Variation in predator communities and anti-predator behaviors of Milne-Edwards' sifakas (*Propithecus edwardsi*) in southeastern Madagascar

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Thesis submitted for the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

Master of Science

in

Fisheries and Wildlife Sciences

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July 19, 2010

Blacksburg, Virginia

Keywords: anti-predator behavior, carnivores, lemurs, local ecological knowledge, Madagascar, Milne-Edwards' sifaka

Abstract

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To advance conservation in the increasingly fragmented landscape of Madagascar, we must examine the persistence and interactions of species in human-disturbed habitats. I investigated lemur-predator interactions in southeastern Madagascar through a comparison of predator communities and anti-predator behaviors of Milne-Edwards' sifakas (*Propithecus edwardsi*) in the continuous rainforest of Ranomafana National Park, and the forest fragments of Ialatsara Forest Station. I confirmed the presence of potential aerial predators at each site, but the sifakas' confirmed native mammalian predator, fossa (*Cryptoprocta ferox*), was absent from the fragmented site. Playbacks of predator vocalizations did not suggest that fragment-living sifakas have weakened anti-predator responses, but that their responses may be less specific than those of conspecifics in the continuous forest. I found that fragment-living sifakas displayed less downward vigilance and more frequently used low canopy heights; these behaviors may increase their vulnerability to recolonizing ground predators. I investigated local ecological knowledge (LEK) of carnivore ecology in communities 0– 20 km from continuous forest to explore the potential for such recolonization. My findings from 182 interviews in 17 communities suggest that the fossa is especially sensitive to anthropogenic disturbance; it was only observed in communities ≤ 2.5 km from the continuous forest within the last five years. In contrast, the introduced small Indian civet (*Viverricula indica*) and wild cat (*Felis silvestris*) were distributed ubiquitously and displayed an affinity to human-dominated habitats. LEK surveys can provide information on the poorly understood responses of the Malagasy carnivores to the threats they face in a changing landscape.

Intended authorship and target journals for manuscripts included in the thesis:

Chapter Two

Variation in predator community and in anti-predator behavior of Milne-Edwards' sifakas, *Propithecus edwardsi*, at continuous and fragmented rainforest sites in southeastern Madagascar

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*To be submitted to *International Journal of Primatology*

Chapter Three

Using local ecological knowledge to investigate carnivore distribution and movements across a human-dominated landscape in southeastern Madagascar

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Acknowledgements

Funding for this project was provided by the Department of Fisheries and Wildlife Sciences of Virginia Polytechnic Institute and State University, and the National Geographic Committee for Research and Exploration (Award # 72504).

I would like to thank Malagasy National Parks (MNP) for permission to conduct research in Ranomafana National Park and the Malagasy Institute pour la Conservation des Environnements Tropicaux (MICET) for their reliable help obtaining necessary research permits and visas, hiring translators, and making travel and lodging arrangements. Special thanks for the amazing staff at Centre Val Bio who facilitated my research projects in and around Ranomafana National park. Merci beaucoup to Daniel and Berenice Rajaona for their permission and encouragement to study the sifakas at Ialatsara Forest Station, and for their friendship during my time there. I am especially grateful to all of the interviewees in southeastern Madagascar who shared their time and experiences with me, and all members of the communities we visited who willingly accepted a stranger such as myself in their midst.

I must acknowledge all of the research technicians with whom I had the pleasure of working with at Ranomafana and Ialatsara, whose amazing skills and incredible patience astound me! I cannot thank them enough for their long hours of hard work, their attention to detail, and their willingness to share knowledge of the forest, Malagasy language, and their culture with me. Their good nature and humor, even during torrential downpours, failed playback attempts, or unforgiving long-distance hikes, were quite contagious and greatly appreciated. Thanks to VELOTSARA Jean-Baptiste, NDRIATAHIANA Aime Noel, VELONABISON Mamitiana Jean Jose, RAZAZAROHAVANA Joseph, RAKOTONIRINA Jean Raymond Richard, RAZAFIMAHENINA Eli Jean Raymond, RAZANAKA Marcel, ANDRIAMIHARISOA Feno Hery, Solo Justin, and RABELAHY Franck Naina. Thank you also to our cook, Manana, whose

meals kept us healthy and happy throughout two field seasons, and to Ranary, who kept our ride running just long enough to get home. Thanks also to Christopher Latimer for volunteering to come to Madagascar and for being a huge help during the initial phase of my first field season.

My project was greatly improved with suggestions from several researchers in Madagascar and at Virginia Tech. Thanks to Dr. Summer Arrigo-Nelson, for her advice and her efforts to capture and recollar sifakas in Valohoaka, and to Dr. Jane Foltz, for her cooperation and trail-blazing work at Ialatsara. At Virginia Tech, thanks to Dr. Jonathan Cohen for his sound statistical advice and his thorough, patient explanations. Thank you to Drs. Steve McMullin and Kathy Alexander for their input in the design of my local ecological knowledge survey. I am grateful for stastistical advice received from Dr. Eric Vance and Hayley Nelson at the Virginia Tech Laboratory of Interdisciplinary Statistical Analysis. Thanks to members of the Karpanty and Fraser lab groups, and to other graduate students in the Department of Fisheries & Wildlife Sciences for help, encouragement, and friendship at Virginia Tech. Special thanks to Brian Gerber for frequent feedback on study design and analysis, for sharing his encyclopedic knowledge of the Malagasy carnivores, and for friendship in Cheatham and Madagascar alike.

I would especially like to thank my committee members for their availability, advice, and encouragement; it has been a pleasure working with them both. Thank you to Dr. Dean Stauffer for frequent and very useful instruction in study design, analysis, and habitat assessment. Thank you to Dr. Jeff Walters, for providing expertise in behavioral studies and primate ecology. I offer enormous thanks to my adviser, Dr. Sarah Karpanty, for her faith in my abilities and her valuable guidance through all aspects of my thesis research. Her perseverance and hard work on this and all other projects she is a part of are inspirational. I feel very grateful to have had the opportunity to conduct this research in Madagascar and to be a part of such a wonderful lab group.

Finally, I would like to acknowledge my family. Thanks to my parents, James and Toni Kotschwar, who raised me to appreciate the natural world and who have always supported and encouraged me as I pursued my interests, even when they took me half-way around the world. Thank you to my sister, Brooke, and my brother, Brett, with whom I shared many outdoor adventures and who continue to be role models of dedication and passion in what they do. Thanks to David Logan for endless support, his visit to Madagascar, and all of those GPS points!

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Chapter One: Introduction

Lemur-predator interactions across a dynamic landscape

Conservationists working to preserve the rich biodiversity in Madagascar face the challenge of managing species and their habitats in an increasingly disturbed landscape. Activities such as timber extraction, mining, and slash-and-burn subsistence farming decrease and fragment the less than 10% original vegetation cover remaining on the island (Myers et al., 2000; Harper et al., 2007). For sustainable conservation initiatives to advance, we need to identify areas in which to create, expand, and connect protected areas based not only on the species present, but also on the goal of protecting and restoring ecosystem integrity (De Leo & Levin, 1997; Kremen et al., 2008; Irwin et al., 2010). Balanced predator-prey interactions are an important component of functional ecosystems, and the loss of top and meso-predators can have cascading trophic effects (Crooks & Soule, 1999; Berger et al., 2001a; Roemer et al., 2009). Due to their large home ranges, high energetic requirements, small population sizes, and direct persecution by humans, many mammalian carnivores and large raptors are especially vulnerable to extirpation from habitat fragments (Crooks 2002, Newton 1979). Thus, habitat fragmentation may result in the loss of important predators and altered predator-prey interactions (Crooks and Soulé 1999, Berger 2007).

The loss of historically important predators has been shown to accompany weakened or inappropriate anti-predator responses among prey within only a few generations (Berger 2007, Gil-da-Costa et al. 2003). This adjusted behavior may be in equilibrium with changes in the predator community, but can lead to hyposensitivity and greater prey mortality if the predator returns (Berger et al., 2001b). Many prey populations adapt quickly to returning predators, reacquiring effective defense tactics within a small number of generations (Berger 2007, Gil-da-

Costa et al. 2003). Small prey populations, however, which are often already limited by other factors, may not survive the costly first contact (Gittleman and Gompper 2001).

Understanding the impacts of forest fragmentation and exposure to predators on prey behavior is especially important for the conservation of lemurs in Madagascar. Of the 92 extant lemur species, 37 are listed as vulnerable, endangered or critically endangered, while the status and population trends for 42 taxa are currently unknown (IUCN, 2010). Predation by mammalian carnivores, hawks, owls, and snakes constitutes a significant source of mortality for many lemur species (Goodman, 2003b; Pochron et al., 2004; Karpanty, 2006), and could lead to the extirpation of small populations in fragmented, degraded habitats (Irwin et al., 2009). Lemurs may also incur extensive sub-lethal effects through the energetic costs of predator avoidance and escape (Lima, 1998), especially in multiple predator communities where risks to a single predator may be enhanced by avoidance of another (Sih et al., 1998; Karpanty, 2003). Predation is believed to be an important selective pressure among primates that has influenced the evolution of physical and behavioral traits in many primate species (Janson, 1998; Zuberbuhler et al., 2002). In the current Madagascar landscape where both habitat degradation and conservation efforts can affect predator communities through local extinctions, introduction of exotic species, and recolonization of historically absent species, it is imperative to better understand lemur behavioral responses to changes in the predator community on an ecological time scale.

Specific study objectives

I explored lemur-predator interactions in the changing landscape of southeastern Madagascar through studies of both predator distribution and lemur behavior, specifically examining the occurrence of different predator species in and between continuous and fragmented rainforest, and variation in anti-predator behavior of lemurs exposed to different predator communities. The first part of my study is an assessment of known and potential predators present within a continuous rainforest site and a fragmented rainforest site in southeastern Madagascar, and a comparison of the anti-predator behavior displayed by groups of an endangered lemur species, Milne-Edwards' sifakas (*Propithecus edwardsi*), living in each of these areas. My specific objectives were to determine 1) the incidence of raptors and mammalian carnivores at each site, 2) if height choice, vigilance, rest/sleep site selection, and alarm calling behaviors of *P. edwardsi* differed between sites, and 3) whether responses of *P. edwardsi* to experimental playbacks of aerial and terrestrial predators differed between sites.

While this comparison provided insight as to the current conditions of lemur-predator interactions in two different habitats, I expanded both the temporal and spatial scale of my research in the second part of my study by investigating local ecological knowledge (LEK) concerning carnivore ecology and movement in the periphery of and matrix between the continuous forest and isolated forest fragments. My objectives in this study were to 1) assess distributions of Malagasy carnivore species outside of the rainforest and relate patterns to landscape- and community-level factors, 2) determine the level of human-carnivore conflict across the landscape, and 3) compare the information obtained through LEK surveys with the findings of other ecological studies conducted in the same region.

Chapter introductions

Chapter 2: I report the results of playback-enhanced raptor point counts and photographic sampling surveys (B. Gerber, Virginia Tech, unpublished data) conducted within intact, primary rainforest of Ranomafana National Park, and fragmented, disturbed rainforest of Ialatsara Forest Station, and describe key differences in the predator communities of the two sites. I describe baseline time allocation, group cohesion, vigilance, height use, and alarm calling of *Propithecus edwardsi* based on group scans and individual focal sampling of 2 sifaka groups within each site, and discuss patterns of habitat selection. Using playbacks of aerial and terrestrial predator vocalizations, I simulated increased predation risk and compare the immediate, short-term, and longer-term behavioral responses of individuals to playbacks between sites, among groups, and among stimuli. I discuss the similarities and differences in sifaka behavior between the fragmented and continuous forest sites in the context of trait loss and persistence, and describe conservation implications.

Chapter 3: I present the results of 182 semi-structured interviews with male heads-of-household from 17 communities located 0 – 20 km from the western border of Ranomafana National Park. I describe distinct patterns of distribution of 2 endemic and 2 introduced carnivore species based on the locations and timing of interviewee observations and relate these patterns to landscape- and community-level factors. I also discuss current and potential human-carnivore conflict based on the accounts of poultry depredation by carnivores, interviewee perceptions of different carnivore species, and reported killing of carnivores across the landscape. The value and limitations of local ecological knowledge in the investigation of carnivore distribution across broad temporal and spatial scales, and the implications of my results, are discussed in context of conservation planning in Madagascar.

Chapter 4: I highlight important findings from the previous two chapters and briefly discuss their conservation implications and directions for future research.

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Chapter Two:

Variation in predator community and in anti-predator behavior of Milne-Edwards' sifakas, *Propithecus edwardsi*, at continuous and fragmented rainforest sites in southeastern Madagascar

Abstract

A better understanding of variation in lemur behavior in response to changing predator communities is necessary for the conservation of lemur populations in increasingly degraded and fragmented habitats of Madagascar. We compared the predator communities and anti-predator behavior of Milne-Edwards' sifakas (*Propithecus edwardsi*) living in the intact, primary rainforest of Ranomafana National Park and the fragmented, disturbed rainforest of Ialatsara Forest Station in southeastern Madagascar. Raptor point counts confirmed the presence of at least one potential aerial predator at each site, while data from concurrent photographic sampling indicated the absence of the sifakas' most significant native mammalian predator, the fossa (*Cryptoprocta ferox*) from the fragmented site. During baseline observations, sifakas at both sites allocated their time similarly, but sifakas in the fragmented site displayed proportionately less downward vigilance and spent a greater percent of the time in low canopy and on the ground than did conspecifics in the continuous forest. Experimental playbacks of predator and potential predator vocalizations did not suggest that sifakas in the fragmented site have weakened anti-predator responses compared to those living in the continuous forest, but that they may lack some specificity. Future research is necessary to determine whether the behavioral differences we observed in fragment-living Milne-Edwards' sifakas would increase their risk of predation by fossa if the species recolonized. Predation risk to small, isolated prey populations by returning predators should be considered in the creation and expansion of protected areas in Madagascar.

Keywords anti-predator behavior, forest fragmentation, Madagascar, Milne-Edwards' sifakas, predation, *Propithecus edwardsi*

Introduction

A better understanding of primate-predator interactions is needed to fully understand the impacts of habitat alteration on primate communities. Predation constitutes a significant source of direct mortality for many primates (Stanford, 2002) and causes extensive sub-lethal effects through the energetic costs of predator avoidance and escape (Lima, 1998). As a strong selective pressure in species with often low fecundities, predation has been implicated in the evolution of primate body size, sociality and activity cycle (Janson, 1998). Trade-offs associated with anti-predator behavior, in terms of energetic costs and/or nonlinear interactions in multiple predator communities (Sih et al., 1998), are important to consider in fragmented landscapes in which primates must adapt to a changing habitat, predator assemblage, or both.

While some predators experience enhanced or equal success in fragments, others are often unable to persist, especially larger mammalian carnivores (Crooks, 2002). Thus, habitat fragmentation may result in the loss of important predators and altered predator-prey interactions (Crooks & Soule, 1999; Berger et al., 2001a). Relaxed predation through the decline or extirpation of one or more predators can produce situations of equilibrium, in which the prey show a reduced response to a reduced risk, or disequilibrium, in which prey exhibit either an exaggerated (hypersensitivity) or inadequate (hyposensitivity) response relative to the predation risk (Berger, 2007). Because the strong selective force exerted by predation results in energetic trade-offs between investment in anti-predator behavior and other fitness enhancing activities, relaxed pressure may lead to shifts in those trade-offs. The loss of historically important predators has been shown to accompany weakened or inappropriate anti-predator responses among prey within only a few generations (Gil-da-Costa et al., 2003; Berger, 2007). While this adjusted behavior may be in equilibrium with changes in the predator community, lost behaviors can lead to hyposensitivity and greater prey mortality if the predator returns. Indeed, studies of large mammal prey have found ‘naïve’ populations subject to higher predation rates during their initial contact with recolonizing predators (Berger et al., 2001b). While prey populations may adapt quickly to returning predators by reacquiring effective defense tactics within a small number of generations, (Gil-da-Costa et al., 2003; Berger, 2007), small prey populations, which are often already limited by other factors may not survive the costly first contact (Gittleman & Gompper, 2001). This suggests that small populations of threatened and endangered prey, such as those living in fragmented, disconnected habitats, may be especially vulnerable after isolation from an important predator.

Understanding the impacts of forest fragmentation and predator experience on primate behavior is especially important for the conservation of lemurs in Madagascar. Primary vegetation has been reduced by over 90% in the approximately 2000 years since human colonization of the island, and continued deforestation alters both the lemurs’ habitat and their predator communities (Myers et al., 2000; Dehgan, 2003; Harper et al., 2007). Lemurs are now known to be vulnerable to predation by a range of predators in diverse guilds (Goodman, 2003; Karpanty, 2006), which in turn, are influenced by landscape changes. The largest mammalian carnivore on the island, the fossa, *Cryptoprocta ferox,* occurs at low densities and it is estimated that only a few protected areas in the country are large enough to support viable populations (Hawkins & Racey, 2005). It is unknown how the loss of this top predator affects the anti-predator behavior of its lemur prey in the wild. However, concentrated and unusually high fossa predation rates on captive-bred black and white ruffed lemurs (*Varecia variegata*) reintroduced to the eastern rainforest of Madagascar suggest that lemurs may be at risk of losing critical predator avoidance techniques (Britt et al., 2004). In another part of the eastern rainforest, the return of fossa, known historically in the region but absent from a site for several years, resulted in the rapid extirpation of critically endangered diademed sifakas (*Propithecus diadema*) from a forest fragment (Irwin et al. 2009). It is hypothesized that several factors, including the prolonged absence of fossa from the fragment, physical crowding, and altered forest structure may interact synergistically to drive unusually high predation in fragments (Irwin et al. 2009). In the increasingly fragmented landscape of Madagascar, we must understand how quickly and under what circumstances lemurs lose predator-defense tactics, which tactics are lost, and how quickly they may be reacquired.

One of the major obstacles in understanding primate-predator interactions is that although primates can be habituated, predators typically remain sensitive to humans and so the presence of human observers may deter already infrequent predation attempts (Janson 1998, Isbell 1994). The impact of predators on primate populations, therefore, often must be studied indirectly. Playbacks of predator vocalizations provide a means to investigate prey response to the presence of a predator. Although many predators are stealthy hunters and do not vocalize before or during an attack, prey may detect the vocalizations of predators engaged in other activities and use these auditory cues in predator avoidance (Blumstein et al. 2008). Several playback experiments conducted with captive and wild lemur populations have confirmed that lemurs use acoustic cues in the recognition and avoidance of aerial and terrestrial predators (Macedonia and Yount 1991, Fichtel and van Schaik 2006, Karpanty and Grella 2001, Karpanty and Wright 2007). Longer-term observational studies of wild lemur groups have provided insight to behaviors believed to be related to predator avoidance, such as vigilance, general and specific alarm calls, the use of different canopy heights, and selection of particular rest and sleep sites (Wright, 1998).

To better understand how the anti-predator behavior of lemurs varies among continuous vs. fragmented habitats, and if any observed behavioral shifts relate to differences in predator communities, we investigated predator assemblages and the anti-predator behavior of Milne-Edwards' sifakas (*Propithecus edwardsi)* in both a continuous and a fragmented forest site in southeastern Madagascar. The species' demography, characterized by seasonal reproduction, low juvenile survival and low fecundity, combined with their relatively low behavioral plasticity, make them especially vulnerable to fragmentation-induced changes in their environment (Dehgan, 2003; Pochron et al., 2004; Lehman et al., 2006). They are listed as endangered (IUCN, 2010) and recent studies of anthropogenic and climatic pressures facing the species support the current listing (Dunham et al., 2008). Furthermore, observational studies of Milne-Edwards' sifakas in Ranomafana National Park reveal that they are highly susceptible to predation by the mammalian carnivore fossa and that they exhibit predator-specific responses to extant raptors (Wright et al., 1997; Karpanty, 2006). Our objectives were to: 1) determine the presence/absence of aerial and terrestrial lemur predators at a continuous and fragmented forest site, 2) compare activity, vigilance, height use and habitat selection of sifakas between these sites, and 3) compare the behavioral responses of sifakas to playbacks of predator and control vocalizations between these sites.

Methods

Study sites and subjects

Our continuous forest sampling occurred in Ranomafana National Park (RNP), located at 47° 18' to 47° 37' E, 21° 02' to 21° 25' S (Fig. 1). Established in 1991, RNP contains 37,367 ha of protected lowland rainforest, cloud forest and moist montane rainforest (Dunham et al., 2008) at elevations ranging between 537 – 1396 m (B. Gerber, unpublished data). The climate is subtropical with average rainfalls of 2,300 to 4,000 mm annually, with considerable seasonal and yearly variation; highest rainfall occurs December through March, while May through October are the driest months (StonyBrook, 2010). Due to selective logging before the park's establishment and the historic presence of villages in the area, RNP now contains a mixture of habitats, ranging from pristine forest to selectively logged and heavily disturbed areas. We conducted this study in the undisturbed primary forest of the Valohoaka trail system and the minimally-disturbed forest of the Vatoarana trail system, from which there has been some selective-logging (Balko, 1998) .

Our fragmented forest sampling occurred at Ialatsara Forest Station (IFS), a private ecotourism reserve and forest station, located at 47^{o} 12' to 47^{o} 15' E, 21^{o} 02' to 21^{o} 06' S (Fig. 1). IFS is owned and managed by two Madagascar residents (D. and B. Rajoana) under a 50-year management convention with the Ministry of Water and Forests. The forest station exists at an altitude range of 1300 – 1500 m and contains about 1000 ha of pine, 500 ha of eucalyptus and 500 ha of natural rainforest in 10 forest fragments of varying size (24-240 ha) surrounded by matrix habitat of grassy or shrubby savannah and agricultural plots. The natural forest was once contiguous with the main eastern rainforest corridor (where RNP is located), but due to deforestation for agricultural activity, the fragments have been isolated for approximately 30 years (Foltz, 2009). We investigated predator communities in and around all fragments of IFS and conducted observations of sifaka groups within the largest natural fragment (240 ha).

At both RNP and IFS we studied groups of Milne-Edwards' sifakas that had previously been habituated, with at least one group member fitted with a radio-collar, as part of earlier studies (Arrigo-Nelson, 2006; Foltz, 2009). Groups ranged in size ranged from 3 – 7 individuals and varied in composition, but all contained at least one adult female, adult male, and a juvenile

(Table 1). All behavior sampling methods were approved by the Virginia Tech Institutional Animal Care and Use Committee (Protocol #08-051-FIW, Appendix A).

Predator community

To compare the raptor communities at each site, we used point counts with playbacks of raptor calls, a technique commonly used to maximize detections in dense habitats (Bibby et al. 2000). We conducted point counts at 24 points in RNP and 26 points at IFS. The points were spaced at least 500 m apart (RNP 512.79 ± 92.84 m SD, IFS 583.87± 85.50 m SD) and were part of established photographic capture survey grids (B. Gerber, Virginia Tech, personal communication). We surveyed each point 4 times from 28 October - 21 November 2008, with approximately 1 week between consecutive observations. To minimize the confounding effects of time of day and weather, we only conducted point counts between one hour after sunrise and 1200 on days with no precipitation, conditions in which other diurnal raptors have been found to be most active and detectable (Fuller and Mosher 1987). We rotated the order in which we visited points among sampling sessions to further reduce time of day effects.

Upon arriving at each point, the observer waited 5 minutes before recording observations to allow birds in the area to settle. After a 5-minute period of silent observation, in which the observer recorded all raptor sightings and vocalizations, the observer began broadcasting playbacks of two species of interest, Henst's goshawk (*Accipiter henstii*) and Madagascar harrier hawk (*Polyboroides radiatus*), which are known to prey on large-bodied lemurs (up to 3.5 kg) in this region (Karpanty, 2006). We broadcast the vocalization of each species 2 times, with 30 seconds of silent observation between them, followed by three minutes of silent observation. We alternated the order of the species' calls among consecutive points. To avoid stimulating the same individuals with playbacks from multiple points and to minimize disturbance to lemur groups in the area, we broadcast the calls at relatively low volumes, heard by humans at maximum distances of 50 – 75 m from the point. During the call playbacks, the observer recorded any vocal responses or visual sightings of raptors, as well as the compass direction and estimated distance from the point.

We calculated the mean number of individuals of each raptor species detected per visit per point as indices of relative abundance of the species at each site. We expected visual detectability of raptors to vary between sites as forest structure varied and only 12 of 26 points in IFS occurred in natural forest fragments. Thus, we included only individuals heard calling at a point, and excluded individuals seen but not heard. For each point, we calculated the mean of individuals heard calling during each repeat visit. We then calculated the mean of all point means within each site.

We provide data on the presence/absence of carnivore species, including known and potential lemur predators, obtained from concurrent photographic capture surveys conducted at both sites (B. Gerber, unpublished data).

Baseline Behavior

We conducted observations of baseline behavior (i.e. behavior in the absence of simulated predator encounters) on two groups of Milne-Edwards' sifakas at each site. Due to logistical constraints, we could not observe groups at both sites over the same time periods (Table 1). Sampling days were dawn to dusk, beginning within one hour of sunrise and ending within one hour of sunset, and usually consisted of locating the group at their sleep sites in the morning (identified by observers the night before) and following them until they settled at a sleep site for the night. During day-long follows, we observed multiple group members using a combination of group scans and instantaneous sampling of focal individuals. For groups RNP1 and RNP2, we sampled all individuals, excluding the infant in RNP1. In groups IFS1 and IFS5, we chose one adult male, one adult female, one juvenile and also one sub-adult for focal sampling and included all members except infants in group scans.

To investigate activity budget, ranging, and group spread of sifakas, we conducted group scans every ten minutes from the time we located a group until the time we left them. During scans, the observers recorded the activity of each group member that could be located within 1 min of the start of the scan. Behavior was divided into 8 mutually-exclusive categories (Table 2). We quantified activity budgets of sifakas at both sites as the mean proportion of group scans during which individuals were engaged in each behavior for each observation day. At the time of each group scan, we also recorded the GPS location of the center of the group and the estimated group spread (distance between the two visible group members farthest apart). We estimated daily path lengths (DPL) of sifaka groups as the sum of the Euclidean distances between consecutive GPS locations of the group's center taken every 10 minutes. As we expected the accuracy of group spread estimates to decrease with increasing distance, we categorized group spread into 6 distance classes (0-2 m, 3-5 m, 5-10 m, 10-20 m, 20-30 m, and > 30 m). We only included scans where all group members were in sight for analyses of group spread.

We used instantaneous focal sampling of individuals to examine vigilance, calling, height use, and group cohesion in sifakas. We sampled individuals in rotation, the order of which was randomly determined for each sampling day before we located the group. At the start and end of each focal sample, we recorded the GPS location of the focal individual and the identity of and distance to the individual's nearest neighbor. Each 10-min focal sample consisted of instantaneous time sampling every 20 s (31 time points per sample) of the focal animal's behavior, vigilance and estimated height. Two observers with synchronized vibrating watches were positioned in different locations to have complementary views of the focal animal's body and face, while a third observer recorded spoken observations. As a proxy for vigilance, we recorded the occurrence and direction of the animal's regard towards anything beyond its immediate surroundings. Thus, if the animal appeared to be looking beyond 0.5 m from itself at a sampling time point, we recorded the direction (upward, downwards, or horizontal) of its gaze in addition to the animal's activity. We continuously recorded all occurrences of vocalizations and discrete vigilance events (staring or scanning in one direction for 3 s or more with a cessation of all other activity) during the sample. We rotated among individuals as efficiently as possible, while maintaining at least 1 hour between consecutive samples of the same individual.

For each focal individual sample, we calculated the proportion of time points the animal displayed vigilance in different directions and occurred in each height category. We removed points for which the observer could not see the animal or classify its behavior, and excluded focal samples with <25 remaining time points. We calculated the mean of proportions taken for each individual per day, then calculated the mean of days for each individual. We also calculated rates of calling and discrete vigilance events as the mean number of occurrences over the 10 min sampling period, and converted the values to hourly rates. We included only loud calls frequently used in response to predators, which could be heard reliably from individuals at any canopy height, in analyses (Table 2). For each individual, we also calculated the mean distance to closest group member at the start of each focal sample. Due to uneven sampling at sleep sites among groups, we excluded focal samples and group scans taken at the group's sleep site before emerging in the morning or after settling in the evening.

Given the unbalanced nature of many of our observations, we used generalized linear models (PROC MIXED, SAS 9.2, Cary, NC, USA) to examine multiple fixed effects on our response variables. We investigated the effects of site (IFS, RNP), group nested within site, and sex/age class on all baseline behaviors including 1) percent of observations in different activity categories, in vigilance, in different height categories, and with a group member at different distances and 2) individual rates of calling and discrete vigilance events. Models for daily path length tested effects of site and group within site, as well as the covariates of rainfall and daylight hours. We conducted pairwise comparisons among levels of fixed effects using t-tests of the difference of least square means. We adjusted the p-values for pairwise comparisons via simulation to protect a family-wise error rate of 0.1 (Litell et al., 2006).

Habitat use

On baseline behavior sampling days (Table 1), we color-flagged and took GPS locations for all diurnal rest locations (where the majority of the group was stationary and resting for ≥ 40 min) and nocturnal sleep locations of the focal study group. We returned on separate days during the same season to measure macro- and micro-habitat characteristics at these flagged sites and two other random locations within each group's day range (area used during dawn to dusk follows). Day ranges were described by minimum convex polygons (MCP) created from the GPS locations taken every 10 minutes during follows. Within each day range MCP, we used Hawth's tools (Beyer 2004) to generate 2 constrained random points at least 50 m from each other and from the rest and sleep locations used that day.

