Human Impact on Space Use, Activity Patterns, and Prey Abundance of Madagascar's
Largest Natural Predator, Cryptoprocta ferox

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This thesis titled
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Largest Natural Predator, Cryptoprocta ferox

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ABSTRACT

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Human Impact on Space Use, Activity Patterns, and Prey Abundance of Madagascar’s Largest Natural Predator, Cryptoprocta ferox

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Madagascar is home to a broad array of intriguing, endemic, and increasingly endangered species. The fosa (*Cryptoprocta ferox*) is the largest living (non-introduced) mammalian carnivore on the island and is considered a keystone species for maintaining ecosystem complexity in a broad range of Madagascar’s forested habitats. Sadly, the fosa is threatened, with viable populations remaining in only two protected areas. In this context, complex interactions among fosa, prey, and myriad introduced species, reveal a dynamic that is increasingly sensitive to human pressures (e.g., hunting, deforestation for agriculture and fuel wood). This project assembles detailed geographic information to augment long-term data collection and help inform the fosa conservation effort.

Research was conducted in Ankarafantsika National Park, a dry deciduous forest in the northwest region of the country, and one of the two places where viable fosa populations still exist. Species encounters and trap rates, roadkill patterns, and the spatial and activity patterns of GPS-collared fosas were analyzed to gather a comprehensive assessment on habitat pressures experienced by the fosa. Species encounter and trap rates documented a shift in prey item encounters over time. Roadkill surveys, together with the roadkill death of one of the GPS-collared study animals, demonstrated failure of current mitigation efforts in addressing roadkill dangers. Fosa space use and activity patterns
clearly reveal that they rely almost exclusively upon forested habitats, and that they avoid human settlements. Interestingly, although fosa do rely heavily on forest habitat, their ability to use forest edges and narrow forested strips suggests that corridors may be a viable method to enhance habitat connectivity and promote positive conservation outcomes.
ACKNOWLEDGMENTS

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CHAPTER 1: INTRODUCTION

Global Human Impact on Species

For thousands of years, humans have played a significant role in shaping the ecosystems in which they reside. Recent research has demonstrated that as far back as the early Holocene (~11,000 years ago), humans induced noticeable shifts in species compositions in North American plant and animal communities (Lyons et al. 2016). Undoubtedly, humans have also profoundly influenced the ecological communities of other regions such as Europe, Asia, and Africa.

The extraordinary rate of human population growth has put extreme pressure on a broad range of species in diverse habitats around the globe. Presently, the extinction rate is 100 times greater than the background rate of 0.1 – 1 species/million species/year. Some of the greatest biodiversity loss is occurring in the tropical rainforests of the economically-developing world. Forested habitats of South America, Indonesia, and Africa represent biodiversity hotspots inhabited by some of the world’s rarest and most endangered species of plants and animals.

Even were humans to cease all destructive practices in the world’s habitats today, the threat of massive levels of species extinction would not vanish. A phenomenon known as “extinction debt” has been demonstrated in fragmented forest habitats. The concept of extinction debt recognizes that some habitats become degraded enough that a population becomes no longer viable, but the currently living adults and juveniles do not immediately die out. Over time, the effects of fragmentation become apparent because species cannot obtain the resources they need to survive and reproduce, and populations
eventually become extinct. Depending on the life history characteristics of a given species, extinction can be delayed for decades, but the outcome remains inevitable (Gibson et al. 2013).

**Effect of Human Impact on Carnivores**

Carnivores experience some of the most adverse effects of human impact. The sensitivity of a number of carnivore species to habitat fragmentation and degradation is well documented globally, whereas the situation for other taxa remain largely unknown. In general, carnivores tend to be more sensitive to habitat fragmentation and encroaching human settlements because of their comparatively large home ranges and solitary habits. Carnivores generally require much more space to obtain sufficient resources for survival and reproduction than do herbivores of similar size, and their elusive behavior can cause difficulties in adapting to life in close proximity to humans. In addition to increased pressure due to their ecological and behavioral characteristics, carnivores are often actively persecuted by humans because they are considered threats to human welfare and livestock, their furs are valuable, and they are reviled or ceremonially hunted in some cultural settings.

Some carnivores, however, are capable of adapting to the presence of humans, and some thrive in even urban environments. In particular, smaller mesopredators, carnivores that are habitat generalists, and species with partially omnivorous diets can persist in areas heavily impacted by human activity. For example, the gray fox diet consists of meat, fruit, and nuts, and it has been shown to live in close proximity to urban environments in California without significant alterations in behavior or ecology (Riley
Their home range sizes and core area sizes were similar to those living in a nearby national park, and half of the collared individuals traveled into residential zones outside the park at least once during the study. In numerous instances, gray foxes even had home ranges adjacent to a housing development (Riley 2006).

