates, were not an available option. Future experiments that provide a 3-dimensional space might reveal a wider range of behaviors. It is, however, also possible that the exhibited response it most appropriate. Predators dangerous to mouse lemurs at night include snakes, the large fosa (up to 12 kgs, Wright personal communication) and possibly some smaller viverrids (*Galidia, Galidictis,* and *Viverricula*), as well as owls. Neither snakes nor the viverrids, especially the large fosa, are likely to be fast or agile enough to chase down a tiny mouse lemur in a tree. Because mouse lemurs have an advantage, and because it is thus very useful to know the exact location of the predator, it might be a very good strategy to first run but then stop and try and locate the predator. I have often encountered mouse lemurs in the forest that use exactly that behavior: either run and stop deeper in the forest or higher up the tree to watch the human, or sometimes I found that I only detected mouse lemurs because they approached me, presumably to watch what I was up to. At night and/or in the forest, predators might heavily rely on the element of surprise, so once they have been informed of their detection, they often give up the hunt [e.g. Caro 2005; Terborgh 1990]. Owls are thought to be one of the greatest threats to mouse lemurs [Goodman et al. 1993]. Forest owls hunt from perches under the canopy, require a clear pounce path, are very visual and highly sensitive to sound. An appropriate response would thus be to run and seek cover, or to freeze, but in an environment with lots of nearby cover, seeking cover might be the first choice. In my experiments, mouse lemurs did not change their behavior in the presence of owl models, nor owl odor, but it is possible that those are not commonly available owl cues in a forest. It should be noted that owls fly silently, and sit silently on lower branches visually scanning for prey. Likewise, mouse lemurs only responded to a model of a ring-tailed mongoose when it moved, and feared moving snakes more often than still ones. Since mouse lemurs never responded with fear (beyond a brief startle) to moving non-predator objects, they must recognize some features specific to predators, which could include shape or pattern (striped tail, scale pattern). This was particularly indicated by the observation that mouse lemurs feared immobile snake shed suggesting pattern recognition. Even though mouse lemurs perceived carnivore urine as dangerous, this fear seems to level off quicker than fear in response to objects. In the forest, where stimuli were present for several hours, mouse lemurs entered traps. Similar observations have been made with rodents in the field [Parson and Bondrup-Nielson 1986]. Since odors do not reliably reveal the predator's whereabouts, predator odors might eventually be ignored in the favor of food if there are no additional cues such as the visual perception or motion.

One of the most interesting finding was that mouse lemurs ignored predator calls, both in my study as well as in a study with captive-born individuals [Bunkus et al. 2005]. Other species of nocturnal lemur, including woolly and sportive lemurs likewise either ignored predator calls, or respond in an inquisitive manner, rather than with flight [Fichtel 2007; Karpanty and Grella 2001]. It is unclear why nocturnal lemurs do not appear to perceive predator calls as indicators of danger. The most often used stimulus was the diurnal raptor call, which might simply be out of context at night [Karpanty and Grella 2001] because diurnal raptors prey on nocturnal primates during the day [Wright and Martin 1995]. Consequently, flight might not be the most adaptive response. Remaining immobile at the sleeping site might be a safer response, because movement attracts attention. Moreover, most nocturnal lemurs sleep in concealed places, which might severely lower the likelihood of being detected by aerial predators. Future experiments should present predator calls to sleeping mouse lemurs to examine whether responses depend on the state of activity.

There is evidence that in some animals predator recognition requires learning [e.g. Lima and Dill 1990]. Observations indicate that predator recognition abilities of primates, as well as other animals, improve with experience. For example, wild macaques show stronger fear responses than captive-born subjects [Mineka et al. 1980], and among wild monkeys, adults were more fearful than young individuals [e.g. Ramakrishnan and Coss 2000]. This might also hold true for nocturnal primates. For example, even though captive-born, predator naïve, mouse lemurs exhibited a mild avoidance of predator odors and predator models [e.g. Bunte 1998; Scheumann et al. 2007], the wild brown mouse lemurs in my study showed behavioral responses such as flight and vigilance, that were more indicative of fear rather than the mild avoidance behaviors exhibited by captive-born subjects. The observation that some brown mouse lemurs were fearful, whereas others were not, might also be an effect of experience. Whether a lack of response is the result of inexperience or a lot of experience remains to be examined. Learning about predators might be adaptive, because it would allow animals to quickly adapt to new habitats with different predator species, or to changes in predator species composition and densities. Such flexibility might explain why mouse lemurs are found in a wide range of habitats all across Madagascar.