For each tree used at a rest or sleep location, and for the nearest tree with diameter at breast height (DBH) ≥ 10 cm at random locations, we recorded the diameter at breast height, tree height (estimated visually and with a clinometer), maximum canopy crown diameter, and % downward slope at the base of the trunk.

We estimated tree density, basal area, and percent cover of different canopy and vegetation types using the point-centered-quarter and point-intercept methods at the center point of each location and one point at a radial distance of 25 m from the center in each of the four cardinal directions. At each of the five points, we recorded the DBH and distance to center of the closest tree ≥ 10 cm DBH in each quadrant (Krebs, 1999). We applied the point-intercept method at five, 2 m intervals from the center of each point in each of the 4 cardinal directions. At each interval, the observer assessed the presence/absence of herbaceous ground cover (leafy vegetation ≤ 0.5 m high) and shrubs (vegetation with woody stems < 10 cm DBH, ≤ 5 m high). All leafy canopy and branches from trees ≥ 10 cm DBH were categorized as low (≤ 5 m high), mid (6 – 15 m high), or high (> 15 m high) canopy.

Calculations of mean tree density, basal area, and proportion of different vegetation types were based on 5 point-quarter points (20 trees) and 100 points for point intercept (20 per point-quarter) at each used or random location. Means of these estimates, as well as dendrometrics of the used and random trees, were calculated for each location type (rest, sleep, and random) within groups. We investigated the effect of site (IFS, RNP), group within site, and type of location (rest, sleep, random), as well as site*location type interactions on all habitat characteristics using generalized linear models, with pairwise comparisons between effect levels as described above. To investigate selective height use among sifakas, we created an index of relative availability of each canopy height (proportion cover of each canopy height/sum of proportions of cover of low, mid and high canopy) at random locations within the daily ranges of each sifaka group. We then compared 95% confidence intervals of proportional use of height classes by sifaka groups with 95% confidence intervals on the relative availabilities of the classes; non-overlapping confidence intervals suggested either positive or negative selection.

Playback experiments

We conducted playbacks with five different stimuli vocalizations: 1) a familiar control (the cuckoo roller, *Leptosomus discolor),* 2) an unfamiliar control (America robin, *Turdus migratorius*), 3) Madagascar harrier-hawk, 4) Henst's goshawk, and 5) the mammalian carnivore, fossa. To avoid pseudoreplication, we created and used digital audio files containing vocalizations of multiple individuals for each predator species. Raptor calls were recorded from birds near their nest sites in and around RNP (S. Karpanty, Virginia Tech, personal communication). Two tapes of the common vocalizations of the fossa were provided by Deutsches Primatenzentrum, recorded from one individual from Zoo Duisburg in Germany, and by Animal Sound Archives (Tierstimmenarchiv) from a collection of calls from three individuals. Wave files containing cuckoo roller and American robin calls were obtained and used with permission from Missouri Botanical Gardens (Parks & Barnes, 2000) and Naturesongs.com (Von Gausig, 1998), respectively. We tested subjects in each group once with each of the five stimuli in random order from August – October 2008 (RNP1 & RNP2), and October-December 2008 (IFS1, IFS4, & IFS5). Consecutive playbacks to a single group were separated by at least 5 days. We conducted playbacks with a group only if there had been no alarm calls or predator encounters within 60 minutes, focal individuals were located in the low to mid-canopy (≤15 m high), the distance between any of the three focal individuals did not exceed 15 m, and all group members were engaged in relatively stationary activity (e.g. feeding, grooming, or resting; not during group travel or intergroup conflict). When all of the conditions above were met and we had already completed at least one hour of observation, a technician silently raised a small set of portable speakers (Philips SBA220/37) camouflaged by natural vegetation to either 2 or 4 meters depending on slope to be as closely level with animals as possible. We varied the distance of the speakers to the group based on the different amplitudes of the calls (Seyfarth et al., 1980). For the lowest amplitude calls of the fossa, we placed the speakers approximately 15 m from the group, while the speakers were placed at approximately 25 m away for the highest amplitude calls of the Madagascar harrier hawk, to maintain sound levels of 51-64 db (Radio Shack Digital Sound Level Meter 33-2055) for all stimuli.

After the speakers were positioned, three observers waited two minutes before beginning pre-playback observation of three group members (1 M, 1 F and 1 JM or JF). Carrying hand-held digital recorders (Sony IC Recorder, 2008), the observers took instantaneous samples of activity, vigilance and height category every 20 s guided by synchronized vibrating watches. We continuously recorded all vocalizations, discrete vigilance events, rapid approaching or fleeing the speakers, and rapid descent or ascent in the canopy. Observers recorded spoken observations during the 5 minutes before the playback, during the playback (20-25 s) and for 10 minutes after.

We transcribed the digitally recorded playback observations using the program Digital Voice Editor (Sony 2008), and scored immediate responses (behaviors that occurred with 1 minute of the start of the playback) for each individual and playback stimulus. The 15-minute observation period was then divided into three 5 minute periods: pre-playback (PRE), post-playback 1 (POST1), and post-playback 2 (POST2). For each 5-minute period, we calculated the proportion of instantaneous samples each individual engaged in each activity category and their mean height in the canopy. For further analyses, we grouped behaviors into only three categories: 1) vigilance (VIG), which included resting alert and headwagging, a repeated side to side motion of the head while looking in one direction, 2) other activity (ACT), which included feeding, social behavior, and self-grooming, and resting down, and 3) travel (TR). To examine the sifakas' short-term responses, we used generalized linear models to test effect of site, group within site, and stimulus on differences between POST1 and PRE proportions in each activity category, and difference in mean height. We also examined the effects of site, group within site, and sex/age class of individuals for the same response variables separately for each stimulus. We conducted the same sets of analyses on the differences between POST2 and PRE activity and mean height to examine longer-term responses.

For all analyses, we tested the normality and heteroscedasticity of model residuals. We used arcsine-square root transformation for proportional data and natural log transformation for continuous data when observations were not normally distributed. We reverse-transformed all least square means and 90 % confidence interval endpoints before reporting them in the results.

Results

Predator communities

We made 62 total raptor call observations at 18 of 25 (75%) different stations in RNP, and 28 total observations at 18 of 27 (69%) stations at IFS. The Madagascar buzzard (*Buteo brachypterus*) and the yellow-billed kite (*Milvus aegyptius*) were the most frequently heard species in RNP and IFS, respectively (Table 3). Of the two larger raptor species known to predate lemurs in the region, Henst's goshawk was heard at 11 stations (46%) in RNP, while the Madagascar harrier hawk was observed at 2 stations (8%) in IFS and an active nest was located within the home range of IFS4. While undetected during point counts at RNP, the Madagascar harrier hawk was visually observed and heard calling in the study area during lemur sampling. Likewise, we did not detect Henst's goshawk during point counts at IFS, but field technicians regularly surveying all fragments reported a nest of this species had been destroyed by local residents shortly before the study period (2008) in a northeastern fragment (J. Randianantenaina, personal communication).

Concurrent photographic capture surveys conducted within the same grids from which our raptor and sifaka data were collected indicated that while 3 out of the 5 native carnivores detected in RNP were absent from IFS (Fossa, Malagasy civet, *Fossa fossana,* and small-toothed civet, *Eupleres goudotii*), the introduced wild cat (*Felis silvestris*) and small Indian civet (*Viverricula indica*) were only detected at IFS (Table 4, B. Gerber, unpublished data).

Baseline behavior

We conducted 5-9 all-day follows for two groups of sifaka at RNP and two groups at IFS (Table 1). Due to logistical constraints, observations at RNP and IFS did not overlap and the mean day length (sunrise to sunset) of sampling days was greater at IFS than RNP (Table 1). Mean daily path length (DPL) traveled by sifaka groups was significantly greater at IFS (1148 m, 90% CI: 933 – 1362 m) than at RNP (736 m, 90% CI: 590 – 881 m, $F_{1,20}$=4.7, p=0.04), but did not differ between groups within a site (Fig. 2, $F_{2,20}$=0.71, p=0.50). We found that DPL generally decreased with increasing rainfall ($F_{1,20}$ =1.37, p=0.25), and generally increased with increasing daylength ($F_{1,20}$=0.71, p=0.41), but the trends were not significant.

We found that group spread differed between sites, with all members of RNP1 and RNP2 usually within closer proximity to each other than individuals in the slightly larger groups at IFS (Fig. 3). However, the mean percent of observations that individual sifakas were in close proximity to their nearest neighbor did not differ between IFS and RNP, or among sex/age classes (Table 5). On average, individuals at both sites were within 10 m of at least one other group member 87-92% of observations, and within 2 m of another group member 40-45% of the observations. Sub-adult males were less frequently observed with neighbors in close proximity, but the trend was not significant (Table 5).

We found that sifakas at both sites displayed similar activity budgets (Table 6), allocating most of their time between sleep sites to resting alert and feeding, followed by resting down and self-grooming, and then travel and social behavior. Sifakas at RNP rested down a greater percent of the day than those at IFS. On average, individual sifakas at IFS were out of sight and away from the group more often than those at RNP, but this difference was confounded by differences between groups and among the sex/age classes. Adult males fed less on average than other sex/age classes, and significantly less than adult females; adult males also engaged in less social behavior than juveniles.

We did not find any overall difference in the proportion of time sifakas spent vigilant (looking beyond 0.5 m from their bodies, regardless of activity) between IFS (37.8%) and RNP (37.0%), however, the directionality of the vigilance varied (Table 7). At both sites, the majority of vigilance was directed horizontally, but sifakas at RNP displayed proportionately greater downward vigilance, while sifakas at IFS displayed proportionately greater horizontal and upward vigilance. The mean individual rate of discrete vigilance events (staring or scanning in a single direction with cessation of other activity for ≥ 3 s), was significantly greater at RNP (4.5 events/hr) than at IFS (2.1 events/hr, Table 8). Sifakas at RNP displayed higher mean rates of discrete downward vigilance events, while rates of horizontal and upward vigilance events were similar between sites.

We observed that sifakas at IFS and RNP emitted roaring barks at similar rates, however, sifakas at IFS emitted zzuss calls at a significantly higher rate (Table 9). We observed that females displayed higher rates of zzuss calling than adult males and juveniles, while sub-adult males displayed significantly higher rates than adult males.

Habitat use

We measured habitat characteristics at used rest and sleep locations on 5 all-day follows for each group at IFS and 7 all-day follows for each group at RNP; we sampled 2 random locations within the daily range for each of these observation days. Sample sizes of rest and sleep locations vary as groups did not always use a diurnal rest location, sometimes used more than one rest location, or individuals separated to use more than one nocturnal sleep location. Additionally, on one observation day group RNP1 remained active after dark and we were unable to locate their sleep tree. Sample sizes by type of locations for groups IFS1, IFS5, RNP1, and RNP2, respectively, are as follows: Random n= 10, 10, 14, 14; Rest n=3, 5, 14, 10; Sleep n=5, 6, 10, 11.

Tree-level characteristics such as mean DBH, mean canopy diameter, mean apex height, and % downward slope at the central tree were greater at RNP than IFS (Fig. 4, Table 10). Mean DBH, canopy diameter and apex height were significantly higher within the ranges of RNP1 than those of RNP2, and downward slope was greater at locations within IFS5, than IFS1. These characteristics also differed among location types. All characteristics were greater at sleep locations than at random locations, and canopy diameter and downward slope were also greater at rest locations than at random locations. Overall, the mean DBH of trees at sleep locations was significantly greater than for either random trees or rest trees, however, within RNP the mean DBH of rest trees was similar to that of sleep trees and significantly greater than that of random trees at RNP.

Mean tree density was also higher at RNP than at IFS, driven by the significantly lower mean tree density of locations within the ranges of IFS5, compared to all other groups (Fig. 5, Table 11). Mean basal area of trees was also significantly greater at RNP than IFS (34.1 m^2/ha vs. 15.4 m^2/ha, respectively). Both tree density and basal area did not differ among location types.

Mean percent cover of different canopy heights and vegetation types varied between IFS and RNP, and among rest, sleep, and random sites (Fig. 6). The most extreme difference between study areas was in mean percent cover of high canopy (> 15 m high), which was significantly greater at RNP (57.2%) than at IFS (7.2%, Table 12). Mean percent mid canopy cover, shrub cover, and herbaceous ground cover were also greater at RNP than IFS; however, differences in mid canopy and herbaceous ground cover were driven by significantly higher values only within the ranges of RNP2. Likewise, mean percent cover of low canopy was significantly higher at IFS, due to higher levels only within the ranges of IFS1 compared to all other groups. Mean percent cover of different vegetation types differed among location types, but these differences varied between sites. At RNP, percent low canopy cover and of shrub cover were higher at rest and sleep locations, than at random locations, while these characteristics did not differ among location types at IFS. Mean percent herbaceous ground cover was higher at sleep sites than random sites at IFS, but highest at random sites at RNP (Fig. 6).

During individual focal samples we found that sifakas at both IFS and RNP used the mid-canopy (5.5 – 15 m high) the majority of sampling periods (57.7% and 58.5%, respectively). We found that sifakas at IFS used the low canopy (≤ 5 m high) more frequently than those at RNP, while sifakas at RNP spent a greater percent of samples in high canopy (> 15 m, Table 13).

Although sifakas at neither site spent a great deal of time on the ground, we did document individual sifakas at IFS on the ground during 0.8% (IFS5) to 1.7% (IFS1) of focal observations, while on-ground observations for sifakas at RNP were at least an order of magnitude lower (RNP1: 0.04%, RNP2: 0.05%). We did not observe that sifakas in RNP selectively-used any canopy class (Fig. 7c, 7d). Sifakas within group IFS1 used the low canopy level proportionally greater than its relative availability (Fig. 7a) and sifakas within group IFS5 used the high canopy level proportionately less than its relative availability (Fig. 7b).

Playback experiments

We observed several behavioral responses within the first minute of the experimental playbacks (Table 14). Looking in the direction of the speakers was the most common response, typically occurring within the first seconds of a broadcast call. Other common responses include head-wagging, ascending or descending in the canopy, fleeing or approaching the speakers, and emitting roaring bark and/or zzuss calls. We found that the immediate responses of sifakas varied among groups and stimuli. To the familiar control, the cuckoo roller, few individuals at IFS and no individuals at RNP responded with more than looking towards the speakers, while some individuals at both sites displayed no immediate response. While we found that the unfamiliar control, American robin, evoked diverse responses from 1 - 3 individuals at IFS; only one individual at RNP responded beyond looking towards the speakers. The fossa and raptor calls evoked a greater array of responses from more individuals within each group than did the controls, with considerable intergroup variation. Sifakas at both sites responded most consistently to the Madagascar harrier hawk playback; all individuals responded by looking towards the speakers and/or head-wagging and by emitting roaring bark vocalizations within 1 min of the playback. At least one individual in all IFS groups approached the speaker, while individuals in IFS5 and RNP1 descended in the canopy. In general, individuals at IFS displayed a wider range of immediate responses to control and predator stimuli, including atypical use of aerial alarm calls in response to the vocalization of the mammalian carnivore, fossa. Sifakas at RNP generally responded to playbacks with a limited number of behaviors, and only gave aerial alarm calls in response to raptor stimuli.

The short-term behavioral responses, quantified as the difference in proportion of time engaged in different behaviors during the five minutes after and five minutes before a playback, also varied by stimulus and among sifaka groups (Fig. 8). All groups responded to playback stimuli with mean increases in vigilant behavior and mean decreases in stationary activity, with the exception of RNP2, which displayed slightly decreased vigilance and increased activity after the playback of Henst's goshawk calls (Fig. 8c). Sifakas did not respond consistently with changes in travel after playbacks. Over all the stimuli, sifakas at IFS responded with greater mean increases in vigilance and decreases in activity, however, this difference was driven primarily by group IFS5, which showed the strongest response to every stimulus except the familiar control (Fig. 8, Table 15). Increases in vigilance and decreases in activity were greatest following the playbacks of the Madagascar harrier hawk and the fossa, and lowest after the cuckoo roller. Similarly, sifakas tended to decrease their mean height after playbacks, but the decrease was significantly greater in magnitude after the Madagascar harrier hawk, than after either control or the fossa (Fig. 9, Table 15).

Examination of site, group, and sex/age class on short term playback responses separately for each stimulus yielded similar results (Appendix B). Sifakas at IFS displayed a greater mean increase in vigilance ($F_{1,8}$=6.29, p=0.037) and travel ($F_{1,8}$=4.71, p=0.06), and a greater mean decrease in activity ($F_{1,8}$=8.58, p=0.02) after the playback of Henst's goshawk vocalizations than did sifakas at RNP. Short term responses to other playback stimuli often varied among groups without consistent between site differences. Responses were also fairly consistent among the sex/age classes of the focal individuals, however, adult females increased travel significantly more than adult males or juveniles after the goshawk playbacks ($F_{2,8}$=4.53, p=0.048) and juveniles responded to fossa playbacks with greater increases in vigilance ($F_{2,8}$=4.23, p=0.056) and greater decreases in activity ($F_{2,8}$=4.12, p=0.059) than adult males.

Longer-term behavioral responses to playbacks, described as the difference in proportion of time points engaged in different behaviors during the 6 – 10 minutes after vs. the 5 minutes before a playback, were generally lower in magnitude and less consistent among individuals and groups than short term responses. As in the short term, mean increases in vigilance and decreases in activity were greatest after the Madagascar harrier hawk; 90% confidence intervals for responses to all other stimuli contained zero (Table 16). Group IFS5 continued to show the strongest overall behavioral response to stimuli in the longer term, and displayed a significantly greater increase in vigilance than groups IFS1 and RNP1, which contributed to an observed site level difference. Group RNP1 increased travel in the period 6-10 minutes after playbacks, compared to all other groups. Sifakas continued to use slightly lower heights than in the period before playbacks, but there were no consistent differences among sites, groups or stimuli in mean height difference (Table 16).

Discussion

Variation in the predator community between fragmented rainforest at Ialatsara Forest Station and continuous rainforest at Ranomafana National Park does not appear to be driving major differences in the anti-predator behaviors of Milne-Edwards’ sifakas, but it may be related to more subtle differences in vigilance behavior, canopy height use, and specificity of anti-predator responses of sifakas at each site. While raptor point counts suggest differences in the occurrence and encounter rates of some species, we detected at least one species of large raptor known to predate lemurs at each site (Karpanty & Goodman, 1999; Karpanty, 2006). Further, additional non-point count observations suggest that Madagascar harrier hawks and Henst's goshawks occurred at both sites within the year prior to this study. Our failure to detect Madagascar harrier hawks during point counts at RNP, despite observing them during sifaka behavioral observations, may be related to the species' preference for nesting in disturbed edge habitats (Karpanty, 2003). Similarly, the preference of Henst's goshawk for nesting in intact forest or large fragments with limited human disturbance may explain their scarcity or absence from IFS (Karpanty, 2003). Despite these differences, it appears that there are currently potential aerial predators of sifakas at both sites.

Arguably the most important difference in predator community between IFS and RNP for sifakas is the absence of fossa from IFS, which was confirmed by photographic camera trap surveys concurrent with our study (B. Gerber, unpublished data). The lack of any observed sifaka mortality due to predation during a demographic study of the entire IFS population from 2006 – 2008 (Foltz, 2009), in comparison to 14 confirmed events of fossa predation on sifakas in RNP from 1986-2007 (Irwin et al., 2009), is further evidence of the absence of fossa from this site. Although it is unknown how long the fossa has been absent from IFS, local ecological knowledge surveys conducted in villages between RNP and IFS suggest that this species does not frequently travel long distances outside of the continuous forest, and the most recent observation of fossa reported by interviewees living on the periphery of IFS was estimated to be 25 years ago (M. Kotschwar, unpublished data). Although Milne-Edwards' sifakas can live > 27 yrs in the wild (King et al., 2005), it is possible that the sifakas we observed at IFS, which were all estimated to be < 15 years old based on dentition (Foltz, 2009), may have had very little to no direct experience with fossa, a predator that constitutes the top source of mortality among sifakas at RNP (Pochron et al., 2004). As many aspects of sifaka behavior evolved under predation pressure from fossa, relaxed predation pressure could result in behavioral changes to reduce fitness costs of non-functional, or non-essential traits. However, the invasive carnivore species we found at IFS, especially dogs and wild cats, are known to kill and harass large diurnal lemurs in other areas of Madagascar (Brockman et al., 2008) and thus may constitute real or perceived predation risk for Milne-Edwards' sifakas at IFS.

Behavioral changes relating to the altered predator community at IFS were not evident in the activity budgets of sifakas at that site, which were very similar to those at RNP, and congruent with levels of feeding, resting and traveling observed in a previous, longer-running study of Milne-Edwards' sifakas in pristine and disturbed areas of RNP (Arrigo-Nelson, 2006). We did not observe a decrease in time allotted to resting alert that corresponded with increases in other fitness-increasing behaviors such as feeding, grooming, or social behavior, such as has been observed in other prey species after loss of an important predator (Blumstein & Daniel, 2005). Seasonal differences, related to fruit abundance and distribution, rather than site level differences in predator community or habitat, may explain the significantly higher levels of resting down, and reduced ranging (shorter mean DPL) by groups at RNP, compared to groups at IFS (Balko, 1998; Arrigo-Nelson, 2006).

We observed no difference in overall percent of time sifakas were vigilant at both sites, but sifakas at IFS and RNP differed in where they looked and with what intensity, in ways that were consistent with differences in their predator communities. When vigilant, sifakas at RNP looked down a greater percent of time, and they displayed significantly higher rates of staring and scanning, especially in the downward and horizontal directions. These discrete vigilance events, which were directed in a single direction and prevented any other activity for at least 3 s, may be indicative of a more intense level of vigilance than simply looking around while resting or feeding. Such intensity may be required to detect a stealth predator, such as the fossa, which likely approaches from lower levels of the canopy where light intensity is decreased (Wright, 1998). At IFS, where the top ground predator is absent, but raptors occur and intergroup encounters are more frequent (M. Kotschwar, unpublished data), sifakas devoted a greater percentage of their vigilance looking in the horizontal and upward directions, and displayed low rates of upward scanning and staring. It is possible that sifakas at both sites have adapted their vigilance behavior to the perceived risks in their respective habitats.

Although differences in vigilance behavior suggest that sifakas at IFS and RNP may perceive different risks, rates of alarm calling indicate that they may perceive some risks at similar frequencies. The specificity and meaning of vocalizations vary widely among primate taxa (Macedonia, 1990; Seyfarth & Cheney, 2003; Zuberbuhler, 2003), however, context specificity is often greater for aerial alarm calls, than terrestrial alarm calls (Seyfarth et al., 1980; Fichtel & Kappeler, 2002). Evidence from playback experiments and observations of raptor encounters indicates that eastern sifakas, including Milne-Edwards' sifakas, use roaring barks as a relatively specific alarm call in response to aerial threats (Patel et al., 2003; Karpanty & Wright, 2007). Although roaring bark calls are occasionally directed towards large, non-predatory birds or falling limbs, the similar rates of aerial alarm calling displayed by sifakas at IFS and RNP may be indicative of similar levels of perceived aerial predation risk between sites, i.e. the frequency of encounters in which sifakas perceive an aerial threat. Sifakas at IFS displayed significantly higher mean rates of zzuss calling than conspecifics at RNP, but the difference cannot be as easily related to differences in predation risk, as eastern sifakas use the zzuss call in a number of different contexts, including terrestrial disturbances such as ground predators, but also general situations of high arousal and social contexts (Wright, 1998; Patel et al., 2003). The significant differences in zzuss calling among the sex/age classes may reflect the social use of the call, rather than differences in perceived risk.

In addition to risk perception, primates may adjust their anti-predator strategies to different habitat structures (Enstam, 2007). Compared to the undisturbed, intact rainforest of RNP, the fragment we studied at IFS was composed of significantly smaller trees, resulting in a lower and less continuous canopy. Constrained by available canopy height, sifakas at IFS spent a much higher percentage of time in low canopy than sifakas at RNP, as expected. While sifakas at RNP appeared to use canopy height classes in proportion to their availability, sifakas at IFS showed preference for low canopy and avoidance of available high canopy. High canopy in IFS typically constitutes the apices of the tallest trees, where branches may be thinner and sifakas more exposed to the elements and to aerial predators, whereas sifakas using high canopy at RNP often had up to several meters of canopy above them. Simply avoiding exposed high canopy does not explain the increased percentage of time that sifakas at IFS played, rested, or traveled on the ground. During our study, sifakas in RNP1 and RNP2 occasionally descended to the ground to feed on dirt (i.e. geophagy), but traveled exclusively in the trees and were rarely observed on the ground during focal samples. This is consistent with the finding that sifakas living in fragments in the eastern periphery of RNP, where fossa were reported to move through, rarely traveled on the ground between fragments (Dehgan, 2003). Although captured only a small percent of time in our study, sifakas at IFS regularly travel on the ground between fragments, and even immigrate from fragments outside of the reserve (Foltz, 2009). This behavior, hypothesized to be the result of relaxed predation pressure, currently promotes gene flow within the IFS population, but could result in greater mortality by recolonizing fossa or introduced terrestrial predators (Foltz, 2009).

The differences in habitat structure between IFS and RNP were also evident in characteristics of diurnal rest and nocturnal sleep locations. We observed significant site differences (though some driven by group within site effects) for every habitat characteristic we measured, which indicate the IFS fragment was generally composed of fewer and smaller trees, with less vegetative cover except at the low canopy level. Despite these general differences, sifakas at IFS and RNP displayed overall similar selection patterns, sleeping in significantly taller trees with greater DBH, and greater canopy diameter, located on steeper slopes (which often increased the height of the sifakas above actual ground) than random trees. Sifakas at RNP also selected diurnal rest trees that were significantly larger than random, while less selection for rest trees was apparent at IFS. Macrohabitat characteristics were similar at used and random sites, however, sifakas at RNP rested and slept at locations with greater percent low canopy and shrub cover, and slept at locations with lower percent herbaceous ground cover than random locations. Increased vegetative cover between the ground and higher canopy may make it harder for a ground predator to detect resting/sleeping groups of sifakas, while lower ground cover may decrease the predator's ability to approach undetected. In contrast, sifakas at IFS displayed little selection for most macrohabitat characteristics, and slept at locations with greater percent herbaceous ground cover than random.

Although we observed subtle differences in directional and discrete vigilance, height use, and habitat selection of sifakas between sites, our experimental playbacks provide little evidence of lost or weakened anti-predator responses at IFS. In our study, Milne-Edwards' sifakas at IFS generally responded to all stimuli with a greater variety and intensity of immediate responses, and greater short term changes in vigilance and activity levels. At RNP, no individuals immediately approached the speakers after a playback, individuals only emitted aerial alarm calls after the playbacks of aerial predators, and they displayed almost no immediate response to either the familiar or unfamiliar control. In contrast, multiple sifakas at IFS approached the speakers after both raptor playbacks, used aerial alarm calls after raptor and fossa playbacks, and displayed a much stronger response, including both aerial and general alarm calls, to the unfamiliar control. The wider range of responses to most stimuli, and use of aerial alarm calls in response to fossa vocalizations, suggest that sifakas at IFS may lack specificity in their repertoire of anti-predator responses, and may be hypersensitive to predator and novel stimuli. However, further research is necessary to determine whether these differences would decrease their ability to avoid fossa predation. Predator recognition through visual cues is typically less experience-based than recognition of acoustic cues (Blumstein, 2006) and tests with predator models may provide a stronger indication of the sifakas' discriminative abilities and predation avoidance strategies (Schel & Zuberbuhler, 2009).

The effects of predator absence on prey behavior vary among taxa, among anti-predator adaptations, and along different time-scales. Generally, hard-wired traits that have developed over evolutionary time will persist longer than relatively experience-dependent or learned traits, and anti-predator adaptations with relatively high fitness costs will respond more quickly than low cost traits to relaxed selection after the loss of a predator (Blumstein, 2006). Further, anti-predator strategies with interrelated mechanisms, or components that serve other functions, will be more likely maintained by the presence of other predators or their use in other functions, when one predator is removed (Blumstein, 2006). These factors help explain the persistence of anti-predator traits in some species after the loss of historically important predators (Blumstein et al., 2009; Schel & Zuberbuhler, 2009), and the loss of traits after both evolutionary isolation from predators (Yorzinski & Ziegler, 2007; Orrock, 2010) and historically recent predator loss (Bshary, 2001; Gil-da-Costa et al., 2003).