Another curious finding of my study was that mouse lemurs differentiated among predator and non-predator objects in the lab, but not in the forest. In the forest, any objects lowered the likelihood of capture. One of the biggest differences between the lab and forest experiments was the availability of sensory information. It was intentionally minimized in the lab, but was naturally abundant in the forest. In the lab, risk perception might have been largely based on the experimental stimulus, whereas under natural conditions a multitude of information was integrated. Since visual information is highly important in the context of predation, and because objects were always placed in clear view, mouse lemurs might have followed a simple rule such as “when in doubt, avoid objects”. A strong selection for visual predator cues would be highly adaptive in visual prey animals such as primates. Tarsiers were also found to be highly sensitive to visual predator cues [Gursky 2003;2007], but comparable data is not available for other nocturnal primate species.

Findings with regards to predator recognition in mouse lemurs are mixed, which could be the result of experimental conditions and choice of subjects. Captive-born naïve subjects seem to respond differently than wild ones, and wild mouse lemurs that were kept in captivity for many weeks [Rahlfs et al. 2006] were less responsive than those held in captivity for very short periods of time [this study; Görlitz 2004]. The differences observed between the lab and forest experiments in this study further suggest that findings are subject to experimental conditions.

Wright [1989] found that anti-predation strategies and adaptations in nocturnal monkeys are contrasting to those of diurnal monkeys. In prosimians, there seems to be less differentiation [Karpanty and Wright 2007]. Findings suggest that visual and olfactory predator recognition abilities might have evolved relatively early in the primate lineage when primates were small and nocturnal [Cartmill 1972]. Alternatively, it is also possible that direct predator mechanisms evolved separately in different suborders or species of primates. Many species, including birds, rodents, marsupials, and even fish use direct predator cues to make risk assessments, which indicates that such mechanisms are of great value to prey, and were selected for in many lineages. The social system, behavior, ecology, and cognitive and physiological systems of any species reflect an optimal balance between the need to find food and mates, and to avoid predation [Janson 1992, 1998, 2003]. Specific, cognitively based, anti-predation strategies might also vary among populations, according to conditions [Dickmann 1992; Caro 2005]. There are few data available regarding predator-prey interactions in primates, and most observations are anecdotal [e.g. Bearder et al. 2002; Isbell 1990, 1994; Miller 2002]. Predation events are rare, and even more rarely is a human observer present. However, now with long-term studies, more data of direct observations are available [e.g. Isbell 1991; Irwin et al. 2010; Wright 1998, 1999]. Nocturnal species in particular are notoriously difficult to study, due to their small size and low light levels during their activity. As more data becomes available about primate and predator behavior, our rudimentary view of nocturnal primates might reveal behaviors and cognitive abilities more complex than previously thought.

5.2. Suggestions for Future Research

The findings from this dissertation have raised a multitude of questions regarding the specificity of recognition mechanism and behaviors, the realism of stimuli, the circumstances of stimuli encounter, the influence of learning, and the apparent lack of predator call recognition in mouse lemurs. There are five main areas for future research:

1) Do mouse lemurs differentiate among different predators? Previous research suggests that many diurnal primates can at least distinguish between terrestrial and aerial predators [e.g. Seyfarth et al. 1980; Macedonia and Polak 1989]. Findings from this study suggest that unlike

many diurnal primates, mouse lemurs do not differentiate among predators, because the behavioral response to feared stimuli was always the same. This observation might however be an artifact of the experimental conditions. In the laboratory, mouse lemurs were largely limited to the horizontal plane. Diurnal primate commonly move down or up in the canopy in response to aerial or terrestrial predators, respectively. A larger apparatus, such as a cage, might reveal more specific, or a wider range of, behavioral responses.