As may be expected, the relatively recent isolation of IFS from the intact eastern rainforest and extirpation of fossa from IFS within the last 30 years did not result in the loss of anti-predator behaviors or a complete break-down in their use in fragment-living Milne-Edwards' sifakas. Individuals at both sites, exposed to potential aerial predators, and either known or potential ground predators, used alarm calls at similar frequencies and in similar contexts, and displayed similar levels of activity and general vigilance. Furthermore, sifakas at both sites displayed mean increases in vigilance and decreases in activity in response to playbacks of vocalizations of potential predators and used lower canopy heights after raptor playbacks. The more diverse and intense immediate responses of IFS sifakas to playback stimuli suggest possible hypersensitivity and a decreased specificity in anti-predator responses in the absence of the species' top predator, fossa (Berger et al., 2001b; Fichtel & van Schaik, 2006). Additionally, whether due to habitat constraints, relaxed predation pressure, and/or other factors, sifakas at IFS displayed greater use of low canopy heights, increased time resting and traveling on the ground, and less downward and discrete vigilance than sifakas at RNP. Rapid reacquisition of lost or weakened anti-predator responses has been observed in several prey species once a predator has returned (Berger et al., 2001b; Gil-da-Costa et al., 2003). The full repertoire of anti-predator responses displayed by sifakas at IFS combined with their continuous experience with potential raptor and novel terrestrial predators, suggest a high potential to rapidly learn appropriate responses to returning fossa. However, the often intense, temporallyspaced, and indiscriminate predation of lemurs of all sex/age classes by fossa may reduce opportunities for learning, especially in isolated fragment-living lemur populations (Berger et al., 2001b; Irwin et al., 2009). Future research is necessary to determine whether the habitat constraints and behavioral differences of Milne-Edwards' sifakas we observed at IFS would increase their risk of predation by fossa if the species recolonized. Predation risk of returning predators to small, isolated prey populations, and the potential need for predator training or 'probing' approaches using acoustic and visual cues, should be considered in the creation and expansion of protected areas in Madagascar (Griffin et al., 2000; Griffin et al., 2001; Gil-da-Costa et al., 2003).

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Figures & Tables

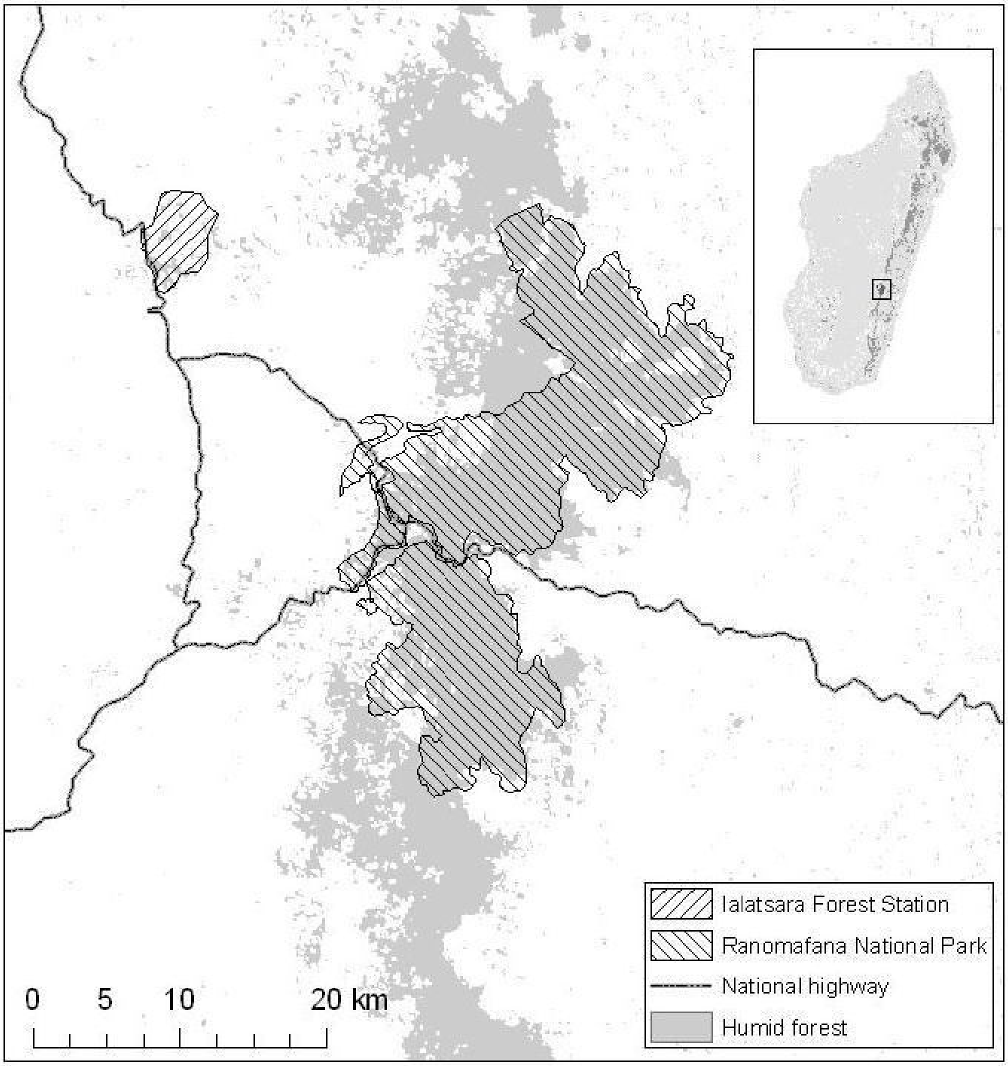


Figure 1. Locations of protected rainforest fragments (Ialatsara Forest Station) and protected continuous rainforest (Ranomafana National Park) in southeastern Madagascar (see inset for general region), in which we investigated the predator community and anti-predator behavior of Milne-Edwards' sifakas (*Propithecus edwardsi*).

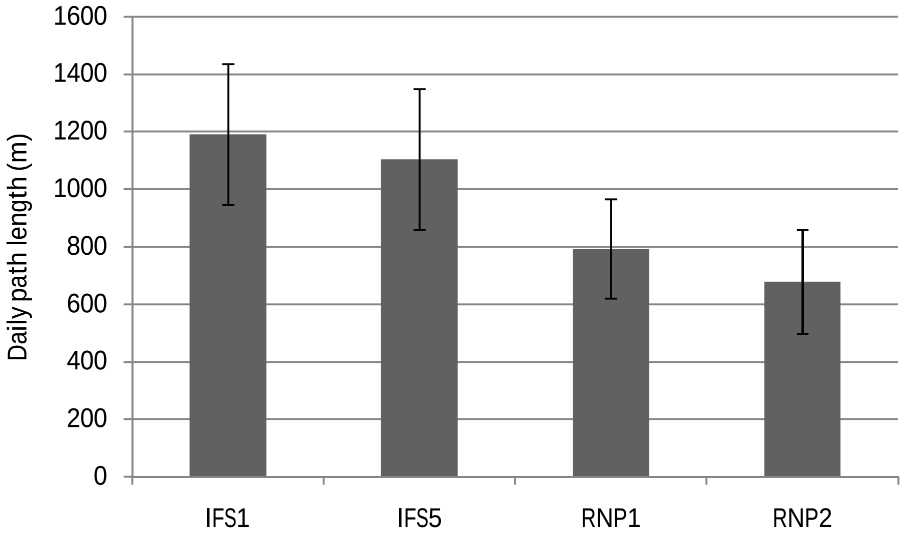
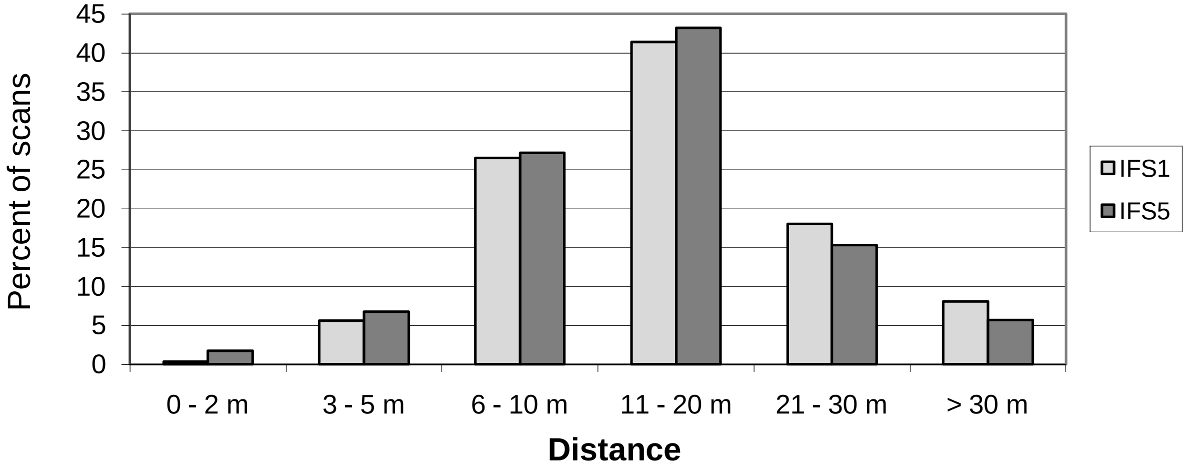


Figure 2. Daily path lengths of groups of Milne-Edwards' sifakas within fragmented rainforest (IFS1 & IFS5) and intact rainforest (RNP1 & RNP2) in southeastern Madagascar. Values represent least square means with 90% confidence intervals estimated with site, group within site, rainfall, and daylength as fixed effects.

(a) IFS



(b) RNP

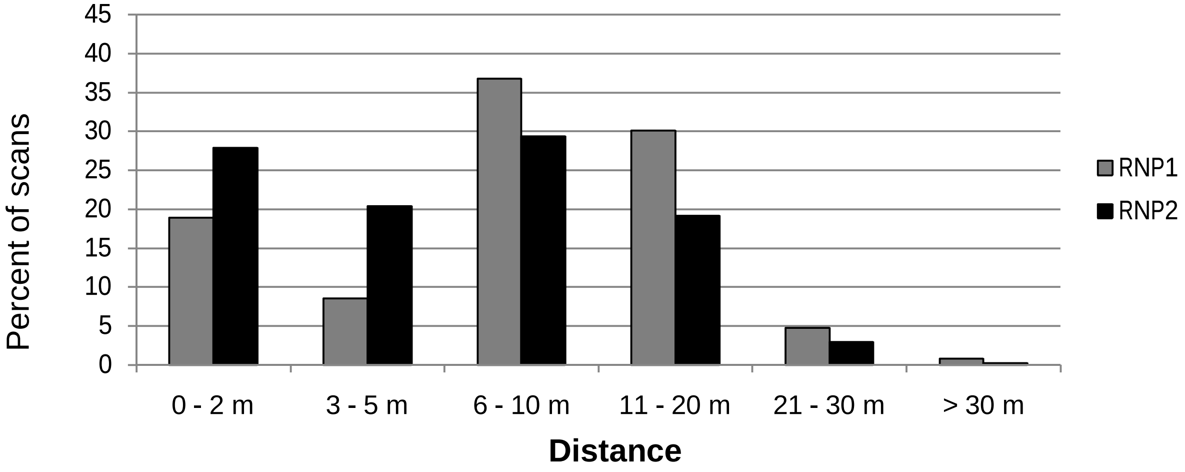


Figure 3. Group spread of Milne-Edwards' sifakas at a fragmented rainforest site (IFS) and a continuous rainforest site (RNP) in southeastern Madagascar. Values represent the percent of instantaneous scans in which all group members were observed within different categories of spread (distance between the two group members farthest apart).

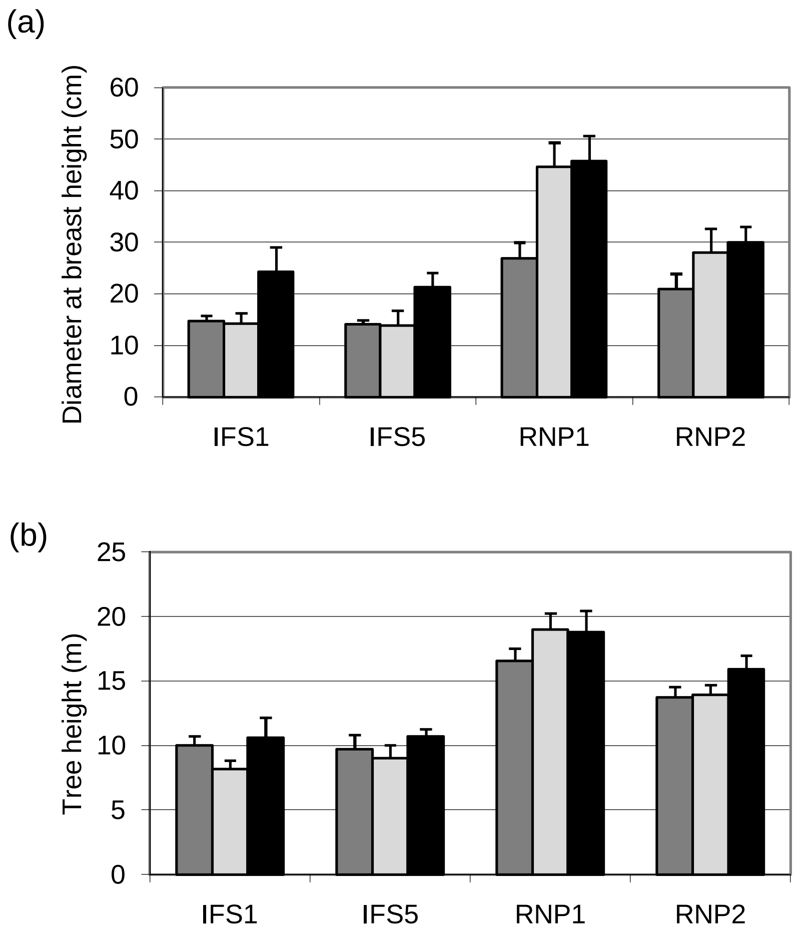


Figure 4. Characteristics of trees used as diurnal rest locations (Rest) and nocturnal sleep locations (Sleep), and central trees at random locations (Random) within the day ranges of Milne-Edwards' sifakas in fragmented rainforest (IFS1 & IFS5) and continuous rainforest (RNP1 and RNP2) in southeastern Madagascar. Values are means (displayed with error bars of ± 1 SE) of characteristics at locations used during all-day follows of sifaka groups, or random locations generated within minimum polygon convexes of those day ranges. (Continued on next page)

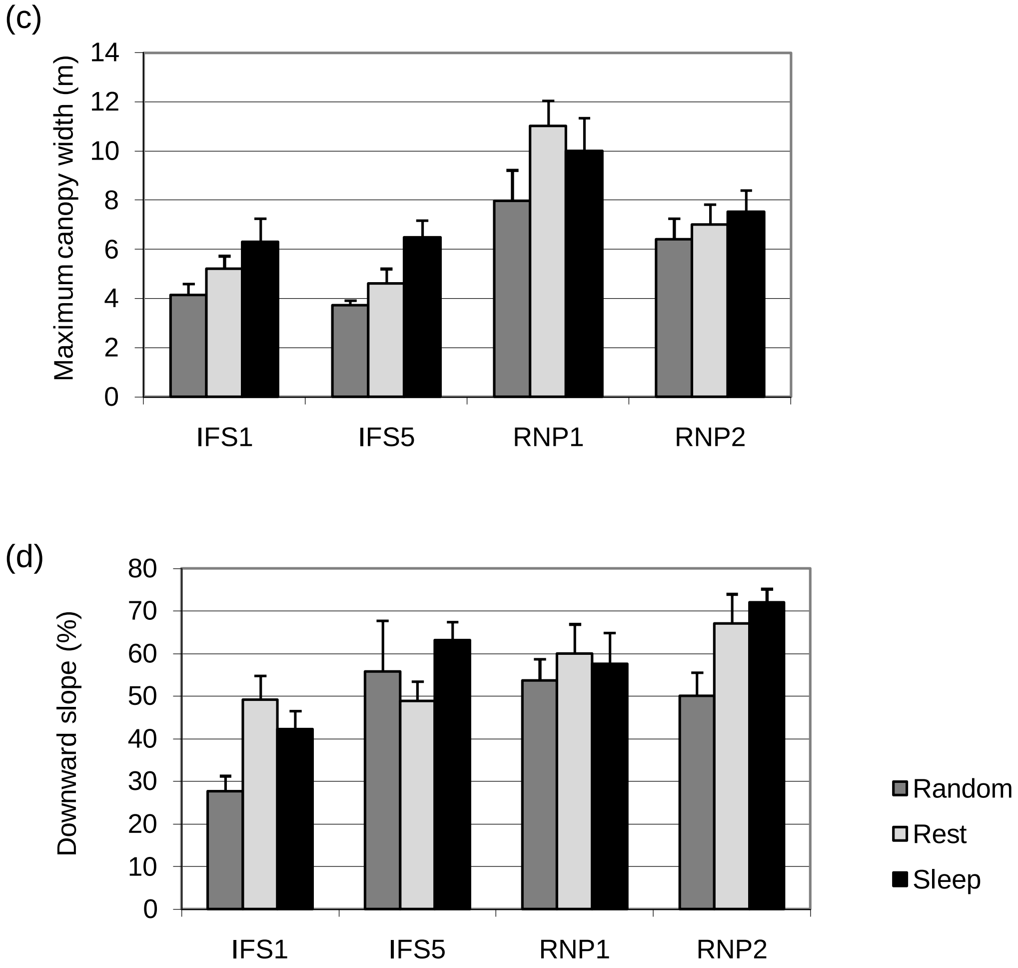
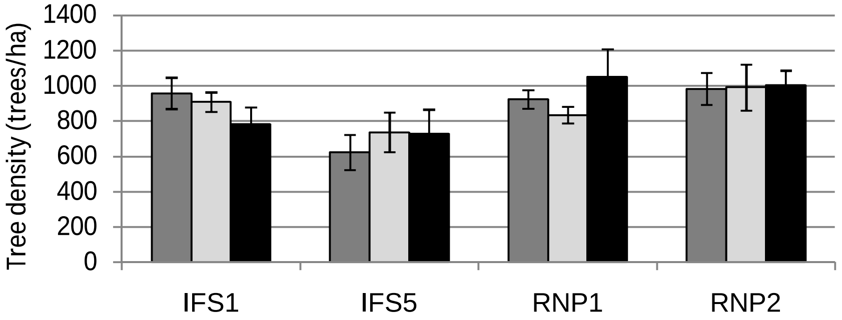


Figure 4. Continued

(a) Tree density



(b) Basal area

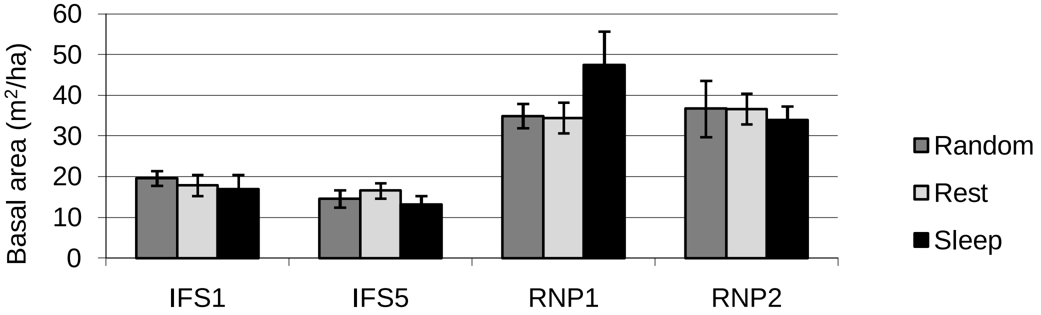
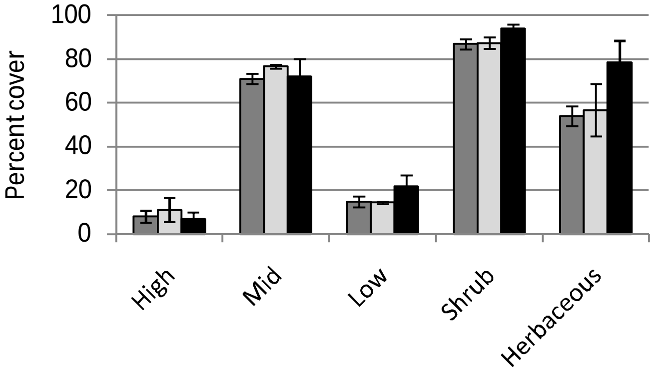


Figure 5. Mean density and basal area of trees ≥10 cm diameter at breast height at diurnal rest locations (Rest) and nocturnal sleep locations (Sleep), and central trees at random locations (Random) within the day ranges of Milne-Edwards' sifakas in fragmented rainforest (IFS1 & IFS5) and continuous rainforest (RNP1 and RNP2) in southeastern Madagascar. Values are means (displayed with error bars of ± 1 SE) of characteristics at sites used during all-day follows of sifaka groups, or random sites generated within minimum polygon convexes of those day ranges.

a. IFS1



b. IFS5

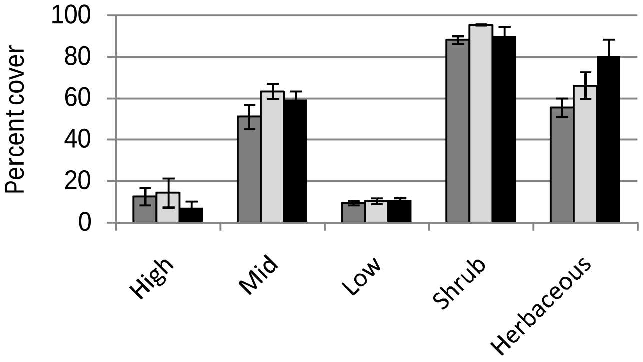
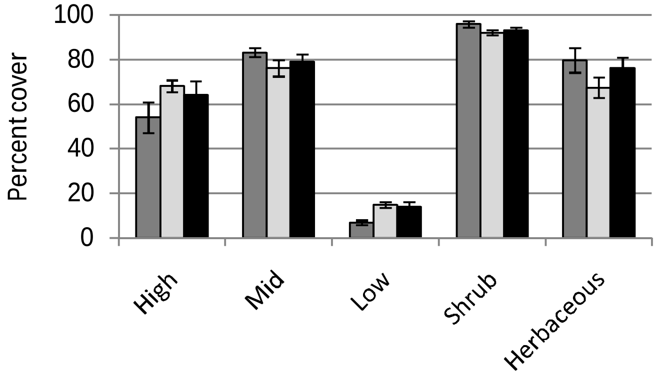


Figure 6. Mean percent cover of different vegetation types at diurnal rest locations (Rest) and nocturnal sleep locations (Sleep), and central trees at random locations (Random) within the day ranges of Milne-Edwards' sifakas in fragmented rainforest (IFS1 & IFS5) and continuous rainforest (RNP1 and RNP2) in southeastern Madagascar. Values represent mean % cover (± 1 SE) of high canopy (>15 m), mid canopy (5.5 – 15 m), and low canopy (≤ 5 m) of trees with ±10 cm dbh, shrubs (≤ 5 m high, < 10 cm dbh), and herbaceous ground cover (<0.5 m high) at sites used during all-day follows of sifaka groups, or random sites generated within minimum polygon convexes of those day ranges. (Continued on next page)

c. RNP1



(d) RNP2

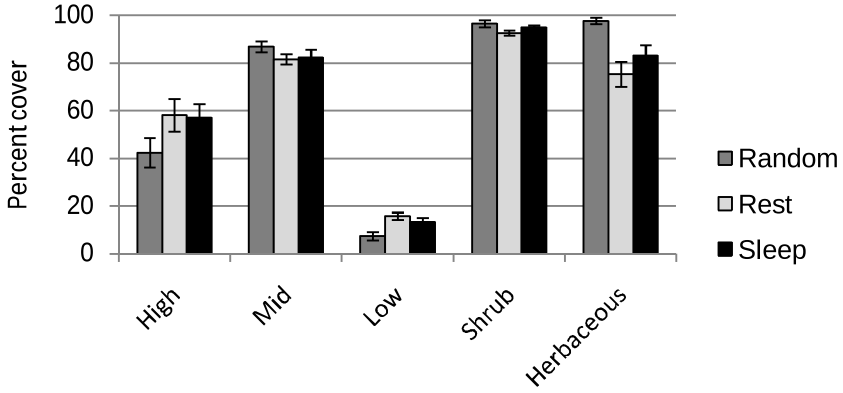
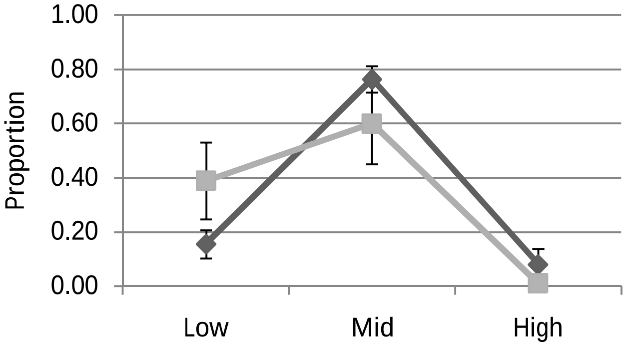
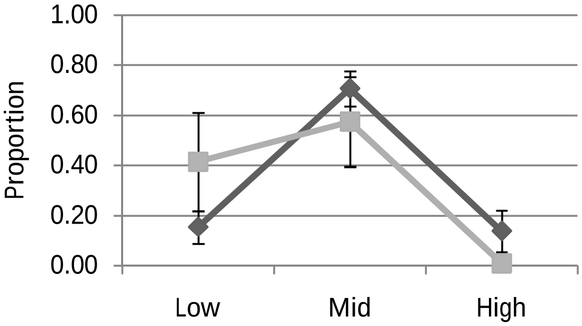


Figure 6. Continued

(a) IFS1



(b) IFS5



(c) RNP1

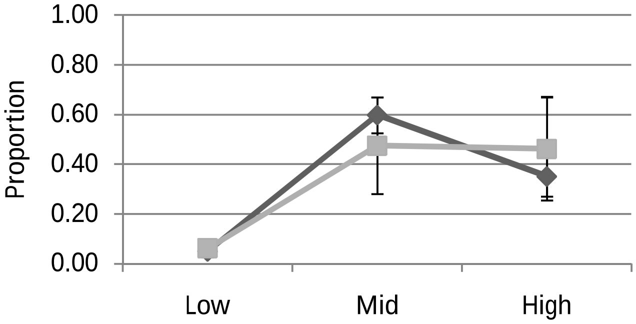


Figure 7. Proportional use vs. relative availability of low (≤ 5 m), mid (5.5 – 15 m), and high (> 15 m) canopy heights by groups of Milne-Edwards' sifakas at a fragmented forest site (IFS1, IFS5) and a continuous forest site (RNP1, RNP2). Error bars represent 95% confidence intervals. (Continued on next page).

(d) RNP2

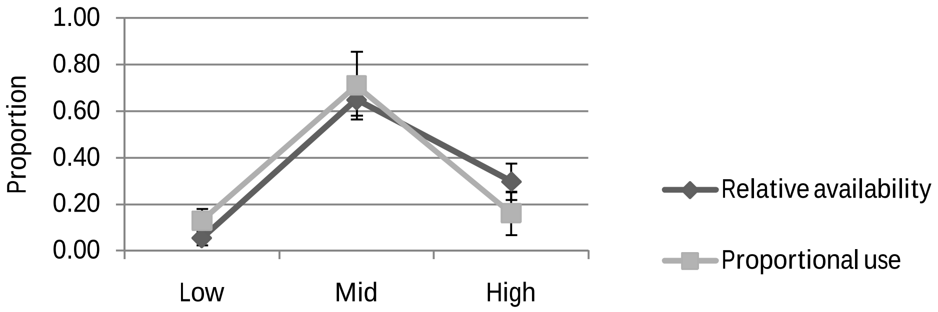
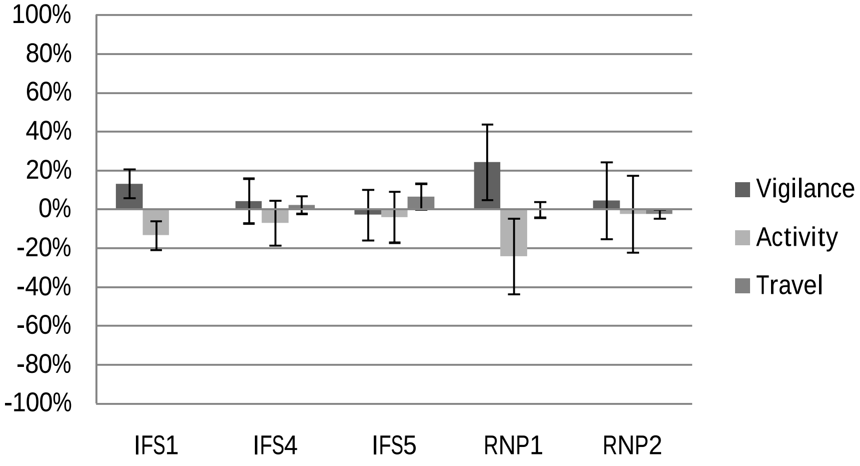


Figure 7. Continued

(a) Cuckoo roller, *Leptosomus discolor*



(b) American robin, *Turdus migratorius*

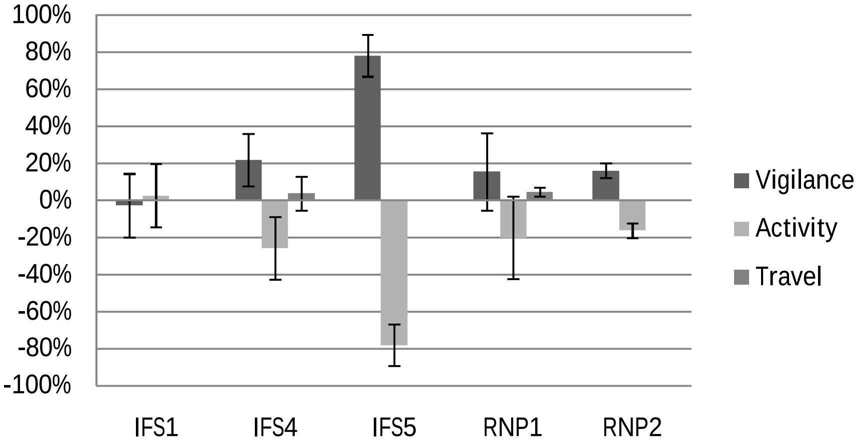
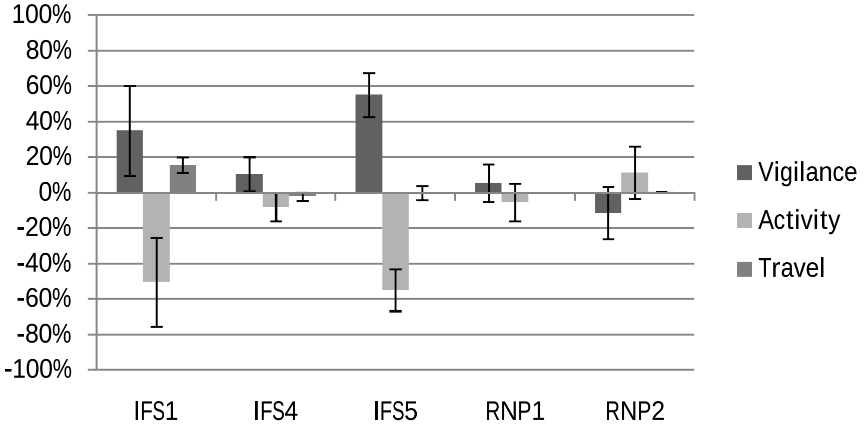
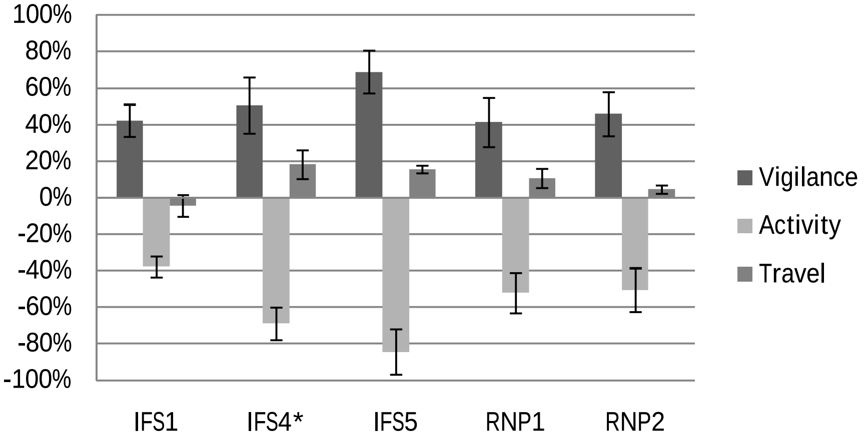


Figure 8. Responses of Milne-Edwards' sifakas in fragmented rainforest (IFS1, IFS4, & IFS5) and continuous forest (RNP1 & RNP2) to experimental playbacks. Values represent the mean difference (± 1 SE) in percent of time individuals (n=3/group) engaged in each behavior during the 5 minutes after the playback and the 5 minutes before the playback, so that bars extending above or below the x-axis signify a mean increase or mean decrease, respectively, in a certain behavior after the playback. Stimuli include two control calls, a familiar non-predatory bird (a) and an unfamiliar non-predatory bird (b), two potential raptor predators (c, d), and a confirmed mammalian carnivore predator (e). * Measures for IFS4 after the *P. radiatus* stimulus were not included in further analysis as an actual hawk began calling during the experiment and might have heightened the group's behavioral response. (Continued on next page)


(c) Henst's goshawk, *Accipiter henstii*


(d) Madagascar harrier hawk, *Polyboroides radiatus*

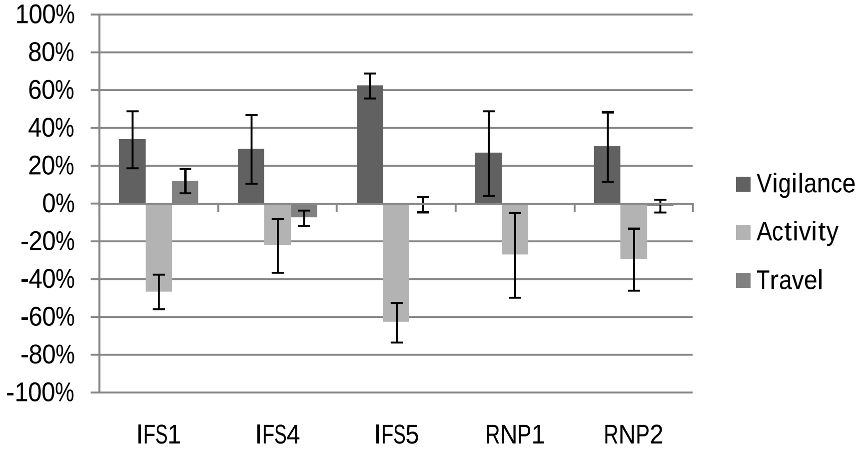
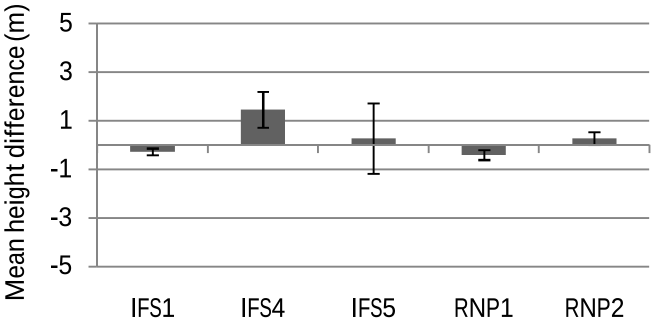
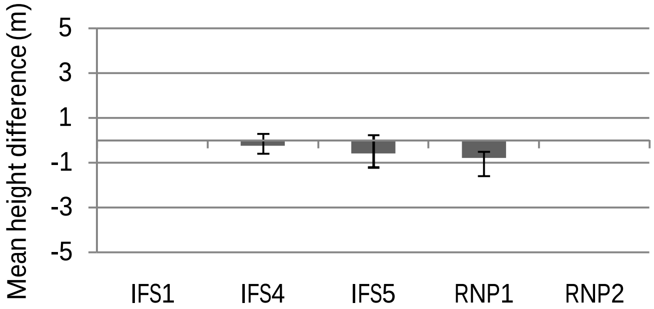

(e) Fossa, *Cryptoprocta ferox*

Figure 8. Continued

(a) Cuckoo roller, *Leptosomus discolor*



(b) American robin, *Turdus migratorius*



(c) Henst's goshawk, *Accipiter henstii*

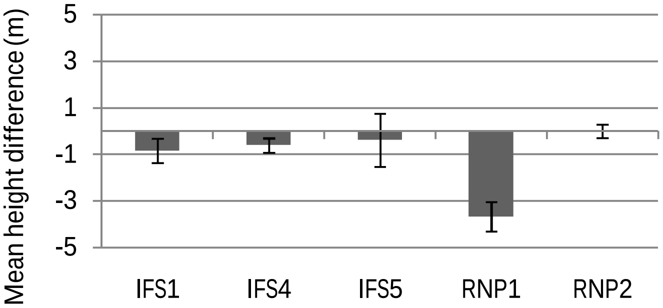
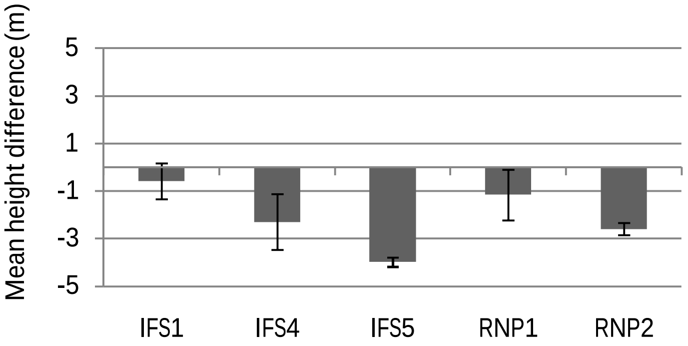
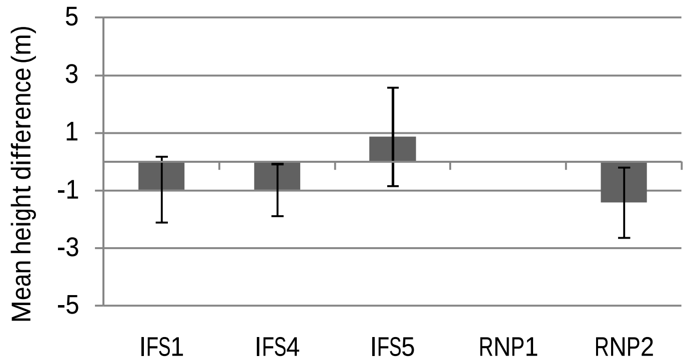


Figure 9. Changes in height use of Milne-Edwards' sifakas in fragmented rainforest (IFS1, IFS4, & IFS5) and continuous forest (RNP1 & RNP2) to experimental playbacks. Values represent the mean difference (± 1SE) in mean height of individuals (n=3/group) engaged in each behavior during the 5 minutes after the playback vs. the 5 minutes before the playback, so that bars extending above or below the x-axis signify a mean increase or mean decrease in height, respectively after the playback. Stimuli include two control calls, a familiar non-predatory bird (a) and an unfamiliar non-predatory bird (b), two potential raptor predators (c, d), and a confirmed mammalian carnivore predator (e). * Measures for IFS4 after the *P. radiatus* stimulus were not included in further analysis as an actual hawk began calling during the experiment and might have heightened the group's behavioral response. (Continued on next page)



(d) Madagascar harrier hawk, *Polyboroides radiatus*



(e) Fossa, *Cryptoprocta ferox*

Figure 9. Continued

Table 1. Group composition and sampling dates of groups of Milne-Edwards' sifakas in a continuous forest site (RNP1 & RNP2) and a fragmented forest site (IFS1, IFS5 & IFS4) in southeastern Madagascar.

Group[a]	Group composition[b]	# focal individuals[c]	Sampling dates (in 2008)	Mean day length[d] (hh:mm)	Focal sampling days[e]	Group scan days[f]	Mean # focal samples/individual
RNP1	1 F, 1 M, 1 JF, 1 IN	3	Jul. 30 - Oct. 08	10:48	5	9	49.5
RNP2	1 F, 1 M, 1 JM	3	Aug. 06 - Oct. 02	11:10	5	7	45
IFS1	1 F, 1 M, 1 JF, 1 SM	4	Oct. 21 - Dec. 03	13:17	5	5	46.3
IFS5	1 F, 1 M, 1 JM, 2 SM, 1 IN	4	Oct. 23 - Dec. 06	12:54	5	5	43.3
IFS4[e]	2 F, 1 M, 2 JF, 2 SM	3	Nov. 12 - Dec. 10				

[a] Group names include identification numbers used in previous studies (RNP groups Valohoaka 1 and 2, Arrigo-Nelson, 2006; IFS groups 1, 5 and 4, Foltz, 2009)

[b] F=adult female, M=adult male, JF=juvenile female, JM=juvenile male, SM=sub-adult male, IN=infant

[c] # individuals sampled for behavior using focal techniques in each group

[d] Length of sampling during all day follows; longer day lengths at IFS reflect increased daylight hours in which sifakas were active

[e] # days on which focal sampling and/or group scans were conducted

[f] IFS4 included in experimental playbacks, but not baseline behavioral observation days

Table 2. Behavioral categories used in instantaneous focal individual sampling and group scans

Category	Definition
Behaviors	
Feeding	Acquisition, manipulation and ingestion of food items
Traveling	Leaping, climbing, and repositioning in the canopy or on the ground.
Self-grooming	Inspection and oral or manual manipulation of the individual's own fur.
Social	Inspection and oral or manual manipulation of another individual's fur; also includes play
Resting alert	Individual stationary and looking at surroundings, unengaged in other activity
Resting down	Individual stationary with eyes closed or head down against body; includes sleeping
Out of sight	Observer cannot see the individual or determine its activity at the time point
Other	All other behaviors not included in a the previous categories; includes calling and scent-marking
Vocalizations	
Roaring barks	High amplitude, open-mouthed vocalizations usually given in response to aerial disturbances
Zzuss calls	Staccato, sneeze-like vocalization given in response to terrestrial disturbance, situations of high arousal, and in response to howls from other group members (Wright 1998, Patel, 2003)

Table 3. Detected raptor species in fragmented (Ialatsara Forest Station) and continuous (Ranomafana National Park) rainforest sites in southeastern Madagascar. Mean number of detected individuals (± 1 SE) are based on point counts, conducted 4 times at each of 26 (IFS) and 24 (RNP) points October – November 2008. As visual detection probability was assumed to differ between sites due to differences in forest structure, mean number of individuals detected by calls only are displayed separately.

		Ialatsara		Ranomafana	
Species		Calls or visuals	Calls only	Calls or visuals	Calls only
Henst's goshawk	*Accipiter henstii*	Undetected[a]	Undetected[a]	0.29±0.11	0.27±0.10
Madagascar buzzard	*Buteo brachypterus*	0.17±0.05	0.10±0.03	0.40±0.09	0.38±0.08
Madagascar kestrel	*Falco newtoni*	0.07±0.03	Undetected	Undetected	Undetected
Banded kestrel	*Falco zoniventris*	0.02±0.01	Undetected	Undetected	Undetected
Yellow-billed kite	*Milvus aegyptius*	0.96±0.20	0.15±0.03	Undetected	Undetected
Madagascar harrier hawk	*Polyboroides radiatus*	0.04±0.02	0.02±0.01	Undetected[b]	Undetected[b]

[a] Henst’s goshawk was not detected during point counts at IFS, but a nest of this species was reported to have been destroyed in a fragment in 2008.

[b] Madagascar harrier hawk was not detected during point counts at RNP, but visually observed and heard calling during observations of sifaka groups.

Table 4. Mammalian carnivore species present within undisturbed, intact rainforest at Ranomafana National Park (RNP) and a fragmented forest site at Ialatsara Forest Station (IFS) in southeastern Madagascar. Presence or absence of species during the study period (RNP: July – Oct. 2008, IFS: Oct. – Dec. 2008) was confirmed in a 2008 photographic capture survey conducted by B. Gerber (unpublished data).

Species		Ialatsara	Ranomafana
Fossa	*Cryptoprocta ferox*	Absent	Present
Ring-tailed mongoose	*Galidia elegans*	Present	Present
Broad-striped mongoose	*Galidictis fasciata*	Present	Present
Malagasy civet	*Fossa fossana*	Absent	Present
Small-toothed civet	*Eupleres goudotii*	Absent	Present
Indian civet	*Viverricula indica*	Present	Absent
Domestic dog	*Canis familiaris*	Present	Present
Wild cat	*Felis silvestris*	Present	Absent

Table 5. Effects of site, group, and sex/age class on the nearest neighbor distances of Milne-Edwards' sifakas at a fragmented rainforest site (IFS) and an intact rainforest site (RNP) in southeastern Madagascar. Values for each effect level are model-based least square means (90% CI) of the percent of observations that individual sifakas were within 2m, 5m, or 10 m of the nearest group member.

Effect	Within 2 m	Within 5 m	Within 10 m
Site			
IFS	43.5 (39.1 - 47.9)	64.8 (59.8 - 69.6)	87.9 (81.9 - 92.8)
RNP	44.7 (39.0 - 50.5)	67.9 (61.6 - 73.9)	91.6 (84.6 - 96.6)
$F_{1,7}$ [a]	0.11	0.55	0.7
P-value	0.75	0.48	0.43
Group[b]			
IFS1	33.2 (27.4 - 39.2) A	62.2 (55.1 - 69.1)	85.1 (75.8 - 92.5)
IFS5	54.0 (47.7 - 60.2) C	67.3 (60.3 - 73.9)	90.4 (82.4 - 96.2)
RNP1	39.0 (31.7 - 46.7) AB	65.2 (56.5 - 73.4)	90.3 (80.2 - 97.1)
RNP2	50.5 (42.8 - 58.1) BC	70.6 (62.2 - 78.3)	92.7 (83.5 - 98.4)
$F_{2,7}$ [a]	12.37	0.9	0.52
P-value	**0.005**	0.45	0.62
Sex/age class[c]			
F	42.6 (36.4 - 48.8)	71.0 (64.2 - 77.3)	90.9 (83.0 - 96.5)
M	45.1 (38.8 - 51.3)	63.0 (55.9 - 69.9)	88.3 (79.7 - 94.8)
J	52.6 (46.3 - 58.8)	70.4 (63.6 - 76.8)	94.9 (88.4 - 98.8)
SM	36.3 (27.4 - 45.8)	60.8 (49.8 - 71.3)	83.6 (68.3 - 94.5)
$F_{3,7}$ [a]	2.91	1.51	1.11
P-value	0.11	0.29	0.41

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male, SM=sub-adult male

Table 6. Effects of site, group, and sex/age class on the allocation of time in activities by Milne-Edwards' sifakas within fragmented rainforest (IFS) and continuous rainforest (RNP) in southeastern Madagascar. Values for each effect level are model-based least square means (90% CI) of percent of focal samples individuals engaged in different behaviors.

Effect	Feeding	Resting alert	Resting down	Self-grooming	Social behavior	Traveling	Out of sight
Site							
IFS	31.1 (29.6 - 32.6)	31.1 (29.1 - 33.1)	8.9 (8.0 - 9.9)	8.8 (7.7 - 10.0)	5.3 (4.0 - 6.7)	9.1 (8.0 - 10.3)	4.4 (3.3 - 5.6)
RNP	30.6 (28.6 - 32.6)	31.0 (28.4 - 33.6)	12.6 (11.2 - 14.2)	10.2 (8.6 - 11.8)	4.5 (3.0 - 6.4)	7.9 (6.5 - 9.3)	2.3 (1.3 - 3.6)
$F_{1,8}$[a]	0.12	0	14.68	1.64	0.39	1.47	4.93
P-value	0.74	0.96	**0.005**	0.24	0.55	0.26	**0.06**
Group[b]							
IFS1	31.5 (29.3 - 33.7) AB	32.9 (30.0 - 35.9)	8.5 (7.1 - 10.0)	9.2 (7.5 - 11.0)	5.4 (3.5 - 7.6)	8.1 (6.5 - 9.8)	3.2 (1.8 - 4.8) B
IFS5	30.6 (28.6 - 32.7) AB	29.2 (26.6 - 31.9)	9.3 (8.0 - 10.7)	8.4 (6.9 - 10.0)	5.2 (3.5 - 7.2)	10.2 (8.6 - 11.9)	5.8 (4.1 - 7.8) B
RNP1	28.0 (25.5 - 30.6) A	32.7 (29.2 - 36.3)	13.6 (11.5 - 15.7)	9.1 (7.1 - 11.3)	4.1 (2.2 - 6.5)	8.1 (6.3 - 10.2)	4.9 (2.9 - 7.3) B
RNP2	33.3 (30.6 - 36.0) B	29.3 (25.9 - 32.8)	11.8 (9.8 - 13.8)	11.3 (9.1 - 13.6)	5.0 (2.9 - 7.6)	7.6 (5.8 - 9.6)	0.7 (0.1 - 1.8) A
$F_{2,8}$[a]	3.81	2.46	1.06	1.12	0.14	1.56	9.24
P-value	**0.07**	0.15	0.39	0.37	0.87	0.27	**0.008**
Sex/age class[bc]							
F	33.1 (30.9 - 35.4) B	32.2 (29.3 - 35.1)	11.3 (9.7 - 12.9)	8.7 (7.1 - 10.4)	3.8 (2.3 - 5.7) AB	7.8 (6.2 - 9.4)	1.7 (0.8 - 3.0) A
M	27.7 (25.5 - 29.8) A	34.1 (31.2 - 37.1)	10.7 (9.2 - 12.4)	11.7 (9.8 - 13.6)	2.8 (1.5 - 4.4) B	8.8 (7.2 - 10.5)	3.7 (2.3 - 5.5) AB
J	32.0 (29.8 - 34.3) AB	29.6 (26.8 - 32.6)	9.8 (8.4 - 11.4)	8.6 (7.0 - 10.3)	6.6 (4.5 - 9.0) A	10.0 (8.3 - 11.9)	2.6 (1.4 - 4.1) AB
SM	30.6 (27.8 - 33.6) AB	28.3 (24.6 - 32.0)	11.0 (9.0 - 13.1)	9.1 (6.9 - 11.4)	7.2 (4.4 - 10.5) AB	7.4 (5.5 - 9.6)	5.7 (3.4 - 8.6) B
$F_{3,8}$[a]	3.99	2.3	0.53	2.26	3.63	1.43	3.21
P-value	**0.05**	0.15	0.67	0.16	**0.06**	0.30	**0.08**

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male, SM=sub-adult male

Table 7. Effects of site, group, and sex/age class on the general vigilance levels of Milne-Edwards' sifakas within fragmented rainforest (IFS) and continuous rainforest (RNP) in southeastern Madagascar. Values for each effect level are model-based least square means (90% CI) of percent of focal samples sifakas looked > 0.5 m from themselves in any direction, and percent of time vigilant spent looking in downward, horizontal, and upward directions.

Effect	Any vigilance	Downward	Horizontal	Upward
Site				
IFS	37.0 (34.0 - 40.1)	19.4 (17.5 - 21.4)	69.7 (67.5 - 71.8)	10.7 (9.0 - 12.5)
RNP	37.8 (33.9 - 41.7)	38.2 (35.2 - 41.3)	56.2 (53.2 - 59.1)	5.2 (3.7 - 6.9)
$F_{1,7}$[a]	0.08	98.02	48.91	17.8
P-value	0.79	**<0.0001**	**0.0002**	**0.004**
Group[b]				
IFS1	36.9 (32.6 - 41.2)	17.5 (14.9 - 20.2)	71.7 (68.7 - 74.7)	10.5 (8.2 - 13.1)
IFS5	37.2 (32.9 - 41.5)	21.4 (18.6 - 24.3)	67.7 (64.5 - 70.7)	10.9 (8.5 - 13.5)
RNP1	35.7 (30.6 - 41.0)	36.9 (32.8 - 41.1)	57.7 (53.6 - 61.6)	5.0 (3.1 - 7.4)
RNP2	39.8 (34.5 - 45.2)	39.5 (35.4 - 43.7)	54.7 (50.6 - 68.3)	5.3 (3.4 - 7.9)
$F_{2,7}$[a]	0.6	2.24	2.18	0.04
P-value	0.57	0.18	0.18	0.96
Sex/age class[bc]				
F	37.0 (32.8 - 41.4)	28.0 (24.9 - 31.1)	64.0 (60.8 - 67.1) AB	7.1 (5.1 - 9.2)
M	42.2 (37.8 - 46.6)	24.6 (21.7 - 27.7)	67.7 (64.5 - 70.7) B	7.2 (5.3 - 9.5)
J	35.8 (31.5 - 40.1)	31.6 (28.4 - 34.9)	61.5 (58.2 - 64.7) AB	6.4 (4.5 - 8.5)
SM	34.7 (28.4 - 41.3)	29.3 (24.6 - 34.3)	59.0 (54.0 - 63.9) A	10.5 (7.0 - 14.5)
$F_{3,7}$[a]	1.78	3.03	3.6	1.28
P-value	0.24	0.10	**0.07**	0.35

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male, SM=sub-adult male

Table 8. Effects of site, group, and sex/age class on the rates of discrete vigilance events (scanning or staring) displayed by Milne-Edwards' sifakas within fragmented rainforest (IFS) and continuous rainforest (RNP) in southeastern Madagascar. Values for each effect level are model-based least square means (90% CI) of mean hourly rates that individual sifakas scanned or stared in one direction and ceased other activities for at least 3 s, calculated from focal samples.

	Discrete vigilance events/hour			
Effect	Total	Downward	Horizontal	Upward
Site				
IFS	2.1 (1.1 - 3.0)	0.3 (-0.2 - 0.8)	1.4 (0.9 - 1.9)	0.3 (0.2 - 0.5)
RNP	4.5 (3.3 - 5.7)	2.0 (1.4 - 2.6)	2.0 (1.4 - 2.7)	0.4 (0.2 - 0.6)
$F_{1,7}$[a]	9.2	16.15	2.36	0.59
P-value	**0.02**	**0.005**	0.17	0.47
Group[b]				
IFS1	2.4 (1.1 - 3.7)	0.2 (-0.5 - 0.9)	1.4 (0.7 - 2.1)	0.7 (0.5 - 1.0) B
IFS5	1.8 (0.5 - 3.1)	0.4 (-0.3 - 1.1)	1.3 (0.6 - 2.1)	0.0 (-0.1 - 0.2) A
RNP1	4.6 (3.0 - 6.2)	2.2 (1.34 - 3.1)	1.9 (1.0 - 2.7)	0.5 (0.2 - 0.8) B
RNP2	4.4 (2.8 - 6.0)	1.8 (0.9 - 2.7)	2.2 (1.3 - 3.1)	0.3 (0.1 - 0.6) AB
$F_{2,7}$[a]	0.2	0.35	0.17	12
P-value	0.82	0.71	0.85	**0.006**
Sex/age class[c]				
F	3.8 (2.5 - 5.1)	1.6 (0.9 - 2.3)	1.8 (1.1 - 2.6)	0.3 (0.1 - 0.5)
M	3.2 (1.9 - 4.5)	0.8 (0.1 - 1.5)	2.2 (1.5 - 2.9)	0.3 (0.1 - 0.5)
J	2.6 (1.2 - 3.9)	1.0 (0.3 - 1.7)	1.3 (0.6 - 2.0)	0.2 (0.1 - 0.4)
SM	3.6 (1.6 - 5.6)	1.2 (0.1 - 2.2)	1.5 (0.4 - 2.6)	0.7 (0.3 - 1.1)
$F_{3,7}$[a]	0.57	0.96	0.89	1.75
P-value	0.65	0.46	0.49	0.24

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male, SM=sub-adult male

Table 9. Effects of site, group, and sex/age class on the mean alarm calling rates of Milne-Edwards' sifakas within fragmented rainforest (IFS) and continuous rainforest (RNP) in southeastern Madagascar. Values for different effect levels are model-based least square means of individual calling rates calculated from focal samples.

Effect	Roaring barks (calls/hr)	Zzuss calls (calls/hr)
Site		
IFS	0.24 (0.08 - 0.41)	0.96 (0.71 - 1.24)
RNP	0.15 (-0.03 - 0.37)	0.51 (0.27 - 0.80)
$F_{1,7}$[a]	0.4	4.99
P-value	0.55	**0.06**
Group		
IFS1	0.37 (0.14 - 0.66)	1.15 (0.78 - 1.60)
IFS5	0.12 (-0.07 - 0.35)	0.79 (0.48 - 1.17)
RNP1	0.21 (-0.04 - 0.52)	0.53 (0.21 - 0.93)
RNP2	0.10 (-0.13 - 0.38)	0.50 (0.19 - 0.90)
$F_{2,7}$[a]	1.27	0.82
P-value	0.34	0.48
Sex/age class[bc]		
F	0.22 (0.01 - 0.47)	1.73 (1.26 - 2.30) C
M	0.09 (-0.10 - 0.31)	0.11 (-0.08 - 0.35) A
J	0.24 (0.03 - 0.50)	0.38 (0.14 - 0.67) AB
SM	0.24 (-0.07 - 0.65)	1.11 (0.58 - 1.82) BC
$F_{3,7}$[a]	0.39	15.41
P-value	0.77	**0.002**

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male, SM=sub-adult male

Table 10. Effects of site, group, and location type on characteristics of diurnal rest trees, nocturnal sleep trees, and central trees of random locations within the daily ranges of Milne-Edwards' sifakas within fragmented rainforest (IFS) and continuous rainforest (RNP) in southeastern Madagascar. Values for each effect level are model-based least square means (90% CI).