2) Is recognition highly specific? Observations and experiments involving diurnal primate species and tarsiers show that the recognition of predators can be very specific with respect to visual features, because subjects distinguished among snake species [Gursky 2005, 2007; Ramakrishnan et al.2005]. The lack of specific behaviors or a lack of recognition observed in my mouse lemur subjects could be due to the absence of features specific to local predator species. Comparing responses to predator models that closely resemble local predators with models that do not might reveal highly specific recognition mechanisms. The variation in perception of predator odors, and a failure to differentiate among them could have been due to odor quality or quantity. Mouse lemurs might make risk assessment based on urine or feces freshness; fresher samples might indicate higher risk than older samples. This could be easily addressed by using odor stimuli of varying freshness. Odor quantity might also be a factor affecting perception. Findings from preliminary trials with much smaller quantities of feces and urine used in this study suggest that larger quantities elicit stronger and more frequent fear responses. Presenting subjects with a variety of quantities might reveal that larger amounts are perceived as more dangerous than smaller ones.

3) Why did mouse lemurs repeatedly re-approach feared stimuli? Mobbing predators is common in many primate and avian species [Frankenberg 1981; Gursky 2005; Outtara et al. 2009]. A re-approach of a real predator is highly dangerous and at first glance doesn’t seem to be a good strategy for survival. However, suggested explanations for the evolution of this behavior include “alerting others” and “perception of detection” (for a review see Gursky 2006; Frankenberg 1981]. A third explanation which I present in this dissertation is that the observed re-approaches reflect a degree of uncertainty. This could be explained by a lack of stimulus realism based on

visual or olfactory characteristics. In my experiments, predators were deliberately reduced to a single sensory modality. This might be confusing to mouse lemurs because under natural conditions, there might be more sensory information. For example, a visual predator that lacks odor or sound might cause uncertainty. The use of multi-sensory stimuli or live predators might not produce repeated approaches.

4) Does learning affect perception? It has long been debated whether predator avoidance is learned or innate in primates [e.g. Janson and van Scaik 1993; Seyfarth et al. 1980]. The observation that some mouse lemur subjects feared stimuli whereas others did not, suggests individual variation in perception. If predator recognition was solely genetic, it would be expected that such a highly beneficial trait would spread through a population very quickly. It is thus more likely that individual variation in perception is due to experience and learning. Repeated testing of the same individuals across time might reveal changes in behavioral responses to the same stimuli. There is also evidence that animals learn from observing others [Janson and van Schaik 1993; Ramakrishnan and Coss 2000] . An experiment where one individual is the observer and another demonstrator of fear, will show if mouse lemurs change their behavior after observing another.

5) Do mouse lemurs lack the ability to recognize predator vocalizations as indicators of danger? There is no evidence that mouse lemurs perceive predator calls as indicators of danger. This might however be due to the predators used, or the time of day the tests took place. At night, mammalian predators might be not a great threat to mouse lemurs due to their agility, and diurnal raptors calls heard at night might be out of context. It is possible that many predators are most dangerous to mouse lemurs during the day when they are sleeping in nests or holes in trees, so future experiments could take place during the day It is also possible that acoustic predator recognition requires learning, because captive born mouse lemurs likewise ignored predator calls. Predator call learning might require the pairing of the sound with another sensory input, for example the visual perception of the predator. Diurnal primates might recognize predator calls, because they usually see the predator more easily at day light, than nocturnal primates at night time. A future experiment could involve the presentation of a predator call with its odor or

a model. Furthermore, it is not known whether diurnal primates have the innate ability to recognize predator calls. Test with naïve monkeys or lemurs might shed light on how much learning factors into call recognition.

In addition to conducting more specific experiments with mouse lemurs, it would be beneficial to have more data regarding other species of nocturnal primates. There are no data regarding visual and olfactory predator recognition regarding species other than mouse lemurs, and there are only few play back studies. It is also clear, that little is known about visual and olfactory predator recognition in diurnal primates; most predator recognition studies have involved predator vocalizations [Macedonia and Polak 1989; Seyfarth et al. 1980; Zuberbuhler 2000]. Olfactory predator recognition studies have been limited to captive-born tamarin monkeys [Buchanan-Smith et al. 199; Caine and Weldon 1989], so it would be interesting to expand studies to other species. There is evidence that in some species, recognition abilities, or specificity, could be dependent of predator densities or abundance. However, little is known about most predator species. As more data becomes available about predator behavior, hunting techniques, prey preferences and predation rates, our knowledge and interpretation of anti-predator behavior in primates might evolve.

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