Effect	DBH (cm)	Canopy diameter (m)	Apex height (m)	Downward slope (%)
Site				
IFS	15.9 (14.4 - 17.6)	4.8 (4.3 - 5.4)	9.5 (8.9 - 10.1)	47.3 (41.6 - 53.0)
RNP	30.8 (30.8 - 1.1)	8.0 (7.3 - 8.8)	16.2 (15.3 - 17.2)	60.9 (55.7 - 66.0)
$F_{1,86}$[a]	63.93	33.05	100.86	8.58
P-value	**<0.0001**	**<0.0001**	**<0.0001**	**0.004**
Group[b]				
IFS1	16.6 (14.3 - 19.3) A	5.0 (4.3 - 5.8) AB	9.5 (8.7 - 10.5) A	37.7 (29.2 - 46.1) A
IFS5	15.2 (13.3 - 17.3) A	4.7 (4.1 - 5.4) A	9.4 (8.6 - 10.2) A	56.9 (49.5 - 64.3) B
RNP1	39.7 (34.9 - 45.1) C	9.9 (8.6 - 11.3) C	18.4 (16.9 - 20.0) C	58.1 (50.8 - 65.4) B
RNP2	23.9 (21.1 - 27.1) B	6.5 (5.7 - 7.4) B	14.3 (13.2 - 15.5) B	63.6 (56.6 - 70.6) B
$F_{3,86}$[a]	11.89	7.19	6.96	4.64
P-value	**<0.0001**	**0.001**	**0.002**	**0.01**
Location type[b]				
Random	17.7 (16.1 - 19.4) A	4.9 (4.4 - 5.4) A	11.8 (11.1 - 12.6) A	46.2 (40.9 - 51.5) A
Rest	21.1 (18.6 - 24.0) A	6.5 (5.7 - 7.5) B	11.8 (10.9 - 12.8) A	57.6 (50.3 - 64.9) B
Sleep	29.0 (25.4 - 33.1) B	7.5 (6.6 - 8.7) B	13.6 (12.4 - 14.8) B	58.5 (51.3 - 65.6) B
$F_{2,86}$[a]	13.03	9.94	2.69	3.56
P-value	**<0.0001**	**0.0001**	**0.07**	**0.03**
Site * Type				
$F_{2,86}$[a]	3.1	0.047	1.02	0.67
P-value	**0.05**	0.63	0.37	0.51

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

Table 11. Effects of site, group, and location type on mean density and basal area of trees ≥ 10 cm DBH at diurnal rest, nocturnal sleep, and random locations within the daily ranges of Milne-Edwards' sifakas within fragmented rainforest (IFS) and continuous rainforest (RNP) in southeastern Madagascar. Values for each effect level are model-based least square means (%90 CI).

Effect	Tree density (trees/ha)	Basal Area (m^2/ha)
Site		
IFS	737.5 (659.8 - 824.3)	15.4 (13.6 - 17.4)
RNP	906.3 (840.1 - 977.8)	34.1 (31.4 - 37.0)
$F_{1,104}$[a]	6.45	81.58
P-value	**0.01**	**<0.0001**
Group[b]		
IFS1	890.1 (758.5 - 1044.5) B	17.9 (15.0 - 21.3) A
IFS5	611.1 (529.2 - 705.7) A	13.2 (11.3 - 15.5) A
RNP1	885.4 (797.1 - 983.5) B	35.4 (31.6 - 39.7) B
RNP2	927.8 (831.7 - 1034.9) B	32.7 (29.1 - 36.9) B
$F_{2,104}$[a]	4.65	2.77
P-value	**0.01**	**0.07**
Location type		
Random	803.7 (731.4 - 883.1)	22.3 (20.2 - 24.7)
Rest	832.3 (729.2 - 949.8)	23.9 (20.7 - 27.6)
Sleep	817.0 (724.7 - 921.0)	22.5 (19.8 - 25.6)
$F_{2,104}$[a]	0.07	0.22
P-value	0.94	0.81
Site * Type		
$F_{2,104}$[a]	0.76	1.19
P-value	0.47	0.31

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

Table 12. Percent cover of different canopy heights and vegetation types at diurnal rest locations, nocturnal sleep locations, and random locations within the daily ranges of Milne-Edwards' sifakas within fragmented rainforest (IFS) and continuous rainforest (RNP) in southeastern Madagascar. Values for each effect level are model-based least square means (%90 CI).

Effect	Low (≤ 5 m)	Mid (5.5 - 15 m)	High (> 15 m)	Shrub	Herbaceous
Site					
IFS	13.0 (11.2 - 14.9)	66.3 (62.7 - 69.8)	7.2 (4.3 - 10.7)	91.6 (89.9 - 93.2)	67.9 (62.4 - 73.2)
RNP	10.9 (9.7 - 12.1)	82.6 (80.6 - 84.5)	57.2 (52.9 - 61.4)	95.3 (94.4 - 96.1)	83.8 (80.8 - 86.6)
$F_{1,104}$[a]	2.76	46.92	163.16	12.14	19.8
P-value	**0.0995**	**<0.0001**	**<0.0001**	**0.0007**	**<0.0001**
Group[b]					
IFS1	16.2 (13.4 - 19.3) B	74.5 (69.6 - 79.1) B	5.9 (2.4 - 10.8) A	90.9 (88.3 - 93.2)	66.6 (58.6 - 74.2) A
IFS5	10.1 (8.1 - 12.4) A	57.6 (52.8 - 62.4) A	8.6 (4.6 - 13.7) A	92.2 (90.1 - 94.2)	69.2 (62.1 - 75.9) A
RNP1	11.0 (9.4 - 12.7) A	80.4 (77.5 - 83.2) B	62.5 (56.7 - 68.2) B	94.8 (93.5 - 96.0)	77.0 (72.2 - 81.4) A
RNP2	10.7 (9.1 - 12.5) A	84.6 (81.9 - 87.2) C	51.8 (45.6 - 57.9) B	95.7 (94.5 - 96.8)	89.6 (85.9 - 92.8) B
$F_{2,104}$[a]	4.37	10.54	2.49	0.63	6.67
P-value	**0.02**	**<0.0001**	**0.09**	0.54	**0.002**
Location type[b]					
Random	8.4 (7.1 - 9.7) A	74.7 (71.8 - 77.4)	24.2 (19.8 - 28.9) A	94.0 (92.7 - 95.1)	77.2 (73.0 - 81.2) AB
Rest	13.7 (11.5 - 16.0) B	75.4 (71.4 - 79.1)	33.6 (26.7 - 40.8) A	92.8 (90.9 - 94.5)	68.3 (61.7 - 74.5) A
Sleep	14.2 (12.2 - 16.3) B	74.7 (71.0 - 78.1)	28.2 (22.3 - 34.5) A	93.9 (92.2 - 95.3)	82.7 (77.8 - 87.1) B
$F_{2,104}$[a]	10.79	0.04	2.49	0.42	4.65
P-value	**<0.0001**	0.97	**0.09**	0.66	**0.01**
Site * Type					
$F_{2,104}$[a]	4.56	4.17	2.09	10.13	15.94
P-value	**0.013**	**0.02**	0.13	**<0.0001**	**<0.0001**

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

Table 13. Effects of site and sex/age class on the percent use of different canopy height classes by Milne-Edwards' sifakas within fragmented rainforest (IFS) and continuous rainforest (RNP) in southeastern Madagascar. Values for each effect level are model-based least square means (%90 CI).

Effect	Low (≤ 5 m)	Mid (5.5 - 15 m)	High (> 15 m)
Site			
IFS	41.4 (38.1 - 44.7)	57.7 (52.8 - 62.6)	0.5 (0.2 - 1.1)
RNP	10.0 (7.5 - 12.8)	58.5 (52.2 - 64.7)	29.1 (25.5 - 33.0)
$F_{1,7}$[a]	1.66	0.03	325.99
P-value	**<0.0001**	0.86	**<0.0001**
Group[b]			
IFS1	40.1 (35.4 - 44.8) C	59.1 (52.2 - 65.9) AB	0.4 (0.0 - 1.2) C
IFS5	42.7 (38.0 - 47.5) C	56.3 (49.3 - 63.2) AB	0.7 (0.2 - 1.7) C
RNP1	6.8 (4.1 - 10.0) A	46.4 (38.0 - 55.0) B	45.3 (39.9 - 50.8) A
RNP2	13.7 (9.9 - 18.0) B	70.1 (62.0 - 77.6) A	15.3 (11.6 - 19.5) B
$F_{2,7}$[a]	4.22	8.25	37.60
P-value	**0.06**	**0.01**	**0.0002**
Sex/age class[bc]			
F	20.3 (16.6 - 24.3)	58.5 (51.5 - 65.3)	14.1 (11.1 - 17.4) B
M	24.2 (20.2 - 28.4)	59.0 (52.0 - 65.8)	11.1 (8.4 - 14.1) AB
J	23.9 (20.0 - 28.1)	60.2 (53.2 - 66.9)	7.0 (4.9 - 9.5) A
SM	27.2 (20.9 - 33.9)	54.8 (44.1 - 65.3)	8.4 (5.0 - 12.7) AB
$F_{3,7}$[a]	1.2	0.22	4.34
P-value	0.3769	0.8804	**0.05**

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male, SM=sub-adult male

Table 14. Immediate responses of Milne-Edwards' sifaka groups in fragmented rainforest (IFS) and intact rainforest (RNP) in southeastern Madagascar to experimental playbacks. Values represent number of focal individuals in each group (n=3) displaying characteristic behavioral responses within 1 minute of broadcast stimulus calls.

Stimulus	IFS1	IFS4	IFS5	RNP1	RNP2
Familiar control Cuckoo roller *Leptosomus discolor*	3 look	1 look	1 look 1 headwag	2 look	1 look
Unfamiliar control American Robin *Turdus migratorius*	3 look 1 approach	2 look 2 descend 1 zzuss call	3 look 3 headwag 1 descend 3 roaring bark	3 look 1 descend	3 look
Henst's goshawk *Accipiter henstii*	3 look 3 headwag 3 approach 3 roaring bark	3 look 1 ascend	3 look 2 headwag 2 approach 3 roaring bark	3 look 2 headwag 1 ascend 3 descend 3 roaring bark	3 look
Madagascar harrier hawk *Polyboroides radiatus*	3 look 3 headwag 1 approach 3 roaring bark	3 look 3 headwag 1 flee 1 approach 3 roaring bark	3 look 2 headwag 3 descend 2 approach 3 roaring bark	2 headwag 2 descend 1 flee 3 roaring bark	3 look 3 headwag 3 roaring bark
Fossa *Cryptoprocta ferox*	3 look 3 headwag 1 flee 3 roaring bark	3 look 1 headwag 2 descend 1 flee	3 look 1 ascend	1 look	2 look 1 descend 2 flee

Table 15. Effects of site, group, and stimulus on the short term behavioral responses of Milne-Edwards' sifakas in a fragmented rainforest site (IFS) and an intact rainforest site (RNP) to experimental playbacks. Values for each effect level are model-based least square means (%90 CI) of differences in percent of sample individuals engaged in vigilance-related behaviors (resting alert or headwagging), stationary activity (feeding, grooming, or social behavior), and travel, and their mean height in the canopy, during the 5 minutes after vs. the 5 minutes before broadcast of playback stimuli.

Effect	Vigilance (%)	Activity (%)	Travel (%)	Mean height (m)
Site				
IFS	32.8 (25.7 - 39.9)	-35.8 (-42.9 - -28.8)	3.0 (0.9 - 5.1)	-0.6 (-1.0 - -0.2)
RNP	19.9 (11.7 - 28.1)	-21.6 (-29.8 - -13.4)	1.7 (-0.8 - 4.1)	-1.0 (-1.4 - -0.5)
$F_{1,63}$[a]	3.93	4.84	0.51	1.25
P-value	**0.05**	**0.03**	0.48	0.27
Group[b]				
IFS1	24.4 (12.7 - 36.0) A	-29.1 (-40.7 - -17.4) A	4.7 (1.2 - 8.1)	-0.5 (-1.2 - 0.1)
IFS4	21.6 (8.3 - 35.0) A	-21.7 (-35.0 - -8.3) A	0.0 (-3.9 - 4.0)	-0.4 (-1.2 - 0.3)
IFS5	52.4 (40.8 - 64.1) B	-56.8 (-68.4 - -45.2) B	4.4 (0.9 - 7.8)	-0.8 (-1.4 - -0.1)
RNP1	22.7 (11.1 - 34.4) A	-25.7 (-37.4 - -14.1) A	3.0 (-0.4 - 6.5)	-1.2 (-1.9 - -0.5)
RNP2	17.1 (5.5 - 28.8) A	-17.4 (-29.0 - -5.8) A	0.3 (-3.2 - 3.7)	-0.7 (-1.4 - -0.1)
$F_{3,63}$[a]	3.87	4.61	1.16	0.35
P-value	**0.01**	**0.01**	0.33	0.79
Stimulus[bc]				
Cuckoo roller	7.5 (-4.2 - 19.2) A	-8.9 (-20.3 - 3.0) A	1.2 (-2.9 - 4.1)	0.2 (-0.4 - 0.9) A
American robin	24.5 (12.8 - 36.2) AB	-26.1 (-37.8 - -14.4) AB	1.5 (-1.9 - 5.0)	-0.4 (-1.0 - 0.3) A
Henst's goshawk	17.6 (5.9 - 29.3) AC	-20.1 (-31.8 - -8.5) AC	2.5 (-1.0 - 6.0)	-1.1 (-1.8 - -0.5) AB
Madagascar harrier hawk	46.8 (33.5 - 60.1) B	-52.7 (-65.9 - -39.4) B	5.9 (1.9 - 9.8)	-2.0 (-2.8 - -1.3) B
Fossa	35.4 (23.7 - 47.1) BC	-36.0 (-47.6 - -24.3) BC	0.6 (-2.9 - 4.1)	-0.5 (-1.2 - 0.1) AB
$F_{4,63}$[a]	4.26	4.98	0.83	4.1
P-value	**0.004**	**0.002**	0.51	**0.01**

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] Scientific names: Cuckoo roller, *Leptosomus discolor*; American robin, *Turdus migratorius*; Henst's goshawk, *Accipiter henstii*; Madagascar harrier hawk, *Polyboroides radiatus*; fossa, *Cryptoprocta ferox*.

Table 16. Effects of site, group, and stimulus on the longer-term behavioral responses of Milne-Edwards' sifakas in a fragmented rainforest site (IFS) and an intact rainforest site (RNP) to experimental playbacks. Values for each effect level are model-based least square means (90% CI) of differences in percent of sample individuals engaged in vigilance-related behaviors (resting alert or headwagging), stationary activity (feeding, grooming, or social behavior), and travel, and their mean height, during the 6 - 10 minutes after vs. the 5 minutes before broadcast of playback stimuli.

Effect	Vigilance (%)	Activity (%)	Travel (%)	Mean height (m)
Site				
IFS	15.0 (5.4 - 24.6)	-16.7 (-26.1 - -7.3)	1.7 (-1.3 - 4.8)	-0.6 (-1.0 - -0.2)
RNP	-1.1 (-12.3 - 10.1)	-6.9 (-17.9 - 4.0)	8.1 (4.6 - 11.6)	-1.0 (-1.4 - -0.5)
$F_{1,63}$[a]	3.33	1.28	5.22	0.81
P-value	**0.07**	0.26	**0.03**	0.37
Group[b]				
IFS1	-4.9 (-20.8 - 10.9) A	5.8 (-9.7 - 21.4) A	-0.9 (-5.8 - 4.1) A	-0.5 (-1.2 - 0.1)
IFS4	13.4 (-4.7 - 31.5) AB	-17.4 (-35.1 - 0.4) AB	4.0 (-1.7 - 9.6) A	-0.4 (-1.2 - 0.3)
IFS5	36.5 (20.7 - 52.3) B	-38.7 (-54.2 - -23.1) B	2.2 (-2.8 - 7.1) A	-0.8 (-1.4 - -0.1)
RNP1	-6.1 (-21.9 - 9.7) A	-9.4 (-24.9 - 6.2) AB	15.5 (10.5 - 20.4) B	-1.2 (-1.9 - -0.5)
RNP2	3.8 (-12.0 - 19.7) AB	-4.5 (-20.0 - 11.0) A	0.7 (-4.3 - 5.6) A	-0.7 (-1.4 - -0.1)
$F_{3,63}$[a]	3.38	3.86	4.53	0.32
P-value	**0.02**	**0.01**	**0.01**	0.40
Stimulus[b,c]				
Cuckoo roller	2.3 (-13.6 - 18.2)	-8.2 (-23.8 - 7.4) AB	5.9 (0.9 - 10.9) AB	0.2 (-0.4 - 0.9)
American robin	3.6 (-12.2 - 19.5)	-4.2 (-19.8 - 11.4) A	0.6 (-4.4 - 5.5) A	-0.4 (-1.0 - 0.3)
Henst's goshawk	-10.0 (-25.9 - 5.9)	8.1 (-7.5 - 23.6) A	2.0 (-3.0 - 6.9) A	-1.1 (-1.8 - -0.5)
Madagascar harrier hawk	25.7 (7.7 - 43.7)	-41.1 (-58.8 - -23.4) B	15.4 (9.7 - 21.0) B	-2.0 (-2.8 - -1.3)
Fossa	13.0 (-2.8 - 28.9)	-13.7 (-29.3 - 1.8) AB	0.7 (-4.3 - 5.7) A	-0.5 (-1.2 - 0.1)
$F_{4,63}$[a]	1.73	3.22	3.64	0.32
P-value	0.15	**0.02**	**0.01**	0.86

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] Scientific names: Cuckoo roller, *Leptosomus discolor*; American robin, *Turdus migratorius*; Henst's goshawk, *Accipiter henstii*; Madagascar harrier hawk, *Polyboroides radiatus*; fossa, *Cryptoprocta ferox.*

Chapter Three:

Using local ecological knowledge to investigate carnivore distribution and movements across a human-dominated landscape in southeastern Madagascar.

Abstract In light of continuing loss and fragmentation of natural forests in Madagascar, it is critical to understand how species persist in and use human-dominated landscapes. We investigated local ecological knowledge of carnivore species using semi-structured interviews in communities 0 – 20 km from the western edge of intact rainforest in southeastern Madagascar. Responses from 182 interviews in 17 different communities indicated distinct distributional patterns for two endemic and two introduced species of carnivores, which suggest a range of tolerances to the anthropogenic landscape. Similar to findings of photographic capture surveys conducted in the same region, the largest endemic carnivore, fossa (*Cryptoprocta ferox*), appeared sensitive to anthropogenic disturbance, and had only been observed in communities ≤ 2.5 km from the continuous forest within the last five years. In contrast, the ring-tailed mongoose (*Galidia elegans*) was found in and around more human-dominated habitats. Both the introduced small Indian civet (*Viverricula indica*) and wild cats (*Felis silvestris*) were ubiquitous throughout the study region and displayed an affinity to human-dominated habitats. The killing of carnivores, although reported by only a minority of interviewees, was motivated primarily by prevention of/retaliation for poultry depredation, but also for bushmeat, and may be an important mortality risk for species living or moving outside of the continuous forest. This local ecological knowledge study provided useful information on carnivore distribution and human-carnivore conflict across a large area of human land-use, such as is needed for multitaxanomic conservation planning in increasingly fragmented landscapes.

Keywords carnivores, forest fragmentation, local ecological knowledge, Madagascar, predation, rainforest

Introduction

Mammalian carnivores are known to significantly influence ecosystem structure and function (Terborgh et al., 2001; Roemer et al., 2009). Their populations may be especially vulnerable to landscape change due to their typically low densities, wide ranging habits, and conflict with humans which increases as habitats shrink and become fragmented (Woodroffe & Ginsberg, 1998; Crooks, 2002). Thus, it is important to understand carnivore population responses to changes in the landscape to best design conservation and management practices. Despite their importance, relatively little is known about the carnivores of Madagascar, where < 10% of primary vegetation remains, and deforestation continued at a rate of 0.9% per year through the previous decade, 1990-2000 (Myers et al., 2000; Harper et al., 2007). Most information about Malagasy carnivores has been collected in protected areas of remaining natural forest (Dunham, 1998; Dollar, 1999; Hawkins & Racey, 2005; Dollar et al., 2007; Hawkins & Racey, 2008; Gerber et al., 2010). Recent photographic sampling surveys conducted in continuous and fragmented rainforest provide evidence of decreasing species richness and density of native carnivores with forest degradation and fragmentation. Two of the larger endemic carnivores, the fossa (*Cryptoprocta ferox*) and Malagasy civet (*Fossa fossana*), appear especially sensitive to these habitat changes (B. Gerber, unpublished data). The decline in native carnivores may be exacerbated by hunting, either for bushmeat (Garcia & Goodman, 2003; Golden, 2009) or due to human-carnivore conflict, which has been found in other areas to be the top source of mortality for adult carnivores, especially for animals living in but ranging beyond protected areas (Woodroffe & Ginsberg 1998).

We need to better understand which carnivore species occur at increasing distances from continuous and/or protected forest and carnivore movement patterns and interactions with humans across Madagascar's diverse landscape (Irwin et al., 2010). This information is important in 1) facilitating the protection and creation of forest corridors as was underway before the 2009 political crisis in Madagascar (Norris, 2006; Brulliard, 2009), 2) understanding behavioral and ecological interactions between Malagasy carnivores and their endangered lemur prey (Irwin et al., 2009), and 3) assessing alternatives for mitigating human-carnivore conflict (Treves et al., 2009). Increasingly, local ecological knowledge (LEK) is recognized as an important complement to other types of data collection in understanding distribution, coarse population trends, response to habitat changes, and harvest of wildlife species (Gilchrist et al., 2005; Brook & McLachlan, 2008; Jones et al., 2008b; Anadon et al., 2009; Brinkman et al., 2009; Golden, 2009). The understanding of natural phenomena gained by local people through their experience in the environment can be important in revealing factors previously unknown to science, in corroborating scientific findings, and in guiding future research efforts. Especially for a guild of species like carnivores that is difficult to study, the input of local people with years of experience living and working in the species' habitats should contribute to a basic understanding of the species' ecology and the design of efficient scientific studies. Furthermore, the use of LEK in conservation-related research increases the involvement of local stakeholders in the development of conservation practices that affect them and the land they use.

In this study, we investigated LEK of carnivore ecology and movement along the edge and in the matrix between intact, primary and fragmented, degraded rainforest in southeastern

Madagascar. Our objectives were to 1) assess distributions of Malagasy carnivore species outside of the rainforest and relate patterns to landscape- and community-level factors, 2) determine the level of human-carnivore conflict across the landscape, and 3) compare the information obtained through LEK surveys with the findings of other ecological studies conducted in the same region.

Study area

We conducted LEK surveys in southeastern Madagascar within 20 km of two protected areas: Ranomafana National Park (RNP) and Ialatsara Forest Station (IFS, Fig. 1). RNP, located at 47^{o} 18' to 47^{o} 37' E, 21^{o} 02' to 21^{o} 25' S, is part of the contiguous forest along the eastern escarpment of Madagascar and contains 37,367 ha (373.67 km) of protected lowland rainforest, cloud forest and moist montane rainforest (Dunham et al., 2008) at elevations ranging between 537 – 1396 m (B. Gerber, unpublished data). Due to selective logging before the park's establishment in 1991 and the historic presence of villages in the area, RNP now contains a mixture of habitats, ranging from undisturbed primary forest to selectively-logged and heavily disturbed areas. The park boasts a high level of biodiversity, including 5 species of endemic carnivores of the family Eupleridae: *C. ferox, F. fossana*, the small-toothed civet (*Eupleres goudotii*), the ring-tailed mongoose (*Galidia elegans*), and the broad-striped mongoose (*Galidictis fasciata,* Gerber et al., 2010). IFS, located about 19 km west of the northern extent of RNP at 47^{o} 12' to 47^{o} 15' E, 21^{o} 02' to 21^{o} 06' S, is a private ecotourism reserve owned and managed by two residents of Madagascar (D. and B. Rajoana). The reserve exists at an altitude range of 1308 – 1563 m and contains about 1000 ha of pine, 500 ha of eucalyptus and 500 ha of natural rainforest in 10 forest fragments of varying size (2 – 240 ha) surrounded by matrix habitat of grassy or shrubby savannah and agricultural plots (Foltz, 2009, B. Gerber, unpublished data). The natural forest was once part of the contiguous eastern rainforest (where RNP is located), but due to deforestation by subsistence-level agricultural activity, the fragments have been isolated for at least 30 years (D. Rajaona, personal communication). Photographic capture surveys conducted in 2008 at IFS confirmed the presence of only two endemic species, *G. elegans* and *G. fasciata* (B. Gerber, unpublished data). The landscape between IFS and RNP is dominated by grassland with some patches of secondary-growth trees, wetlands used widely for rice cultivation, other types of cultivation, and some interspersed natural forest fragments (Moat and Smith 2007).

We selected communities randomly in ArcMap 9.2 (ESRI, Redlands, CA), using Hawth's Tools (Beyer 2004) to generate random points at least 3 km apart within 20 km of the western boundary of RNP. Using satellite imagery available on Google Earth (Google Inc., 2009) and data from the Malagasy National Parks association, we identified the village nearest to each random point. The selected villages included both Tanala and Betsileo communities, representing the two major ethnic groups in the region.

Methods

Between October-December 2009, we interviewed adult male heads of households from 17 communities at varying distances (0.2 – 20 km) from the western border of RNP (Virginia Tech Institutional Review Board Protocol #09-280, Appendix C). Participants were individuals at least 20 years of age, who had lived in the focal community for at least 5 years. We identified an initial group of informants with the aid of village elders and located additional informants through chain referral (Huntington, 2000). The exact number of participants in each community varied with the number of people available and willing to participate, as well as the time constraints of the research team, but fell between 8 – 13 (mean 11 ± SD 1.4) participants per village.

We conducted semi-structured interviews, consisting of primarily open-ended questions that guided the interview, but also allowed respondents to discuss related information as they saw fit (Appendix C). A trained Malagasy technician from the study area conducted the interview in Malagasy, while MK, proficient in conversational Malagasy, and a second Malagasy translator took written notes and asked questions when additional information or clarification was needed. We digitally recorded the interviews (Sony IC Recorder, 2008) with the informants' verbal consent.

We asked informants about three main topics: 1) the informant's experience with different wild carnivore species, 2) livestock and poultry husbandry and depredation, and 3) the informant's residency and regular activities within the region. First, we verified each participant's identification of a species based on their descriptions of morphology and behavior, as well as their identification of color photographs. We provided multiple exemplars of five native species (*C. ferox*, *E. goudotii*, *F. fossana*, *G. elegans*, *G. fasciata*) and two introduced species (wild cat *Felis silvestris*, small Indian civet *Viverricula indica*) known to occur in the region based on photographic capture carnivore surveys within RNP and IFS (Appendix B, Gerber et al. 2010, B. Gerber, unpublished data) and asked if they had observed any other carnivore species not included in our photographs. We grouped responses related to feral cats and larger, distinct morphs believed to be introduced wildcats (Brockman et al., 2008). Both subspecies occurred in the region, were infrequently distinguished by informants, and were reported to interbreed. We asked informant's about their experience with each species of carnivore identified, focusing on the frequency, locations, and timing of observations. We also asked about their perceptions of the species, and whether or not the species was hunted in their community.

After informants discussed their observations and perceptions of carnivore species, we asked them about their livestock and poultry. Informants described the number of each type of animal they raised (e.g. chickens, ducks, pigs), how many years they had been raising them, and how/where they were kept during the day and night. We then asked about depredation of the informant's poultry and/or livestock, focusing on when, where, and how often it occurred, by which predators, and how the informants identified the predator for particular events. Finally, we also asked informants to describe the methods used to prevent depredation of poultry and livestock.

To gain an understanding of both the temporal and spatial context for carnivore observations within a community, we recorded how long each informant had lived within the community and how far they ranged outside the village on a regular basis. We collected data on the informants' travel to work sites, agricultural fields, forests, and markets.

Data analyses

The team conducting the interviews (SJ, FR and MK) translated all interviews into English and MK extracted and coded pertinent data. The interviewing team considered the interviewees' identification of each species based on photograph identification and descriptions of morphology and behavior and removed reports from further analyses when conflicting descriptions suggested confusion with another species. We categorized observations of carnivore species spatially by estimating locations based on reported distances and directions from a known location. When informants reported travel times rather than distances, we estimated distance using a conversion rate of 4158 m/hr calculated using the mean of reported travel times by informants between locations for which we obtained GPS coordinates (n=124). The limits of a community were described as the mean of the maximum distances to field or forest locations to which each informant reported to travel at least once a week.

For carnivore species observed by at least 15 interviewees within the last five years, we modeled proportions of interviewees observing each species within their communities using logistic regression (PROC Logistic, SAS 9.2, Cary, NC) to examine landscape- and community-level factors that may influence the proportion of interviewees reporting a species' occurrence. We quantified three landscape characteristics using ArcMap 9.2. We estimated distance to continuous forest (DistForest) as the straight-line distance from village to nearest patch of humid forest cover visibly connected to the contiguous forest of the eastern escarpment, based on available data from the Critical Ecosystem Partnership Fund Madagascar Vegetation Mapping Project (Moat and Smith 2007). We measured distance from village to national highway (DistRoad) based on data provided by Malagasy National Parks. We quantified village spread (Spread) as the area of the minimum convex polygon (MCP) containing all interviewed households divided by the magnitude of the largest MCP (100 ha). We collected data on four community characteristics during the surveys: number of households (#Houses), the proportion of interviewees owning dogs (*Canis familiaris*) and cats (Dogs and Cats, respectively) and a poultry index (Poultry), which was the product of the proportion of interviewees owning poultry and the mean flock size they reported. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) to determine the best-fitting 1-3 parameter (including intercept) models for each carnivore species and calculated the relative importance (R_i) of model variables by summing the Akaike model weights of all candidate models containing the variable. As candidate models included all possible pairings of explanatory variables, each variable was present in equal numbers of models for each species. We examined the model-averaged β-coefficients of all variables in the candidate models and report significantly positive or negative effects if 95% confidence intervals of the estimates did not contain zero (Burnham & Anderson, 2002).

We used similar analyses to explore patterns of predation by wild carnivores. As almost all interviewees owned poultry, and poultry were the most commonly reported livestock lost to carnivore predation, we modeled 1) the proportion of poultry owners within a community losing poultry to predation by wild carnivores among villages (n=17) and 2) poultry predation by wild carnivores among individual poultry owners (n=170). We again used logistic regression with AIC_c model selection to rank 1-3 parameter models containing combinations of the seven landscape- and community level variables described above to explain variation in the proportion of poultry owners experiencing personal poultry loss to predation by wild carnivores within the last year (2008 – 2009). We also used logistic regression to model the probability of an individual poultry owner experiencing poultry loss to predation within the last year; this model contained three household-level variables that we believed were pertinent to animal husbandry and predation risk: number of poultry owned (#Poultry), the dichotomous categorical variable of whether or not the individual owned dogs (Dog: Yes vs. No), and whether poultry were kept inside the house or in an outdoor enclosure at night (PoultryNight; Inside vs. Outside).

To explore reported habitat use, perceptions, hunting of carnivore species, and livestock predation prevention methods in different communities, we grouped related responses and report the percentages of interviewees expressing different views. We performed Pearson's chi-square tests of independence to test whether habitat use factors and reported hunting varied among species for which there were enough observations, and whether perceived effectiveness varied among predation prevention methods.

Results

We conducted 182 interviews with male heads of households aged 21 – 85 years (mean 44 ± SD 14), who had lived in their respective communities for 33 ± SD 16 years. The interviews ranged in duration from 18 - 84 min (45 ± SD 13 min). We found that the interviewees were primarily agricultural cultivators (89%) and/or animal breeders (21%), while wood-cutting (5%) and iron forging (3%) were also reported as primary occupations. Fewer than 5 people (<3%) each reported honey collection, crayfish collection/fishing, carpentry, vendor, paid labor, or other occupations as their livelihood. The mean maximum distance traveled by interviewees to field or forest locations at least once a week was 2531 ± SD 1000 m, thus we considered a community to comprise the land within a 2500 m radius from the village center.

We found that all five native species and two introduced species of wild carnivore known to occur in the region were identified and recently observed by interviewees from communities at different maximum distances from the continuous rainforest (Table 1). The two introduced species (*F. silvestris* and *V. indica*) and the native *G. elegans* were the most commonly observed and widespread carnivores as reported by interviewees. We documented that the largest endemic carnivore, *C. ferox*, was recently (within the last 5 years) observed by only 15 of 182 interviewees, within communities at a maximum distance of 2.5 km from continuous rainforest. Both native and non-native carnivores were found in diverse habitats, ranging from rainforest to villages; no species' observations were confined to less than three different types of habitat (Fig. 2). Reported habitat used differed among species (χ^2 =39.072, p=0.0001), with *C. ferox* observed more than expected in villages and along roads, and *F. silvestris* observed more than expected in non-native forest. Few villagers observed the highly nocturnal endemic species, *E. goudotii*, *F. fossana*, and *G. fasciata*, even at close proximity to continuous forest. We summarized observations and responses for these species, but could not include them in statistical analyses.

When we considered observations within increasing time intervals, we found different spatial and temporal trends. The percent of interviewees reporting observations of each carnivore species within their communities increased when observations within the last year (2008 - 2009), last 5 years (2004 – 2009), last 10 years (1999 – 2009), and all years were sequentially included (Fig. 3a). The number of villages where *F. silvestris* and *V. indica* had been observed only increased when the time interval was extended from 1 to 5 years, and both were observed at maximum distances of 18.7 km from the continuous forest within the last year (Fig. 3b-c). The number of villages where *C. ferox* and *G. elegans* were observed increased with each increased time interval, and the maximum community to forest distance increased when the time interval was extended from 5 to 10 years (Fig. 3b-c). *C. ferox* was observed at a maximum village to forest distance of 18.7 km within the last 10 years, but only in communities at 2.5 km from the forest within the last 5 years (Fig. 3c).

We found that DistForest was an important explanatory variable for the proportion of interviewees reporting observations of three carnivore species within their community in the last 5 years (2004-2009, Table 2). For *C. ferox* (R_i DistForest=1.00) and *G. elegans* (R_i DistForest=1.00), the probability of observation decreased significantly with increasing distance to continuous forest, while for *F. silvestris* (R_i DistForest=0.98), the opposite trend was observed (Table 3). The number of households within a village was the most important variable explaining the proportion of interviewees observing *V. indica* (R_i #Houses=0.50), which generally decreased with increasing numbers of households, but the directionality of the relationship was indeterminate (Table 3).

While 95.6% of interviewees owned livestock, including poultry (93.4%), pigs (44.0%), cattle (53.3%), rabbits (9.3%) and fish (7.7%), only 46.2% of the informants reported personal loss of livestock within the last year (2008-2009). Of the interviewees reporting recent losses, 96.4% reported loss of poultry, while only small percentages reported loss of rabbits (4.7%) or fish (1.2%). The largest domestic animals reportedly killed by wild animals within any time frame were dogs (n=3) and pigs (n=1). The most commonly reported predators responsible for kills, based on direct observations of the event or on signs around a kill such as tracks, were raptors, mainly the yellow-billed kite (*Milvus aegyptius*, Table 4). Among reports of recent depredation of livestock/poultry by wild carnivores, wild or feral cats (*F. silvestris*) were the most commonly reported predators (14.4% of poultry/livestock owners), followed by *G. elegans* (7.5% of poultry/livestock owners); recent loss of livestock due to predation by *C. ferox* or *V. indica* was uncommon (Table 4).

We found that no single variable or model strongly explained the variation in proportion of interviewees within each community experiencing poultry loss to wild carnivores within the last year (Table 5). Analyses of whether or not individual households experienced poultry depredation by wild carnivores revealed that the probability of a household losing poultry increased with the number of poultry owned ($\beta=0.0211 \pm 0.0120$ SE, $p=0.08$). The probability of predation was estimated to increase for households without dogs ($\beta=0.3422 \pm 0.2394$ SE, $p=0.15$), and to decrease if poultry were kept inside a house at night ($\beta=-0.3644 \pm 0.2339$ SE, $p=0.12$), but these effects were not significant.

Nearly all interviewees (180 of 182) discussed methods of preventing poultry predation. The most common methods included watching over poultry or restricting their ranging during the day (N = 51), keeping dogs (N =40), keeping poultry indoors at night (N =37), non-lethal predator deterrence including scaring or chasing potential predators away and clearing shrubs around the village (N =33), and using secure outdoor coops at night (N = 21). A small number of interviewees described lethal methods of predator control, such as trapping or killing the predators directly when seen (N = 5). A fairly large group (N = 28) responded that there was nothing they could do to prevent predation of their poultry. Perceptions of the effectiveness of each method varied significantly (χ^2 =39.072, p=0.0001); keeping dogs and keeping poultry indoors at night were regarded as effective more frequently than expected (67.7% and 65.5% of interviewees reporting the methods, respectively) while non-lethal predator deterrence was regarded as effective less frequently than expected (38.5% of interviewees reporting the method). Watching over poultry or restricting their movement during the day, and keeping poultry in outdoor coops at night, were considered effective by 44.2% and 50.0% of the informants reporting them, respectively. Only one of four interviewees reporting lethal predator control felt that it was an effective method of predation prevention.

When we asked whether interviewees viewed a species as beneficial, harmful, or of no importance to their lives, 40 – 65% of all interviewees familiar with *C. ferox, G. elegans, F. silvestris,* and *V. indica*, responded that they were harmful or both harmful and beneficial (Table 6). The negative perceptions primarily related to the species' depredation of their livestock, namely poultry. We found that beneficial views of the native carnivores were explained as relating to the species' importance in the forest or uniqueness in Madagascar, the aesthetic and/or educational value of simply observing the species in the wild, or the inherent value of every living organism. Our interviews revealed more utilitarian values such as food and rodent control for the introduced wild cat, *F. silvestris*, which was often described as both beneficial and harmful for killing mice and rats, but also poultry. The rarely observed *E. goudotii*, was described as a valuable food source by 4 out of the 6 interviewees familiar with this species.

We found that slightly less than half of the responding interviewees (44.1%), but almost all villages (94.1%), reported that *F. silvestris* was hunted within their communities, either for food, or because the animal preyed on poultry (Table 7, 8). We documented that *G. elegans* and *V. indica* were also killed for food or because of their role in poultry depredation, while *C. ferox* was almost exclusively reported as killed because of poultry depredation. The percent of interviewees reporting a species was killed varied significantly among species ($\chi^2 = 22.21$, $p < 0.0001$), as *F. silvestris* was more frequently reported to be killed relative to *G. elegans*. Of the rarely observed carnivores, *F. fossana* and *G. fasciata* were seldom or never reported as hunted, while 4 out of 6 interviewees reported that *E. goudotii* was hunted and/or trapped for food (Tables 7, 8).

Discussion

Our study of LEK revealed distinct patterns in the distribution and habitat use of native Malagasy and exotic carnivores across a human-dominated landscape. The proximity to the continuous rainforest explained more variation in the probability of observing *C. ferox*, *G. elegans*, and *F. silvestris* than any community characteristic such as number of households, village spread, or relative abundance of domestic animals. The differing distributions and frequencies of observations among these three species suggest a range of tolerances for habitat types outside of continuous rainforest. The largest endemic species, *C. ferox*, may be most sensitive to human-dominated landscapes, as the probability of observing them decreased with increasing distance to continuous forest, and they had only been observed in communities ≤ 2.5 km from the continuous forest from 2004 – 2009. The probability of observing *G. elegans* also decreased with increasing distance to continuous forest; however, interviewees reported this species in a majority of communities 0 - 13.3 km from continuous forest, and observations were more evenly distributed among different habitat types, suggesting a greater tolerance for anthropogenic landscapes. *F. silvestris* appeared to have the strongest affinity for the anthropogenic landscape, having been observed in all villages. The probability of observing this species increased with increasing distance to continuous forest and almost twice as many interviewees reported observing the species in non-native eucalyptus or pine forest (n=59) than reported observing them in natural rainforest (n=30, Figure 3).

Despite the combined domestic and international conservation efforts focused on preserving Madagascar's biodiversity (Myers et al., 2000; Norris, 2006), there has been little research into human-wildlife conflict on the island. In other continents and in mainland Africa, however, where larger carnivore species pose direct threats to both humans and their livestock, researchers are using LEK to identify the extent and implications of the conflicts, as well as alternatives to mitigate them (Dar et al., 2009; Hemson et al., 2009; Inskip & Zimmermann, 2009; Treves et al., 2009). Due to the relatively small size of the Malagasy carnivores, human-carnivore conflict is primarily limited to depredation of poultry, although *C. ferox* was also reported to occasionally kill small pigs and dogs, and *V. indica* was reported to degrade crop value with its musky scent. Our results indicate that poultry loss to wild carnivores appears to be impacting a minority of households in the region, yet we discovered predominantly negative perceptions of the wild carnivores based on their role as predators and informants most frequently cited this reason for the killing of carnivores in their communities. While well less than the majority of informants reported that native species were hunted in their communities, it is alarming that at least one informant reported it in so many of the communities where the species occurs or occurred in the past. Previous surveys conducted on the sensitive issues of wildlife hunting and natural resource extraction in Madagascar were conducted by teams working in an area for several years and rely on informant-researcher confidence built up through extensive interaction for the accuracy of their results (Jones et al., 2008a; Golden, 2009). Although we assured informants of their anonymity and our independence from local agencies, we assume that not all informants were willing to report illegal or perceived illegal activity to us. Thus, the percentages of informants and villages reporting that carnivore species are killed in their communities are likely conservative estimates. There is increasing evidence of bushmeat hunting in Madagascar (Garcia & Goodman, 2003; Goodman, 2006), and the first quantitative assessments, conducted in northern Madagascar, suggest that the bushmeat harvest of several species, including *C. ferox*, is unsustainable in the region (Golden, 2009). While bushmeat hunting was not the primary motivation for killing carnivores in this study, the fact that it was reported for three of the endemic species, including *C. ferox,* currently classified as Vulnerable (IUCN, 2010), and the very rarely observed *E. goudotii* (Near Threatened, IUCN, 2010), suggest that it may be a direct threat to carnivores outside of the continuous forest. Even targeted hunting for other species poses a potential risk to native carnivores. Many interviewees hunt with dogs, which were reported to occasionally chase and kill prey other than the species their owners intended to catch.

Mitigating human-carnivore conflict can be approached directly with methods aimed to reduce the probability or adverse effects of carnivore encounters, or indirectly, by increasing the tolerance of stakeholders to the encounters (Treves et al., 2009). Our results suggest the potential need for both approaches in this region of Madagascar. Direct measures should focus on reducing human-carnivore conflict and decreasing financial losses of villagers by adapting current livestock and poultry husbandry practices. A relatively large percentage of villagers reported that there was nothing they could or knew how to do to prevent depredation of their poultry and livestock, and substantial percentages of villagers were using particular methods they felt were not effective or only conditionally effective. Workshops focused on determining and implementing combinations of practical methods to protect poultry during the day and the night may help villagers reduce their risk of losing poultry to wild carnivores, thereby reducing the motivation for lethal predator control and possibly impacting villager perceptions regarding these species.

While relatively limited poultry predation by wild carnivores fuels widespread negative perceptions and is the primary motive for killing these species, the positive values of these species across the landscape are largely overlooked. Villagers rarely attributed a utilitarian value of rodent control to the commonly observed native carnivore species, which were usually classified as harmful because of poultry predation, and occasionally beneficial for a non-specific importance to the environment, but not to the villagers themselves. Indirect mitigation could include educational programs that highlight the fact that native carnivore species also prey on rodents, birds, and insects that may damage crops (Goodman, 2003; Dollar et al., 2007; Hawkins & Racey, 2008), as well as the general importance of carnivores to the integrity of forests.

With increasing study and application of local knowledge in conservation planning, there has been increasing demand to validate this information using supplemental types of data collection (Gilchrist & Mallory, 2007). Studies that incorporate both LEK and more traditional ecological survey methodologies indicate that LEK may be limited or partially inaccurate and should not be the sole source of data to inform management and conservation practices, however, it fulfills a purpose often complementary to other forms of data collection (Gilchrist et al., 2005; Msoffe et al., 2007; Can & Togan, 2009). Recommended reliance and application of LEK varies with the methods of the study, study species, and providers of LEK. It ranges from guiding further scientific sampling, especially for more rare and elusive species (Msoffe et al., 2007), to estimating abundance within desired confidence intervals (Anadon et al., 2009). The LEK recorded in our study provides important insight concerning the distribution of two endemic and two exotic carnivore species in southeastern Madagascar that is congruent with and complementary to other data collected in the same region. Recent photographic capture surveys conducted in RNP, IFS and an additional fragmented forest site along the eastern forest corridor indicate a similar range of tolerance among these species for human-disturbed habitats, as that suggested by LEK collected in our study (B. Gerber, unpublished data). Photographic sampling only detected *C. ferox*, the least tolerant species in our study, within protected, intact forest sites in RNP and forest fragments ≤ 2.5 km from intact forest, while *G. elegans* was detected in intact forest and forest fragments 2.5 km and 15 km from the continuous forest, and was observed using primarily rainforest patches, but also matrix habitat consisting of burned shrub areas with interspersed pine (B. Gerber, unpublished data). *V. indica* was detected in fragmented forest, surrounding matrix of open burned shrub, shrub, and interspersed pine, and in the edge of continuous forest near a national highway, while *F. silvestris* was detected only in fragmented forest and matrix habitat (Gerber et al., 2010, B. Gerber, unpublished data). These surveys also detected *G. fasciata* within intact forest and forest fragments, and detected *F. fossana* and *E. goudotii* only within intact rainforest. Too few interviewees in our study had observed these almost exclusively nocturnal species to suggest reliable patterns of distribution and habitat use, or population trends.

Unlike photographic capture and other ecological surveys, which have assessed conditions within specific continuous forest and fragmented forest sites over relatively brief periods of time, our LEK survey investigated trends over a vast area of a human-dominated landscape and a broad time interval. Consistent with previous findings, informants reported observations of *G. elegans* in communities along the periphery of RNP and around the forest fragments of IFS, both protected areas where photographic capture surveys detected the species (B. Gerber, unpublished data). Informants also reported observations of *G. elegans* in several communities at intermediate distances 4-9 km from the forest with less substantial rainforest cover (Moat & Smith, 2007), providing novel distribution data from areas where ecological surveys for carnivores have not been conducted. The lack of observations of *C. ferox* in any communities > 2.5 km from the continuous forest within the last five years also provides previously missing information on the limited ranging of *C. ferox* outside of the contiguous natural forest. LEK reported in surveys such as this, or in longer-term community monitoring programs, can and should be used to provide information on the poorly understood responses of the Malagasy carnivores and the threats they face across a gradient of disturbance and human-land use, such as is needed for multitaxa conservation planning in an increasingly fragmented landscape (Kremen et al., 2008; Irwin et al., 2010).

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Figures & Tables

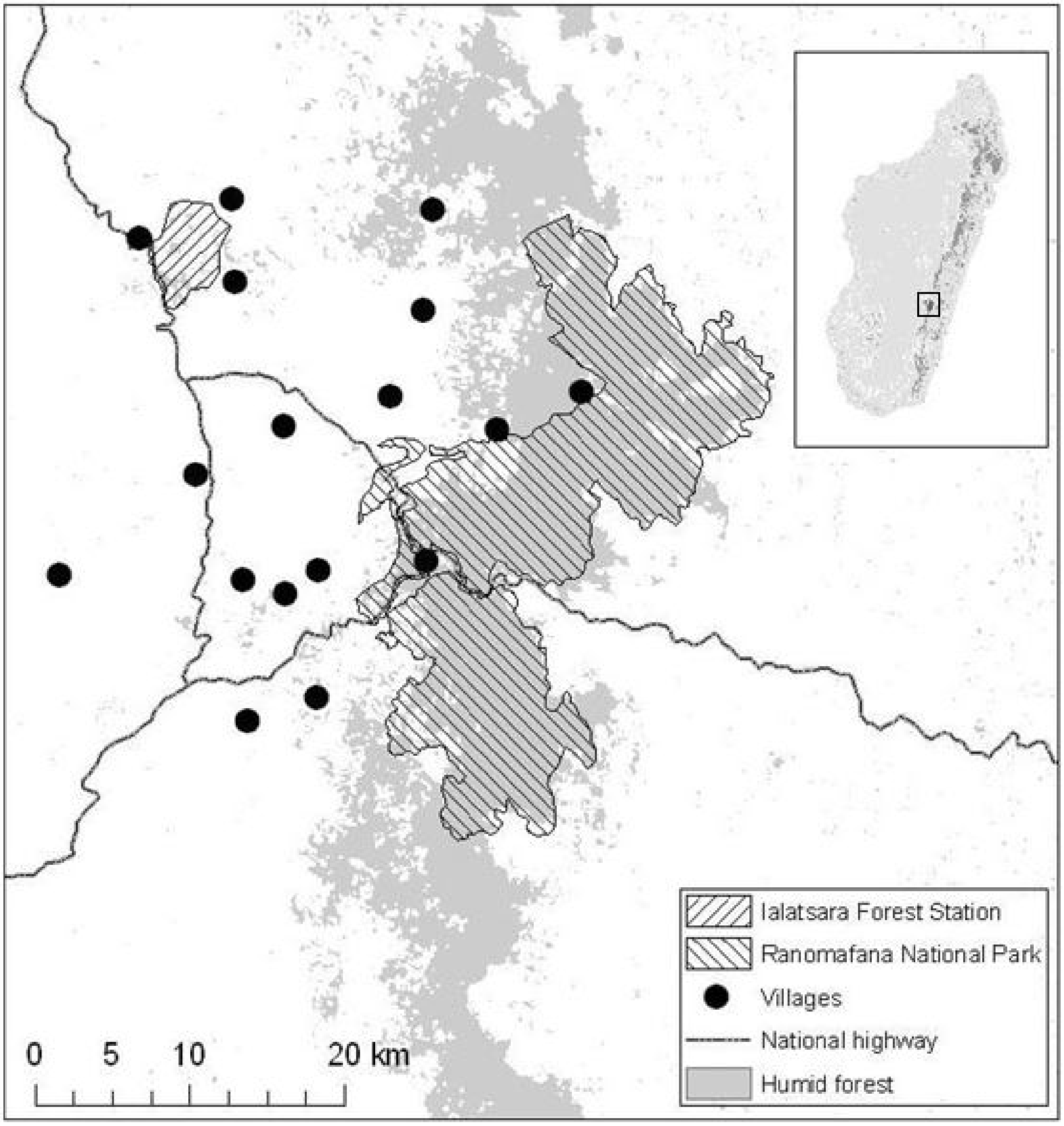

Figure 1. Locations of the 17 communities in southeastern Madagascar (see inset for general region) in which we investigated human observations and perceptions of carnivores. The communities are located at varying distances from the protected continuous rainforest of Ranomafana National Park and rainforest fragments of Ialatsara Forest Station.

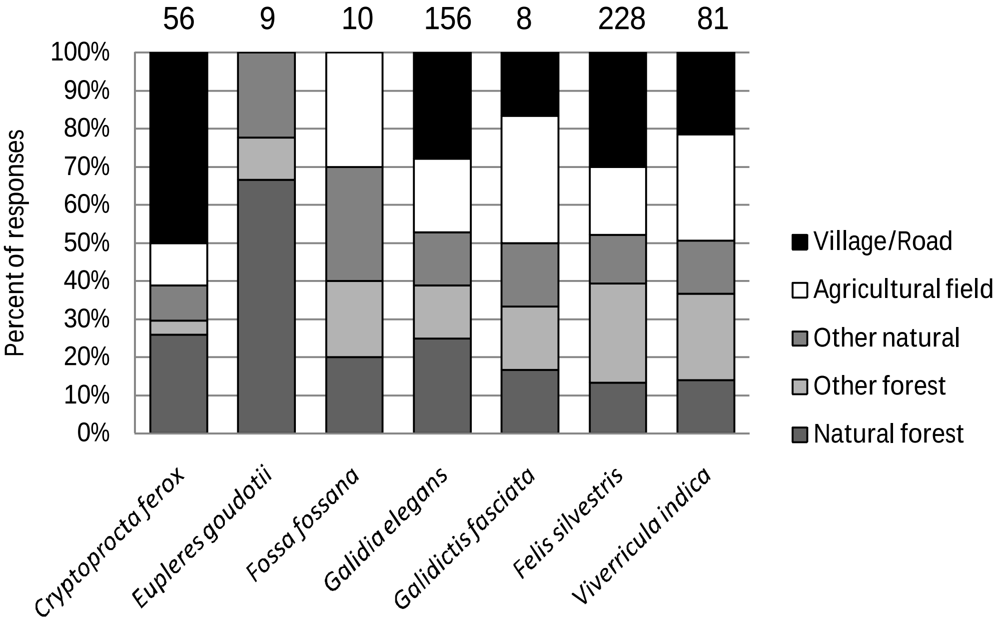

Figure 2. Habitat types in which interviewees reported observations of carnivore species in southeastern Madagascar. Values shown above stacked bars represent the total number of interviewee reports of habitat use by the species and may exceed total number of interviewees observing each species because many informants reported seeing a species in multiple habitat types. Habitat types included: 1) natural forest, composed primarily of native species, 2) other forest, including eucalyptus (*Eucalyptus spp*.) and pine (*Pinus spp*.) plantations, 3) other natural areas which included grasslands, shrubs, and riparian zones, 4) agricultural fields, and 5) villages and roads.

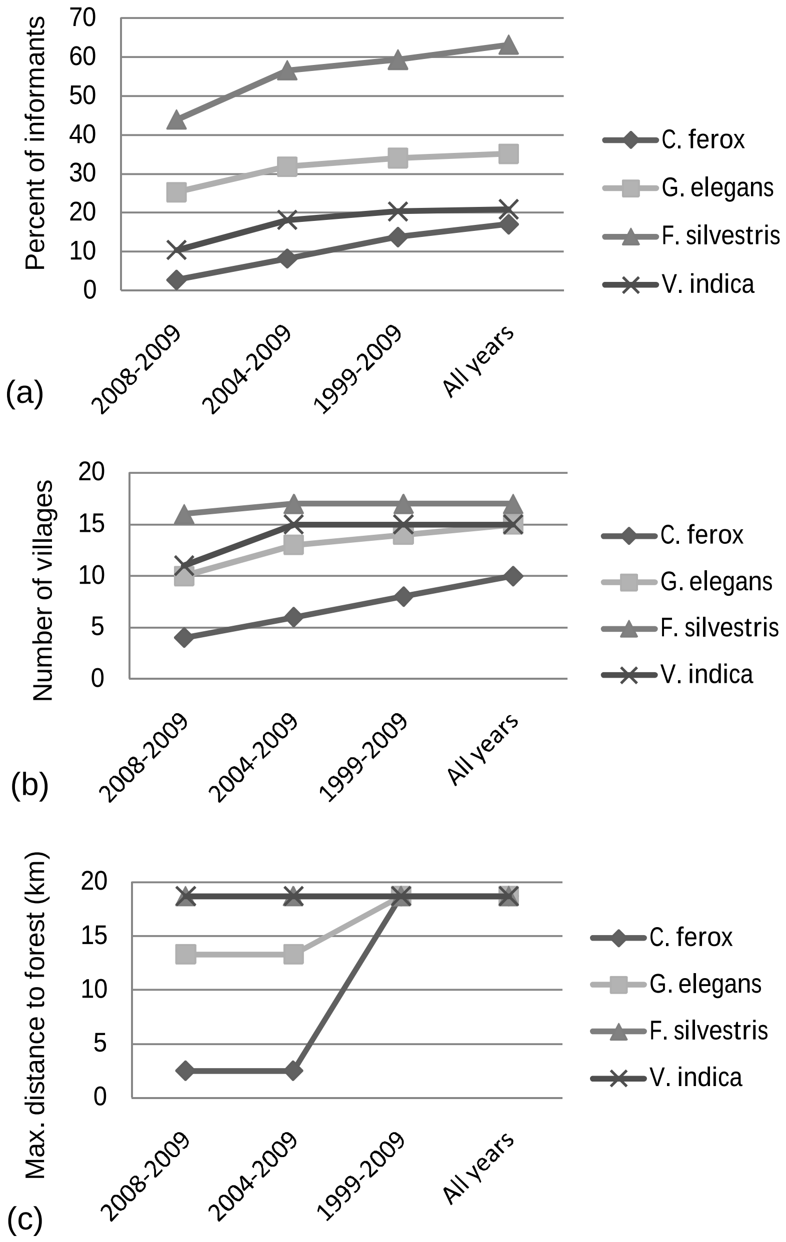

Figure 3. Spatio-temporal summary of reported carnivore observations in southeastern Madagascar within the last year (2008-2009), within the last 5 years (2004-2009), within the last 10 years (1999-2009), and ever (all years through 2009): (a) the cumulative percent of interviewees (n=182) reporting observations of species within their communities within these time frames, (b) the number of villages (n=17) in which at least one interviewee reported an observation of a species within their communities within the described time frames, (c) the village center to forest distance of the village furthest from the continuous forest where a species observation was reported within each time frame.

Table 1. Percent of interviewees (n=182) and villages (n=17) reporting carnivore observations within their communities in southeastern Madagascar within the last five years (2004 – 2009).

Species	% Interviewees [1]	% Villages [2]	Max. village distance to continuous forest (km) [3]
Fossa (*Cryptoprocta ferox*)	8.2	35.3	2.5
Small-toothed civet (*Eupleres goudotii*)	2.2	17.6	4.7
Malagasy civet (*Fossa fossana*)	3.8	17.6	8.5
Ring-tailed mongoose (*Galidia elegans*)	31.9	76.5	13.3
Broad-striped mongoose (*Galidictis fasciata*)	1.1	11.8	0.2
Wild cat (*Felis silvestris*)	56.6	100.0	18.7
Small Indian civet (*Viverricula indica*)	18.1	88.2	18.7

[1] The percent of interviewees that reported observing a species within 2500 m of their village center within the five years prior to the survey

[2] The percent of villages in which at least one interviewee reported observing a species within 2500 m of their village center within the five years prior to the survey

[3] Distance between the village center and the edge of continuous forest for the village farthest from the forest where a species was observed.

Table 2. Top models (ΔAICc < 2, likelihood >0.125) of factors affecting the proportion of interviewees in southeastern Madagascar reporting observations of each carnivore species within 2.5 km of their village in the last 5 years (2004 – 2009).

Species	Model$^{1, 2}$	K^3	AIC_c^4	ΔAIC_c^4	ω_i^4	Model likelihood
Fossa *(Cryptoprocta ferox)*	DistForest, #Houses	3	70.04	0.00	0.25	1.00
	DistForest, Spread	3	70.47	0.43	0.20	0.81
	DistForest	2	70.73	0.69	0.17	0.71
	DistForest, Dogs	3	71.04	1.01	0.15	0.60
	DistForest, Poultry	3	71.28	1.24	0.13	0.54
	DistForest, DistRoad	3	71.72	1.69	0.11	0.43
Ring-tailed mongoose *(Galidia elegans)*	DistForest, Spread	3	181.99	0.00	0.61	1.00
	DistForest, Poultry	3	183.75	1.76	0.25	0.41
Wild cat *(Felis silvestris)*	DistForest, DistRoad	3	226.37	0.00	0.27	1.00
	DistForest, #Houses	3	226.67	0.30	0.23	0.86
	DistForest	2	227.86	1.49	0.13	0.48
	DistForest, Dogs	3	228.33	1.96	0.10	0.38
	DistForest, Cats	3	228.57	2.20	0.09	0.33
	DistForest, Spread	3	228.60	2.23	0.09	0.33
	DistForest, DistRoad	3	228.85	2.48	0.08	0.29
Small Indian civet *(Viverricula indica)*	#Houses	2	169.65	0.00	0.12	1.00
	#Houses, Spread	3	170.41	0.76	0.08	0.69
	#Houses, Poultry	3	170.47	0.82	0.08	0.66
	DistForest, #Houses	3	170.58	0.92	0.08	0.63
	#Houses, DistRoad	3	170.61	0.96	0.07	0.62
	#Houses, Dogs	3	170.65	0.99	0.07	0.61
	Poultry	2	171.23	1.57	0.05	0.46
	Spread	2	171.56	1.91	0.05	0.39
	Spread, Dogs	3	171.60	1.95	0.05	0.38
	Spread, DistRoad	3	171.70	2.04	0.04	0.36
	Poultry, Dogs	3	171.85	2.20	0.04	0.33
	Poultry, Spread	3	172.00	2.35	0.04	0.31
	Poultry, DistRoad	3	172.06	2.40	0.04	0.30
	DistForest, Poultry	3	172.13	2.48	0.03	0.29
	Intercept only	1	172.31	2.66	0.03	0.26
	DistForest, Spread	3	172.49	2.84	0.03	0.24
	Dogs	2	173.24	3.59	0.02	0.17
	DistForest	2	173.25	3.60	0.02	0.17
	DistRoad	2	173.28	3.63	0.02	0.16

[1] No. of models evaluated for *C. ferox* and *V. indica*=22, for *G. elegans* and *F. silvestris* = 29.

Table 2. Continued

[2] DistForest=distance to continuous forest, DistRoad=distance to national highway, #Houses=number of households, Spread=area of the minimum convex polygon containing all interviewed households (ha)/100, Dogs=proportion of interviewees owning dogs, Cats=proportion of interviewees owning cats, Poultry=proportion of interviewees owning poultry x mean flock size

[3] No. of parameters, including intercept.

[4] AICc = Akaike's Information Criterion corrected for sample size. ΔAICc = the difference between a model's AICc and that of the best-fitting model. ω_i= Akaike model weight. Statistics are only comparable within species.

Table 3. Relative importance of landscape- and community-level factors in explaining proportion of interviewees observing different carnivore species within their communities in southeastern Madagascar. Values are shown in bold for the variable with the highest relative importance for each species. Variables for which the 95% confidence intervals around the model-averaged β coefficient did not contain zero are indicated as negative (-) or positive (+) to show the directionality of the relationship.

	Relative importance of variable by species[1]			
Variable[2]	*Cryptoprocta ferox*	*Galidia elegans*	*Felis silvestris*	*Viverricula indica*
DistForest	**1.00 (-)**	**1.00 (-)**	**0.98 (+)**	0.18
#Houses	0.25 **(-)**	0.04 **(-)**	0.24	**0.50**
Spread	0.20	0.61	0.09	0.28
Dogs	0.15	0.02	0.10	0.20
Poultry	0.13	0.25	0.08	0.29
Cats	N/A[3]	0.06	0.09	N/A[3]
DistRoad	0.11	0.01	0.29	0.20

[1] Relative importance = the sum of the Akaike model weights of all tested models containing the variable.

[2] DistForest=distance to continuous forest, DistRoad=distance to national highway, #Houses=number of households, Spread=area of the minimum convex polygon containing all interviewed households (ha)/100, Dogs=proportion of interviewees owning dogs, Cats=proportion of interviewees owning cats, Poultry=proportion of interviewees owning poultry x mean flock size.

[3] Variable not included in candidate models for a species.

Table 4. Livestock and poultry depredation events by various predators in southeastern Madagascar. Values represent the number and percent of interviewees owning poultry and livestock (n=174) who reported depredation of their livestock and/or poultry within the previous year (2008-2009). Only reports in which the predator was directly observed or identified by signs were included in the categories by species/predator type.

Predator	%
Any predator	45.4
Any wild carnivores	21.3
F. silvestris	14.4
G. elegans	7.5
C. ferox	0.6
V. indica	0.6
Raptors	19.0
Domestic dogs	4.0
Snakes	1.7
Other	1.7
Unknown	5.2

Table 5. Top models (ΔAICc < 2, likelihood >0.125) of factors affecting the proportion of interviewees in southeastern Madagascar reporting predation of their poultry by wild carnivores within the last year (2008-2009).

Model[1, 2]	K[3]	AIC_c[4]	ΔAIC_c[4]	ω_i[4]	Model likelihood
Spread, DistRoad	3	168.98	0.00	0.18	1.00
Spread, #Houses	3	169.20	0.21	0.16	0.90
DistRoad	2	169.94	0.96	0.11	0.62
Spread, Poultry	3	170.39	1.41	0.09	0.50
Poultry, DistRoad	3	170.52	1.54	0.08	0.46
#Houses, DistRoad	3	170.56	1.57	0.08	0.46
Dogs, DistRoad	3	170.68	1.70	0.08	0.43
DistForest, DistRoad	3	170.94	1.96	0.07	0.38
Spread	2	171.80	2.81	0.04	0.25
Spread, DistForest	3	172.10	3.12	0.04	0.21
Spread, Dogs	3	172.38	3.39	0.033	0.18

[1] No. of models evaluated = 22.

[2] DistForest=distance to continuous forest, DistRoad=distance to national highway, #Houses=number of households, Spread=area of the minimum convex polygon containing all interviewed households (ha)/100, Dogs=proportion of interviewees owning dogs, Poultry=proportion of interviewees owning poultry x mean flock size

[3] No. of parameters, including intercept.

[4] AICc = Akaike's Information Criterion corrected for sample size. ΔAICc = the difference between a model's AICc and that of the best-fitting model. ω_i= Akaike model weight.

Table 6. Percent of interviewees in southeastern Madagascar reporting beneficial, harmful, and/or neutral perceptions of wild and introduced carnivore species.

	% of informants[1]						
Perceptions	*Cryptoprocta ferox (n=32)*	*Eupleres goudotii (n=6)*	*Fossa fossana (n=6)*	*Galidia elegans (n=84)*	*Galidictis fasciata (n=6)*	*Felis silvestris (n=143)*	*Viverricula indica (n=49)*
Beneficial	**18.8**	**66.7**	**16.7**	**28.6**	**33.3**	**28.7**	**22.4**
Intrinsic/educational	9.4	.	.	13.1	33.3	2.1	6.1
Environmental	3.1	.	.	7.1	.	0.7	2.0
Endemicity/tourism	6.3	.	.	3.6	.	1.4	6.1
Food	.	66.7	.	1.2	.	2.8	2.0
Rodent control	.	.	.	3.6	.	18.9	4.1
Other	.	.	16.7	.	.	3.5	2.0
Harmful	**62.5**	**0.0**	**16.7**	**50.0**	**16.7**	**65.0**	**40.8**
Harms livestock	62.5	.	.	50.0	16.7	64.3	32.7
Harms people	6.2	.	.	.	.	.	.
Harms crops	.	.	.	.	.	.	8.2
Other	.	.	16.7	.	.	0.7	.
Neutral	**25.0**	**33.3**	**66.7**	**39.3**	**50.0**	**18.2**	**42.9**
No importance	12.5	16.7	50.0	25.0	33.3	11.9	30.6
Unknown	12.5	16.7	16.7	14.3	16.7	6.3	12.2

[1] The variable sample size (n) reported for each species indicates the total number of interviewees from the 17 villages samples who were familiar enough with the species to describe their perceptions of its value. The sum of percentages may exceed 100 as some informants described species as both beneficial and harmful, and/or listed more than one positive or negative value.

Table 7. Percent of informants and villages reporting hunting or killing of carnivores in southeastern Madagascar.

	Informants		Villages	
Species	n[1]	%	n[1]	%
Fossa (*Cryptoprocta ferox*)	31	32.3	9	44.4
Small-toothed civet (*Eupleres goudotii*)	6	66.7	4	50.0
Malagasy civet (*Fossa fossana*)	6	16.7	3	33.3
Ring-tailed mongoose (*Galidia elegans*)	91	15.4	16	56.3
Broad-striped mongoose (*Galidictis fasciata*)	5	0.0	5	0.0
Wild cat (*Felis silvestris*)	143	44.1	17	94.1
Small Indian civet (*Viverricula indica*)	47	29.8	17	42.9

[1] The variable sample sizes (n) reflect the number of informants familiar enough with each species to respond, and the number of villages where at least one informant responded to the question.

Table 8. Percent of interviewees in southeastern Madagascar reporting whether or not different carnivore species are killed within their communities and the reasons they are or are not hunted.

	% of informants[1]						
Hunting status	*Cryptoprocta ferox* (n=32)	*Eupleres goudotii* (n=6)	*Fossa fossana* (n=6)	*Galidia elegans* (n=84)	*Galidictis fasciata* (n=6)	*Felis silvestris* (n=143)	*Viverricula indica* (n=49)
Hunted/trapped	**32.3**	**66.7**	**16.7**	**15.4**	**0.0**	**44.1**	**31.0**
Stealing/village	25.8	.	.	3.3	.	5.6	7.1
Harms poultry	.	.	.	4.4	.	16.1	9.5
Food	3.2	66.7	.	7.7	.	21.0	16.7
Accident	.	.	.	.	.	1.4	2.4
Reason not given	3.2	.	16.7	.	.	.	.
Not hunted	**67.7**	**33.3**	**83.3**	**84.6**	**100.0**	**55.9**	**69.0**
Not eaten or used	19.4	16.7	16.7	25.3	.	12.6	16.7
Not harmful	3.2	16.7	.	7.7	20.0	2.8	9.5
Protected	3.2	.	16.7	4.4	20.0	0.7	4.8
Taboo/bad omen	.	.	16.7	6.6	.	0.7	4.8
Impractical	9.7	.	.	15.4	.	14.7	2.4
Unfamiliar	16.1	.	.	7.7	20.0	1.4	7.1
Wild animal	6.5	.	16.7	13.2	40.0	.	.
Doesn't know	9.7	.	16.7	4.4	.	7.7	.

[1] The variable sample sizes (n) reflect the number of informants familiar enough with each species to respond.

Chapter Four: Conclusion

Conservation implications and directions for future research

Due to historical and continued deforestation in Madagascar, which has resulted in an 80% reduction of core forest (> 1 km from a forest edge) since the 1950s, conservation activities in Madagascar must include efforts to connect remaining forest patches that support high levels of diversity (Harper et al., 2007; Kremen et al., 2008). In addition to simply identifying areas of high taxa diversity, we must understand species' responses to anthropogenic disturbance to best predict which species may persist in isolated, connected, and disturbed habitats (Irwin et al., 2010). Information on lemur-predator interactions in continuous vs. fragmented forest sites, and predator distribution and movement in the largely anthropogenic habitats between continuous and fragmented forests, contributes to this greater understanding.

Lemur-predator interactions

From baseline observations and experimental playbacks, I found that Milne-Edwards' sifakas (*Propithecus edwardsi*) living in an isolated forest fragment of Ialatsara Forest Station (IFS) did not lose anti-predator responses or significantly alter time allocation in the absence of their most significant native mammalian predator, the fossa (*Cryptoprocta ferox*). However, I found that fragment-living sifakas spent more time at low canopy heights and on the ground than sifakas living in the intact forest of Ranomafana National Park (RNP); this difference may be related to habitat constraints, namely a lower canopy and the necessity of ground travel between fragments, coupled with relaxed predation pressure from native ground predators and/or other unknown factors. These habitat and behavioral differences, in addition to proportionately lower downward vigilance and less frequent scanning and staring displayed by sifakas in the forest fragment, could initially make fragment-living sifakas more vulnerable to predation by recolonizing or transient fossa. The presence of all predator detection and escape elements in the repertoire of these fragment-living sifakas suggests that this population could quickly reacquire appropriate response to a returning predator; however, fossa have been known to rapidly decimate sifaka groups, leaving little opportunity for learning. The potential for predator-related local extinctions is an especially relevant concern at IFS where 4 sifaka groups live in the largest fragment, but other fragments are each inhabited by only 1 - 2 groups (Foltz, 2009). Sifakas may be less likely to recolonize empty fragments than previously occupied home ranges in continuous forest (Irwin et al., 2009).

My research, focused on a single lemur species and its known and potential predators in one region of Madagascar, highlights the need for further investigations of predator-prey interactions in fragmented landscapes in Madagascar. Additional research is needed to determine whether the behavioral differences we observed in fragment-living sifakas would result in increased predation mortality by recolonizing or novel predators, such as has been observed in other prey systems (Berger et al., 2001). Predator model exposure experiments, which test predator discrimination based on visual cues, may provide a more accurate depiction of how sifakas would respond to a predator encounter and further insight to how predator recognition and response may vary between sifaka groups exposed to different predator communities. If evidence from such experiments suggest that lemurs isolated from one or more natural predators for only 30 years could be at risk of especially high predation mortality and local extinction with the predator's return, the implementation and efficacy of predator conditioning in naïve populations should be explored. Although more frequently applied to captive-bred or translocated animals, predator conditioning has been used to train naïve prey to recognize predators and to enhance weak anti-predator responses with some, albeit variable, success (Griffin et al., 2000; Shier & Owings, 2006). The continued exposure of sifakas at IFS to potential aerial and novel ground predators, and their full repertoire of anti-predator responses, suggest that they might respond well to such techniques (Griffin et al., 2000). Finally, it would be useful to examine the impact of introduced carnivore species on lemur populations in IFS, as feral dogs (*Canis familiaris*) and wild cats (*Felis silvestris*) are known predators of large-bodied, diurnal lemurs in the dry and spiny forests of southern Madagascar (Brockman et al., 2008), but little is known about their interactions with lemurs of the eastern rainforest.

Carnivore distribution and movement across a human-disturbed landscape

My investigation of local ecological knowledge (LEK) also provides important insight to species distribution and persistence in disturbed habitats in southeastern Madagascar, and suggests possibilities for future research and outreach in the region. The locations and dates of reported observations of carnivores in the LEK survey suggest distinct distribution patterns for different carnivore species, ranging from the seemingly forest-dependent fossa, which had not recently been observed in communities > 2.5 km from continuous forest, to wild cats, which were more frequently observed at greater distances from the continuous forest. My survey also highlights ongoing human-carnivore conflict, which was previously undocumented in southeastern Madagascar, and at least some hunting of native carnivore species in many of the villages we surveyed. This conflict, which stems from poultry predation by native and introduced carnivores, would likely be exacerbated with increased fragmentation as human activity increases along the forest edge, but could also worsen with movement of previously absent carnivores into new areas through established forest corridors (Woodroffe & Ginsberg, 1998; Crooks, 2002).

In addition to providing previously missing information about the persistence or movement of Malagasy carnivores, and threats they face in the landscape between remaining natural forest patches, my study suggests a potentially important role of LEK in future studies of species distribution. With relatively little investment, monitoring programs in which local inhabitants regularly reported and pooled observations of focal species could provide real-time data on carnivore ecology as the landscape changes, and more accurate insight to trends over time than isolated, short-term surveys can provide. Additionally, the ongoing use of LEK in conservation-related research increases the involvement of local stakeholders in the development of practices that affect them and can provide an outlet for their concerns (Treves et al., 2009). A community-based monitoring program, drawing from the experience of inhabitants regularly using and traversing both natural and anthropogenic habitats, would provide useful information on the frequency of carnivore movements in these areas, rare events, and the full extent of human-carnivore conflict, such as is needed for better understanding of predator-prey interactions, the functionality of forest corridors, and the sustainability of conservation efforts.

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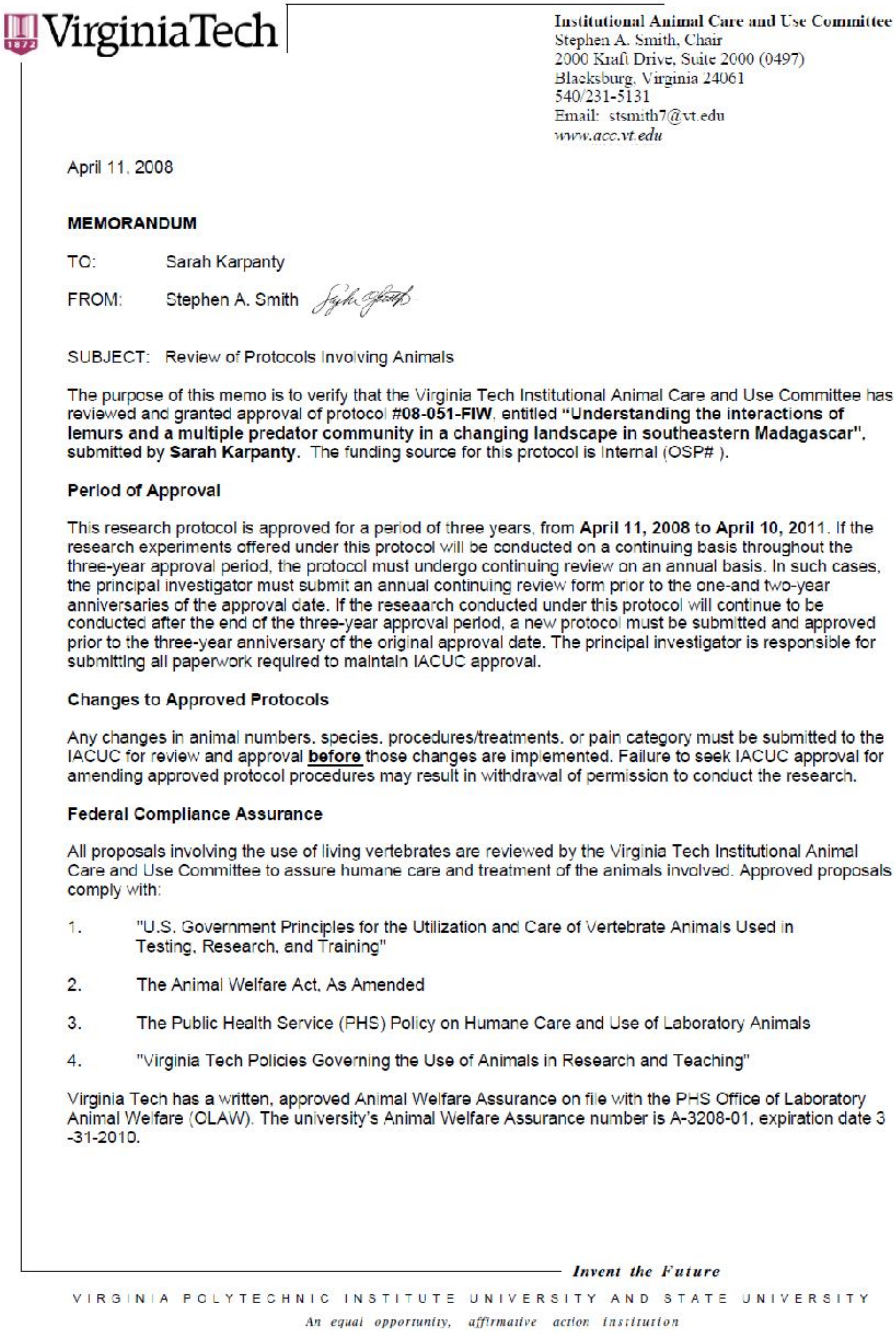
Appendix A: Institutional Animal Care and Use Committee approval letter



VirginiaTech

Institutional Animal Care and Use Committee
Stephen A. Smith, Chair
2000 Kraft Drive, Suite 2000 (0497)
Blacksburg, Virginia 24061
540/231-5131
Email: stsmith7@vt.edu
www.acc.vt.edu

April 11, 2008

MEMORANDUM

TO: Sarah Karpanty

FROM: Stephen A. Smith

SUBJECT: Review of Protocols Involving Animals

The purpose of this memo is to verify that the Virginia Tech Institutional Animal Care and Use Committee has reviewed and granted approval of protocol **#08-051-FIW**, entitled **"Understanding the interactions of lemurs and a multiple predator community in a changing landscape in southeastern Madagascar"**, submitted by **Sarah Karpanty**. The funding source for this protocol is Internal (OSP#).

Period of Approval

This research protocol is approved for a period of three years, from **April 11, 2008 to April 10, 2011**. If the research experiments offered under this protocol will be conducted on a continuing basis throughout the three-year approval period, the protocol must undergo continuing review on an annual basis. In such cases, the principal investigator must submit an annual continuing review form prior to the one-and two-year anniversaries of the approval date. If the reseaarch conducted under this protocol will continue to be conducted after the end of the three-year approval period, a new protocol must be submitted and approved prior to the three-year anniversary of the original approval date. The principal investigator is responsible for submitting all paperwork required to maintain IACUC approval.

Changes to Approved Protocols

Any changes in animal numbers, species, procedures/treatments, or pain category must be submitted to the IACUC for review and approval **before** those changes are implemented. Failure to seek IACUC approval for amending approved protocol procedures may result in withdrawal of permission to conduct the research.

Federal Compliance Assurance

All proposals involving the use of living vertebrates are reviewed by the Virginia Tech Institutional Animal Care and Use Committee to assure humane care and treatment of the animals involved. Approved proposals comply with:

1. "U.S. Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research, and Training"
2. The Animal Welfare Act, As Amended
3. The Public Health Service (PHS) Policy on Humane Care and Use of Laboratory Animals
4. "Virginia Tech Policies Governing the Use of Animals in Research and Teaching"

Virginia Tech has a written, approved Animal Welfare Assurance on file with the PHS Office of Laboratory Animal Welfare (OLAW). The university's Animal Welfare Assurance number is A-3208-01, expiration date 3-31-2010.

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Appendix B: Effects of site, group, and sex/age class on behavioral responses of Milne-Edwards' sifakas by playback stimulus

Table B1. Effects of site, group, and sex/age class on the short term behavioral responses of Milne-Edwards' sifakas in a fragmented rainforest site (IFS) and an intact rainforest site (RNP) to playback of vocalizations of cuckoo roller (*Leptosomus discolor*). Values for each effect level are model-based least square means of differences in percent of sample individuals engaged in vigilance-related behaviors, stationary activity, and travel, and their mean height in the canopy, during the 5 minutes after vs. the 5 minutes before broadcast of playback stimuli.

Effect	Vigilance (%)	Activity (%)	Travel (%)	Height difference (m)
Site				
IFS	5.0 (-12.4 - 22.4)	-8.0 (-25.4 - 9.3)	3.0 (-1.6 - 7.6)	0.6 (-0.3 - 2.5)
RNP	14.4 (-6.9 - 35.8)	-13.2 (-34.4 - 8.1)	-1.3 (-6.9 - 4.4)	-0.1 (-0.6 - 1.4)
$F_{1,8}$[a]	0.4	0.12	1.19	0.7
P-value	0.54	0.74	0.31	0.43
Group[b]				
IFS1	13.3 (-16.8 - 43.5)	-13.3 (-43.4 - 16.7)	0.0 (-8.0 - 8.0)	-0.2 (-0.8 - 1.9)
IFS4	4.4 (-25.7 - 34.6)	-6.8 (-36.9 - 23.2)	2.4 (-5.6 - 10.4)	3.3 (0.1 - 15.7)
IFS5	-2.7 (-32.9 - 27.5)	-4.0 (-34.0 - 26.1)	6.7 (-1.3 - 14.7)	0.3 (-0.7 - 4.1)
RNP1	24.3 (-5.9 - 54.4)	-24.1 (-54.2 - 5.9)	-0.2 (-8.2 - 7.9)	-0.3 (-0.8 - 1.6)
RNP2	4.6 (-25.5 - 34.8)	-2.2 (-32.3 - 27.8)	-2.4 (-10.4 - 5.6)	0.3 (-0.7 - 4.1)
$F_{3,8}$[a]	0.41	0.37	0.45	1.14
P-value	0.75	0.78	0.72	0.39
Sex/age class[c]				
F	20.6 (-3.0 - 44.1)	-18.7 (-42.1 - 4.7)	-1.9 (-8.1 - 4.4)	0.1 (-0.6 - 2.1)
M	4.6 (-19.0 - 28.1)	-8.1 (-31.6 - 15.3)	3.6 (-2.7 - 9.8)	1.4 (-0.1 - 6.0)
J	4.1 (-19.4 - 27.6)	-5.0 (-28.4 - 18.4)	0.9 (-5.3 - 7.2)	-0.3 (-0.8 - 1.0)
$F_{2,8}$[a]	0.56	0.33	0.66	1.26
P-value	0.59	0.73	0.54	0.33

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male

Table B2. Effects of site, group, and sex/age class on the short term behavioral responses of Milne-Edwards' sifakas in a fragmented rainforest site (IFS) and an intact rainforest site (RNP) to playback of vocalizations of American robin (*Turdus migratorius*). Values for each effect level are model-based least square means of differences in percent of sample individuals engaged in vigilance-related behaviors, stationary activity, and travel, and their mean height in the canopy, during the 5 minutes after vs. the 5 minutes before broadcast of playback stimuli.

Effect	Vigilance (%)	Activity (%)	Travel (%)	Height difference (m)
Site				
IFS	32.5 (14.9 - 50.0)	-33.7 (-52.3 - -15.1)	1.3 (-3.4 - 5.9)	-0.2 (-0.6 - 0.3)
RNP	15.9 (-5.6 - 37.3)	-18.2 (-41.0 - 4.6)	2.3 (-3.4 - 8.0)	-0.3 (-0.7 - 0.3)
$F_{1,8}$[a]	1.24	0.97	0.07	0.06
P-value	0.30	0.35	0.80	0.81
Group[b]				
IFS1	-2.7 (-33.0 - 27.7) A	2.7 (-29.5 - 34.9) A	0.0 (-8.0 - 8.0)	0.0 (-0.6 - 1.6)
IFS4	21.9 (-8.4 - 52.3) AB	-25.7 (-58.0 - 6.5) AB	3.8 (-4.2 - 11.8)	-0.2 (-0.7 - 1.0)
IFS5	78.2 (47.8 - 108.5) B	-78.2 (-110.4 - -45.9) B	0.0 (-8.0 - 8.0)	-0.4 (-0.8 - 0.4)
RNP1	15.6 (-14.8 - 45.9) AB	-20.2 (-52.4 - 12.1) AB	4.6 (-3.4 - 12.6)	-0.5 (-0.8 - 0.2)
RNP2	16.2 (-14.2 - 46.5) AB	-16.2 (-48.4 - 16.0) AB	0.0 (-8.0 - 8.0)	0.0 (-0.6 - 1.6)
$F_{3,8}$[a]	4.3	3.74	0.36	0.63
P-value	**0.04**	**0.06**	0.78	0.62
Sex/age class[c]				
F	24.0 (0.3 - 47.6)	-22.6 (-47.8 - 2.5)	-1.3 (-7.6 - 4.9)	-0.3 (-0.7 - 0.4)
M	26.0 (2.3 - 49.6)	-28.6 (-53.8 - -3.5)	2.7 (-3.6 - 8.9)	-0.1 (-0.6 - 0.8)
J	22.6 (-1.1 - 46.3)	-26.6 (-51.7 - -1.4)	4.0 (-2.2 - 10.3)	-0.4 (-0.7 - 0.3)
$F_{2,8}$[a]	0.02	0.05	0.69	0.16
P-value	0.98	0.95	0.53	0.85

a F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

b Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

c F=adult female, M=adult male, J=juvenile female or male

Table B3. Effects of site, group, and sex/age class on the short term behavioral responses of Milne-Edwards' sifakas in a fragmented rainforest site (IFS) and an intact rainforest site (RNP) to playback of vocalizations of Henst's goshawk (*Accipiter henstii*). Values for each effect level are model-based least square means of differences in percent of sample individuals engaged in vigilance-related behaviors, stationary activity, and travel, and their mean height in the canopy, during the 5 minutes after vs. the 5 minutes before broadcast of playback stimuli.

Effect	Vigilance (%)	Activity (%)	Travel (%)	Height difference (m)
Site				
IFS	33.5 (16.4 - 50.6)	-37.9 (-54.3 - -21.5)	4.4 (2.0 - 6.7)	-0.5 (-0.7 - 0.0)
RNP	-3.0 (-24.0 - 18.0)	2.9 (-17.1 - 23.0)	0.1 (-2.8 - 2.9)	-0.8 (-0.9 - -0.7)
$F_{1,8}$[a]	6.29	8.58	4.71	5.3
P-value	**0.037**	**0.019**	**0.06**	**0.05**
Group[b]				
IFS1	34.9 (5.3 - 64.6)	-50.5 (-78.9 - -22.1)	15.6 (11.5 - 19.6) B	-0.6 (-0.9 - 0.3) A
IFS4	10.5 (-19.2 - 40.1)	-8.3 (-36.6 - 20.1)	-2.2 (-6.3 - 1.8) A	-0.4 (-0.8 - 0.6) A
IFS5	55.1 (25.4 - 84.7)	-54.9 (-83.3 - -26.5)	-0.2 (-4.2 - 3.9) A	-0.3 (-0.8 - 1.0) A
RNP1	5.4 (-24.2 - 35.0)	-5.4 (-33.8 - 23.0)	0.0 (-4.1 - 4.1) A	-1.0 (-1.0 - -0.9) B
RNP2	-11.4 (-41.0 - 18.3)	11.3 (-17.1 - 39.6)	0.1 (-3.9 - 4.2) A	0.0 (-0.7 - 2.0) A
$F_{3,8}$[a]	1.49	2.1	13.25	6.63
P-value	0.29	0.18	**0.0018**	**0.01**
Sex/age class[bc]				
F	5.0 (-18.1 - 28.2)	-9.9 (-32.1 - 12.2)	4.9 (1.7 - 8.1) B	-0.5 (-0.8 - 0.2)
M	27.4 (4.3 - 50.5)	-31.0 (-53.2 - -8.9)	3.7 (0.5 - 6.8) A	-0.9 (-0.9 - -0.7)
J	13.3 (-9.8 - 36.4)	-11.4 (-33.6 - 10.7)	-1.9 (-5.0 - 1.3) A	-0.6 (-0.8 - -0.2)
$F_{2,8}$[a]	0.84	0.99	4.53	2.3
P-value	0.47	0.41	**0.048**	0.16

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male, SM=sub-adult male

Madagascar harrier hawk (*Polyboroides radiatus*)

Table B4. Effects of site, group, and sex/age class on the short term behavioral responses of Milne-Edwards’ sifakas in a fragmented rainforest site (IFS) and an intact rainforest site (RNP) to playback of vocalizations of Madagascar harrier hawk (*Polyboroides radiatus*). Values for each effect level are model-based least square means of differences in percent of sample individuals engaged in vigilance-related behaviors, stationary activity, and travel, and their mean height in the canopy, during the 5 minutes after vs. the 5 minutes before broadcast of playback stimuli.

Effect	Vigilance (%)	Activity (%)	Travel (%)	Height difference (m)
Site				
IFS	55.6 (38.9 - 72.2)	-61.1 (-77.3 - -45.0)	5.6 (-0.1 - 11.3)	-0.9 (-1.0 - -0.8)
RNP	43.6 (26.9 - 60.3)	-51.3 (-67.4 - -35.1)	7.7 (2.0 - 13.4)	-0.8 (-0.9 - -0.7)
$F_{1,6}$[a]	0.97	0.7	0.26	0.5
P-value	0.3621	0.4347	0.6269	0.5075
Group				
IFS1	42.2 (18.7 - 65.8)	-37.8 (-60.6 - -14.9) A	-4.4 (-12.5 - 3.6) A	-0.4 (-0.8 - 0.7) A
IFS5	68.9 (45.3 - 92.4)	-84.4 (-107.3 - -61.6) A	15.6 (7.5 - 23.6) B	-1.0 (-1.0 - -0.9) B
RNP1	41.3 (17.8 - 64.9)	-52.1 (-74.9 - -29.3) A	10.8 (2.7 - 18.8) AB	-0.7 (-0.9 - 0.0) A
RNP2	45.9 (22.3 - 69.4)	-50.5 (-73.3 - -27.6) A	4.6 (-3.5 - 12.7) AB	-0.9 (-1.0 - -0.8) AB
$F_{2,6}$[a]	1.25	3.95	6.37	10.15
P-value	0.3529	**0.0805**	**0.0328**	**0.0119**
Sex/age class				
ADF	55.9 (35.5 - 76.3)	-61.4 (-81.1 - -41.6)	5.5 (-1.5 - 12.4)	-0.8 (-0.9 - -0.4)
ADM	53.1 (32.7 - 73.5)	-56.6 (-76.3 - -36.8)	3.4 (-3.5 - 10.4)	-0.9 (-1.0 - -0.9)
JUV	39.7 (19.3 - 60.1)	-50.7 (-70.4 - -30.9)	11.0 (4.0 - 17.9)	-0.8 (-0.9 - -0.5)
$F_{2,6}$[a]	0.68	0.28	1.17	2.42
P-value	0.5421	0.7675	0.3716	0.1699

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male, SM=sub-adult male

Table B5. Effects of site, group, and sex/age class on the short term behavioral responses of Milne-Edwards' sifakas in a fragmented rainforest site (IFS) and an intact rainforest site (RNP) to playback of vocalizations of fossa (*Cryptoprocta ferox*). Values for each effect level are model-based least square means of differences in percent of sample individuals engaged in vigilance-related behaviors, stationary activity, and travel, and their mean height in the canopy, during the 5 minutes after vs. the 5 minutes before broadcast of playback stimuli.

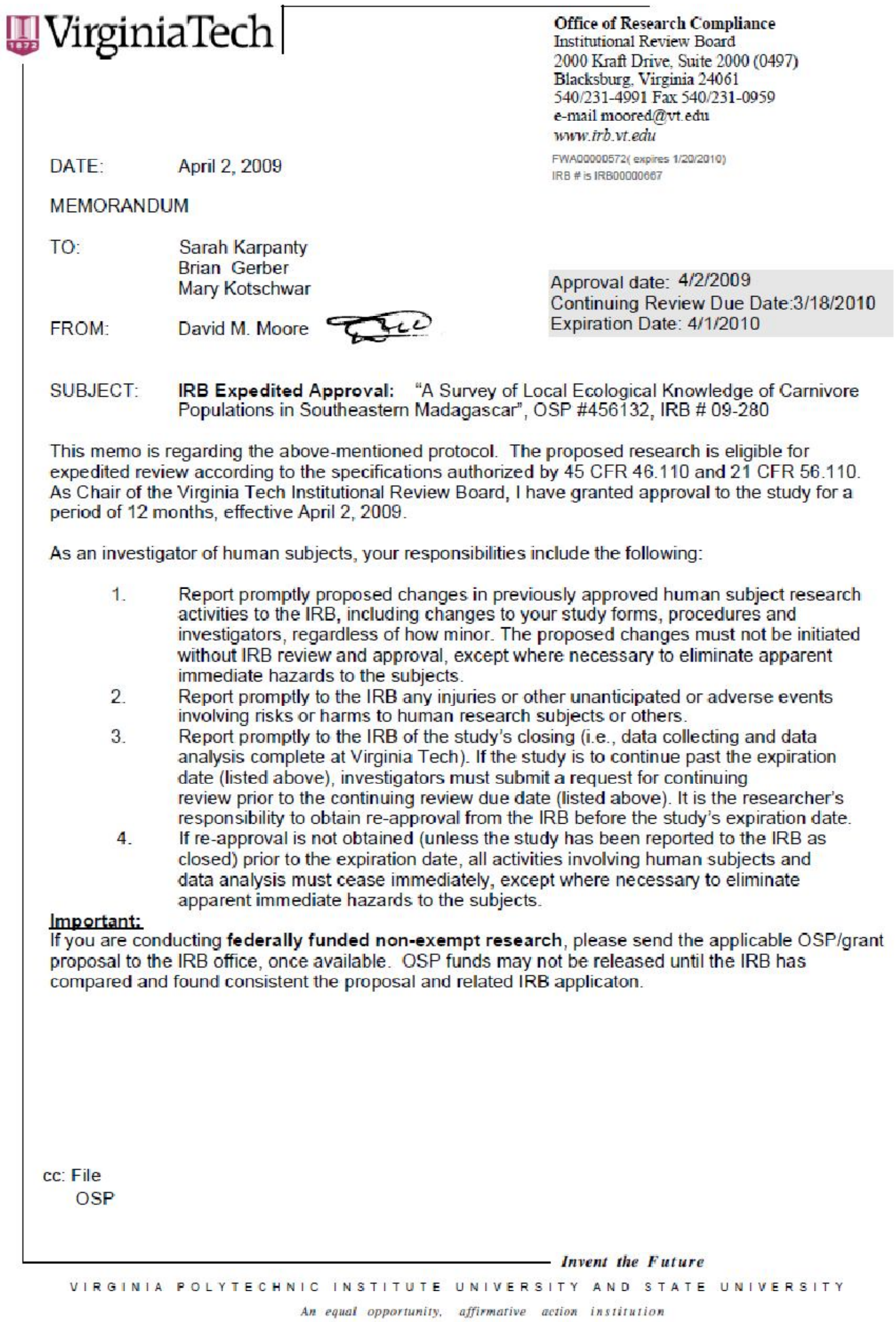
Effect	Vigilance (%)	Activity (%)	Travel (%)	Height difference (m)
Site				
IFS	42.0 (27.8 - 56.2)	-43.6 (-56.4 - -30.7)	1.6 (-2.9 - 6.1)	-0.3 (-0.8 - 1.4)
RNP	28.6 (11.2 - 46.0)	-28.1 (-43.8 - -12.4)	-0.5 (-6.0 - 5.0)	-0.5 (-0.9 - 1.2)
$F_{1,8}$[a]	1.23	2.01	0.3	0.11
P-value	0.3002	0.1941	0.5988	0.7464
Group[b]				
IFS1	34.1 (9.5 - 58.7)	-46.3 (-68.6 - -24.1)	12.3 (4.5 - 20.1) A	-0.6 (-1.0 - 2.1)
IFS4	29.2 (4.6 - 53.8)	-21.9 (-44.1 - 0.4)	-7.3 (-15.1 - 0.5) B	-0.6 (-1.0 - 2.1)
IFS5	62.7 (38.1 - 87.3)	-62.5 (-84.8 - -40.3)	-0.2 (-8.0 - 7.6) AB	1.4 (-0.7 - 18.6)
RNP1	26.9 (2.3 - 51.5)	-26.9 (-49.2 - -4.7)	0.0 (-7.8 - 7.8) AB	0.0 (-0.9 - 7.2)
RNP2	30.3 (5.7 - 54.9)	-29.3 (-51.5 - -7.1)	-1.0 (-8.8 - 6.8) AB	-0.8 (-1.0 - 1.0)
$F_{3,8}$[a]	1.26	1.96	3.74	0.84
P-value	0.3515	0.1984	**0.0602**	0.5076
Sex/age class[bc]				
F	35.0 (15.8 - 54.1) AB	-33.4 (-50.8 - -16.1) AB	-1.5 (-7.6 - 4.6)	-0.5 (-0.9 - 1.7)
M	14.4 (-4.8 - 33.6) A	-18.4 (-35.7 - -1.0) A	4.0 (-2.1 - 10.1)	-0.7 (-1.0 - 0.3)
J	56.5 (37.4 - 75.7) B	-55.7 (-73.1 - -38.4) B	-0.8 (-6.9 - 5.3)	0.5 (-0.7 - 7.0)
$F_{2,8}$[a]	4.23	4.12	0.85	1.08
P-value	**0.0557**	**0.0589**	0.4623	0.3836

[a] F-ratio (df numerator, df denominator) from type III test of fixed effects (PROC MIXED, SAS 9.2, Cary, NC)

[b] Pairwise comparisons conducted only when significant effect observed, estimates with the same capital letter are not significantly different (pairwise t-tests, adjusted p-value < 0.1).

[c] F=adult female, M=adult male, J=juvenile female or male, SM=sub-adult male

Appendix C: Institutional Review Board approval letter



VirginiaTech

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FWA00000572(expires 1/20/2010)
IRB # is IRB00000667

DATE: April 2, 2009

MEMORANDUM

TO: Sarah Karpanty
Brian Gerber
Mary Kotschwar

FROM: David M. Moore

Approval date: 4/2/2009
Continuing Review Due Date:3/18/2010
Expiration Date: 4/1/2010

SUBJECT: **IRB Expedited Approval:** "A Survey of Local Ecological Knowledge of Carnivore Populations in Southeastern Madagascar", OSP #456132, IRB # 09-280

This memo is regarding the above-mentioned protocol. The proposed research is eligible for expedited review according to the specifications authorized by 45 CFR 46.110 and 21 CFR 56.110. As Chair of the Virginia Tech Institutional Review Board, I have granted approval to the study for a period of 12 months, effective April 2, 2009.

As an investigator of human subjects, your responsibilities include the following:

1. Report promptly proposed changes in previously approved human subject research activities to the IRB, including changes to your study forms, procedures and investigators, regardless of how minor. The proposed changes must not be initiated without IRB review and approval, except where necessary to eliminate apparent immediate hazards to the subjects.
2. Report promptly to the IRB any injuries or other unanticipated or adverse events involving risks or harms to human research subjects or others.
3. Report promptly to the IRB of the study's closing (i.e., data collecting and data analysis complete at Virginia Tech). If the study is to continue past the expiration date (listed above), investigators must submit a request for continuing review prior to the continuing review due date (listed above). It is the researcher's responsibility to obtain re-approval from the IRB before the study's expiration date.
4. If re-approval is not obtained (unless the study has been reported to the IRB as closed) prior to the expiration date, all activities involving human subjects and data analysis must cease immediately, except where necessary to eliminate apparent immediate hazards to the subjects.

<u>Important:</u>
If you are conducting **federally funded non-exempt research**, please send the applicable OSP/grant proposal to the IRB office, once available. OSP funds may not be released until the IRB has compared and found consistent the proposal and related IRB applicaton.

cc: File
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Appendix D: Photograph exemplars of carnivore species used in local ecological knowledge interviews

Scientific name: *Cryptoprocta ferox*
Common name: Fossa
Local names: Fosa, fosa varika, viro

Scientific name: *Eupleres goudotii*
Common names: Small-toothed civet, falanouc
Local names: Fanaloka, fanalo, tombosodina, renibetrandraka

Scientific name: *Fossa fossana*
Common names: Malagasy civet, fanaloka
Local names: Fanaloka, fanalo, halazana, atamba

Scientific name : *Galidia elegans*
Common name : Ring-tailed mongoose
Local names: Vontsira

Figure D1. Example photographs used in local ecological knowledge survey for species identification. Images from photographic capture surveys in southeastern Madagascar (Gerber et al., 2010), used with permission from B. Gerber. (Continued on next page)

Scientific name: *Galidictis fasciata*
Common name: Broad-striped mongoose
Local names: Vontsira fotsy

Scientific name: *Felis silvestris*
Common names: Wild cat, feral cat
Local names: Ampaha, piso dia
*Introduced species

Scientific name : *Viverricula india*
Common name : Small Indian civet
Local names: Jaboady, halazana, ampaha
* Introduced species

Figure D1 continued

Appendix E: Outline of questions in English and Malagasy used in local ecological knowledge interviews

English version

CARNIVORE OBSERVATIONS AND EXPERIENCE

1. Do you know this animal? What is it called? (Showing photographs of species and asking clarification questions if needed)
2. Have you seen this species?
    a. When? (Since the last rice harvest? During the dry or rainy season? At night or day? (If a long time use presidents, cyclones, park creation as time references)
    b. How often? (1x a day, 1x a week, 1x a month, a few times a year, only a few times ever)
    c. Where? (in the village, in the fields, in the forest, on the road etc.)
    d. What was the animal doing? (Moving quickly or slowly, resting, eating, other, don't know)
    e. What were you doing at the time?

3. Have you observed feces or tracks of any of this animal? If no, skip to 4
    a. How are the feces (tracks) of this animal different from another (ex: dog or cat)?
    b. Where do you find the feces (tracks)? (in the village, in the fields, in the forest, on the road etc.)
    c. When? (Since the last harvest? During the rainy season? At night or day? If a long time, use presidencies or cyclones as references)
    d. How often? (1x a day, 1x a week, 1x a month, a few times a year, only a few times ever)

4. Is there a special time or season when you see the animal more often?
    a. Why do you think that is?

5. Do you see this species more often, less often, or the same amount as before (again, use presidencies and cyclones as time references)?
    a. Do you have any ideas about why you see them more/less often?

6. Do you consider this species to be beneficial, harmful, or of no importance in your life?
    a. Why?

7. Is this species hunted in this community? (Why or why not?)

BIOGRAPHICAL QUESTIONS

8. Do you raise animals? Which kinds (chickens, ducks, zebu, pigs, dogs, cats, etc.)? For each kind mentioned, ask:
    a. How many?
    b. Since when/for how many years?
    c. Where do you keep them in the day and at night?

9. Have any of your animals been killed by wild predators?

10. Do you know of other people who have lost livestock to wild predators?

11. What do people here do to prevent livestock predation by wild predators?

12. Do you feel that this/these method(s) are effective?

13. How long have you lived in this commune?

14. In which villages?

15. How long have you lived in this village?

16. What is your primary occupation? Secondary occupation(s)?

17. Where are your fields? How often do you go there? With how many people?

18. Do you go to the natural forest? Eucalyptus forest? Pine forest?
    a. Where is the forest you go to?
    b. How often do you go there?
    c. With how many people?

19. Do you go to market?
    a. Which market(s)?
    b. How often do you go?
    c. With how many people?

Malagasy version

CARNIVORE OBSERVATIONS AND EXPERIENCE:

1. Fantatrao ve ity biby ity? Inona no anarana iantsoanareo azy? (Manehoa sary biby)

2. Efa hitanao ve ity karazam-biby ity?
    a. Impiry? (Isan'andro, isan-kerinandro, isam-bolana, indraindray isan-taona, mahalana dia mahalana)
    b. Oviana? (Taona? Volana? Fahavaratra/Ririnina/Lohataona? Tamin'ny antoandro sa tamin'ny alina? Raha efa ela dia afaka mampiasa anarana mpitondra fanjakana, cyclone na ny fotoana nisokafan'ny parc)
    c. Taiza? (teto an-tanana, tany an-tsaha, tany anaty ala, tany an-dalana…)
    d. Inona no nataon'ilay biby? (Mandeha miadana sa mihazakazaka, maka aina, mihinan-kanina, zavatra hafa, tsy fantatra)
    e. Inona no nataonao tamin'izay fotoana izay?

3. Fantatrao tsara ve ny dian-tongony sy tainy?
    a. Manahoana no anavahanao ny tongony sy ny tainy?
    b. Aiza no nahitanao azy?
    c. Ary impiry? Oviana?

4. Amin'ny fotoana inona izany no tena fahitanao azy? (Oh: .....)
    a. Moa ve efa mba nieritreritra ianao hoe maninona?

5. Ary mitovy amin'ny taloha ve? Fahitanao azy amin'izao?
    a. Moa ve efa mba nieritreritra ianao hoe maninona?

6. Ahoana ny fiheveranao an'ireo biby ireo eo amin'ny fiainanao: ahitana soa, tsy misy dikany, miteraka fatiantoka?
    a. Nahoana?

7. Misy mihaza na misambotra an'ireny biby ireny ve eto amin'ity faritra ity? Nahoana?

LIVESTOCK PREDATION:

8. Miompy biby ve ianao? Manana alika sy saka na biby hafa ve ianao?
    a. Firy?
    b. Hatramin'ny oviana?
    c. Aiza no ametrahanao azy ireo? (trano, vala…)

9. Moa ve nisy tamin’ny biby fiompinao novonoin’ny bibidia?

10. Mahafantatra biby fiompin’olon-kafa notafihin’ireny biby ireny teto an-tanana ve ianao?

11. Inona no ataon’ny mponina eto an-tanana mba hisorohana ny fandripahana biby fiompy ataon’ireny biby ireny?

12. Moa mahomby ve ireny fomba ireny?

BIOGRAPHICAL QUESTIONS

13. Efa hatramin’ny oviana no nipetrahanao teto amin’ity faritra ity?

14. Aiza ny tanananao?

15. Efa hatramin’ny oviana ianao no nipetraka tao amin’io Tanana io?

16. Inona no tena asanao? Moa ve mbola misy asa hafa ankoatra izay ataonao?

17. Aiza ny tanimbolinao ary impiry ianao no miasa any?
    a. Firy ny olona miaraka?

18. Impiry ianao no mandeha any anaty ala?
    a. Aiza?
    b. Firy ny olona miaraka?
    c. Inona no atao?

19. Impiry ianao mandeha any an-tsena?
    a. Aiza?
    b. Firy ny olona miaraka?

Appendix F: Candidate models of landscape- and community-level factors affecting proportion of interviewees observing carnivore species

Table F1. Logistic regression models of factors affecting the proportion of interviewees in southeastern Madagascar reporting observations of *Cryptoprocta ferox* within 2.5 km of their village in the last 5 years (2004 – 2009).

Model[1]	K^2	AIC_c^3	ΔAIC_c^3	ω_i^3	Model likelihood
DistForest, #Houses	3	70.04	0.00	0.24	1.00
DistForest, Spread	3	70.47	0.43	0.20	0.81
DistForest	2	70.73	0.69	0.17	0.71
DistForest, Dogs	3	71.04	1.01	0.15	0.60
DistForest, Poultry	3	71.28	1.24	0.13	0.54
DistForest, DistRoad	3	71.72	1.69	0.11	0.43
#Houses, DistRoad	3	91.57	21.53	0.00	0.00
#Houses, Spread	3	91.82	21.78	0.00	0.00
Poultry, DistRoad	3	92.10	22.06	0.00	0.00
#Houses, Dogs	3	93.11	23.07	0.00	0.00
#Houses	2	94.27	24.23	0.00	0.00
Spread, DistRoad	3	94.78	24.74	0.00	0.00
#Houses, Poultry	3	94.85	24.81	0.00	0.00
Poultry, Dogs	3	95.15	25.12	0.00	0.00
DistRoad	2	95.56	25.52	0.00	0.00
Dogs, DistRoad	3	95.79	25.75	0.00	0.00
Poultry, Spread	3	96.49	26.45	0.00	0.00
Poultry	2	100.10	30.06	0.00	0.00
Spread, Dogs	3	101.60	31.56	0.00	0.00
Dogs	2	102.67	32.64	0.00	0.00
Intercept only	1	103.61	33.57	0.00	0.00
Spread	2	104.61	34.57	0.00	0.00

[1] DistForest=distance to continuous forest, DistRoad=distance to national highway, #Houses=number of households, Spread=area of the minimum convex polygon containing all interviewed households (ha)/100, Dogs=proportion of interviewees owning dogs, Cats=proportion of interviewees owning cats, Poultry=proportion of interviewees owning poultry x mean flock size

[2] No. of parameters, including intercept.

[3] AICc = Akaike's Information Criterion corrected for sample size. ΔAICc = the difference between a model's AICc and that of the best-fitting model. w_i= Akaike model wt. Statistics are only comparable within species.

Table F2. Logistic regression models of factors affecting the proportion of interviewees in southeastern Madagascar reporting observations of *Galidia elegans* within 2.5 km of their village in the last 5 years (2004 – 2009).

Model[1, 2]	K[3]	AIC_c[4]	ΔAIC_c[4]	ω_i[4]	Model likelihood
DistForest, Spread	3	181.99	0.00	0.60	1.00
DistForest, Poultry	3	183.75	1.76	0.25	0.41
DistForest, Cats	3	186.71	4.72	0.06	0.09
DistForest, #Houses	3	187.21	5.22	0.04	0.07
DistForest, Dogs	3	188.51	6.52	0.02	0.04
DistForest, DistRoad	3	189.61	7.62	0.01	0.02
DistForest	2	191.14	9.15	0.01	0.01
Poultry, Dogs	3	210.69	28.70	0.00	0.00
Cats, DistRoad	3	216.22	34.23	0.00	0.00
Poultry, DistRoad	3	216.44	34.45	0.00	0.00
Poultry, Cats	3	218.77	36.78	0.00	0.00
#Houses, Cats	3	219.00	37.01	0.00	0.00
Dogs, Cats	3	219.17	37.18	0.00	0.00
Spread, Poultry	3	220.04	38.05	0.00	0.00
Spread, Cats	3	220.45	38.46	0.00	0.00
#Houses, Dogs	3	220.70	38.70	0.00	0.00
Cats	2	220.70	38.71	0.00	0.00
Spread, Dogs	3	221.29	39.30	0.00	0.00
Spread, DistRoad	3	221.72	39.73	0.00	0.00
#Houses, DistRoad	3	221.82	39.83	0.00	0.00
Poultry	2	222.13	40.14	0.00	0.00
#Houses, Poultry	3	222.20	40.21	0.00	0.00
#Houses	2	223.99	42.00	0.00	0.00
DistRoad	2	224.44	42.45	0.00	0.00
#Houses, Spread	3	224.54	42.55	0.00	0.00
Dogs, DistRoad	3	225.43	43.44	0.00	0.00
Dogs	2	226.59	44.60	0.00	0.00
Intercept only	1	227.82	45.83	0.00	0.00
Spread	2	228.40	46.41	0.00	0.00

[1] DistForest=distance to continuous forest, DistRoad=distance to national highway, #Houses=number of households, Spread=area of the minimum convex polygon containing all interviewed households (ha)/100, Dogs=proportion of interviewees owning dogs, Cats=proportion of interviewees owning cats, Poultry=proportion of interviewees owning poultry x mean flock size

[2] No. of parameters, including intercept.

[3] AICc = Akaike's Information Criterion corrected for sample size. ΔAICc = the difference between a model's AICc and that of the best-fitting model. w_i= Akaike model wt. Statistics are only comparable within species.

Table F3. Logistic regression models of factors affecting the proportion of interviewees in southeastern Madagascar reporting observations of *Felis silvestris* within 2.5 km of their village in the last 5 years (2004 – 2009).

Model[1]	K[2]	AIC_c[3]	ΔAIC_c[3]	ω_i[3]	Model likelihood
DistForest, DistRoad	3	226.37	0.00	0.27	1.00
DistForest, #Houses	3	226.67	0.30	0.23	0.86
DistForest	2	227.86	1.49	0.13	0.48
DistForest, Dogs	3	228.33	1.96	0.10	0.38
DistForest, Cats	3	228.57	2.20	0.09	0.33
DistForest, Spread	3	228.60	2.23	0.09	0.33
DistForest, Poultry	3	228.85	2.48	0.08	0.29
DistRoad	2	234.60	8.23	0.00	0.02
#Houses, DistRoad	3	234.67	8.30	0.00	0.02
Poultry, DistRoad	3	235.02	8.65	0.00	0.01
Cats, DistRoad	3	235.50	9.13	0.00	0.01
Spread, DistRoad	3	235.53	9.16	0.00	0.01
Dogs, DistRoad	3	235.55	9.18	0.00	0.01
#Houses, Spread	3	235.59	9.22	0.00	0.01
#Houses, Dogs	3	238.44	12.07	0.00	0.00
Poultry, Dogs	3	240.00	13.63	0.00	0.00
Spread, Poultry	3	241.14	14.77	0.00	0.00
Dogs	2	242.15	15.78	0.00	0.00
Spread, Dogs	3	243.05	16.68	0.00	0.00
Dogs, Cats	3	243.15	16.78	0.00	0.00
Spread, Cats	3	244.03	17.66	0.00	0.00
Spread	2	244.98	18.61	0.00	0.00
#Houses, Poultry	3	247.87	21.50	0.00	0.00
#Houses	2	248.42	22.05	0.00	0.00
#Houses, Cats	3	248.64	22.27	0.00	0.00
Intercept only	1	249.13	22.76	0.00	0.00
Cats	2	249.97	23.60	0.00	0.00
Poultry	2	250.06	23.69	0.00	0.00
Poultry, Cats	3	250.96	24.59	0.00	0.00

[1] DistForest=distance to continuous forest, DistRoad=distance to national highway, #Houses=number of households, Spread=area of the minimum convex polygon containing all interviewed households (ha)/100, Dogs=proportion of interviewees owning dogs, Cats=proportion of interviewees owning cats, Poultry=proportion of interviewees owning poultry x mean flock size

[2] No. of parameters, including intercept.

[3] AICc = Akaike's Information Criterion corrected for sample size. ΔAICc = the difference between a model's AICc and that of the best-fitting model. w_i= Akaike model wt. Statistics are only comparable within species.

Table F4. Logistic regression models of factors affecting the proportion of interviewees in southeastern Madagascar reporting observations of *Viverricula indica* within 2.5 km of their village in the last 5 years (2004 – 2009).

Model[1]	K[2]	AIC_c[3]	ΔAIC_c[3]	ω_i[3]	Model likelihood
#Houses	2	169.65	0.00	0.12	1.00
#Houses, Poultry	3	170.41	0.76	0.08	0.69
#Houses, Spread	3	170.47	0.82	0.08	0.66
#Houses, DistForest	3	170.58	0.92	0.08	0.63
#Houses, DistRoad	3	170.61	0.96	0.07	0.62
#Houses, Dogs	3	170.65	0.99	0.07	0.61
Poultry	2	171.23	1.57	0.05	0.46
Spread	2	171.56	1.91	0.05	0.39
Spread, Dogs	3	171.60	1.95	0.05	0.38
Spread, DistRoad	3	171.70	2.04	0.04	0.36
Poultry, Dogs	3	171.85	2.20	0.04	0.33
Poultry, Spread	3	172.00	2.35	0.04	0.31
Poultry, DistRoad	3	172.06	2.40	0.04	0.30
DistForest, Poultry	3	172.13	2.48	0.03	0.29
Intercept only	1	172.31	2.66	0.03	0.26
DistForest, Spread	3	172.49	2.84	0.03	0.24
Dogs	2	173.24	3.59	0.02	0.17
DistForest	2	173.25	3.60	0.02	0.17
DistRoad	2	173.28	3.63	0.02	0.16
Dogs, DistRoad	3	174.03	4.37	0.01	0.11
DistForest, DistRoad	3	174.11	4.45	0.01	0.11
DistForest, Dogs	3	174.22	4.57	0.01	0.10

[1] DistForest=distance to continuous forest, DistRoad=distance to national highway, #Houses=number of households, Spread=area of the minimum convex polygon containing all interviewed households (ha)/100, Dogs=proportion of interviewees owning dogs, Cats=proportion of interviewees owning cats, Poultry=proportion of interviewees owning poultry x mean flock size

[2] No. of parameters, including intercept.

[3] AICc = Akaike's Information Criterion corrected for sample size. ΔAICc = the difference between a model's AICc and that of the best-fitting model. w_i= Akaike model wt. Statistics are only comparable within species.