Coyotes are partially omnivorous and highly elusive, but have also adapted to human environments particularly well. After the extirpation of gray wolves, the coyote’s range expanded far eastward from its original range in the central United States’ grasslands, eventually approximating the wolf’s previous niche (Gompper 2002). Coyotes have been reported to subsist in environments heavily impacted by humans, including locations as urban as Central Park in New York City (Martin 1999). Coyotes successfully occupy urban areas in many states without a significant change in survival rate, and in some cases without even an alteration in diet (Grubbs and Krausman 2009). To compensate for habitat fragmentation, however, coyote home range size tends to significantly increase, and population densities significantly decrease (Riley et al. 2003).

Successful adaptation to human presence is not entirely limited to smaller mesopredator carnivores, however. Hyenas are apex predators that are entirely carnivorous and live in complex social groups, yet they too have successfully colonized peri-urban environments. In Africa, spotted hyena clans occupy spaces in urban areas, acclimating to areas lacking native prey by hunting livestock and scavenging materials from urban waste (Abay et al. 2011).

Other carnivores, unfortunately, are not as well equipped to adapt to expanding human populations and growing urban areas. Species such as the American bobcat avoid
urban areas and roads more than do other carnivores such as gray foxes (Riley 2006). Large carnivores are also actively persecuted by human populations, leading to their endangerment and eventual extinction. The gray wolf was extirpated from much of the continental United States, and only after being listed under the Endangered Species Act did the species manage to bounce back in some areas like Yellowstone National Park. Despite being listed as endangered in some states, wolves are also still heavily persecuted as a species, particularly in areas where livestock husbandry makes up a great proportion of livelihoods.

Large, solitary predators also sometimes have difficulty adapting to human presence. Many extant big cats are good examples, as they are becoming increasingly endangered. This includes the leopard, which resides in Caucasus, Middle East and central Asia. Studies using radiotelemetry have shown that leopards actively avoid regions near any sort of urban development (Gavashelishvili and Lukarevskiy 2008). Their avoidance of urban areas makes it increasingly difficult for these solitary animals to establish sufficient home ranges to feed themselves without overlapping with human habitations. To survive, leopards will have to either adapt to smaller home ranges or to greater spatial overlap with humans.

Madagascar and its Species

The unique ecology of Madagascar is best understood in the context of its geography. Today’s Madagascar was once a small piece of Godwanaland in the mid-Jurassic. About 157 Ma, Madagascar separated from the shore of the Somali Basin and began moving south-southeast along the African continental shoreline. At this time, the
northern part of the island was much closer to the equator (Wells and Andriamihaja 1993). As the tectonic movements of Africa and Eastern Gondwanaland extended the Somali-Madagascar gulf, Madagascar continued to move southward until it reached its present position at about 124.5 Ma, during the Late Cretaceous (Harland et al. 1990). Madagascar’s eastern edge separated from India by around 84 MYBP, finally isolating the island from neighboring landmasses (Royer et al. 1992). In the last 15 to 20 million years of this epoch, Madagascar was reduced to its present size, with significant separation from India (Wells and Andriamihaja 1993).

The latitudinal movements of Madagascar back and forth toward the equator and the poles are largely responsible for its highly endemic, unique flora and fauna. Equatorward movements of the landmass moved it through the arid sub-tropics. As a result, it is likely that much of the biota previously living there were exterminated, making Madagascar a largely empty island and a candidate for colonization from chance immigrants. Immigrants that established themselves on the island then underwent extraordinary evolutionary radiation throughout the Cenozoic (Wells and Andriamihaja 1993). The timeframe in which the radiation that formed Madagascar’s present-day biomes is outdated, but it provides a general frame of reference as to their development and the levels of endemism that occur in each (Appendix A).

Today, Madagascar is the world’s fourth largest island at 587,045km². A variety of biomes occur in Madagascar, including lowland rainforests, dry forests, savannahs, and deserts (White 1983). The eastern region of the country contains lowland rainforests, as well as coastal, central plateau, and montane forests (Alonso et al. 2002). In contrast,
the western region contains dry deciduous forests, coastal plains, limestone plateaus, and spiny deserts (Alonso et al. 2002). Here, about 25% of Africa’s plants and 13% of the world’s primate species are found (Alonso et al. 2002). Madagascar has an extraordinarily high level of endemism as well. At least 80% of its flowering plant species, over 90% of its reptiles, and all of the lemurs found in the world are endemic to the island (Alonso et al. 2002). Although precise counts vary from study to study (Mittermeier et al. 2010, Schwitzer et al. 2013), dozens of lemur species are found occupying most of the biomes in the country including humid, dry, and spiny forests, with a higher number of vulnerable and endangered primate species than found in practically any other country (Mittermeier et al. 2010).

Human Impact in Madagascar and on its Species

Ecosystems across Madagascar have been significantly altered in recent decades by anthropogenic habitat change, and contiguous habitats continue to disappear at an alarming rate. From the 1950s to 2000, forest cover across the entire country decreased by almost 40%, and core forests decreased by almost 80% (Harper et al. 2007). In the dry deciduous forests of Madagascar, more than 50% were lost during these five decades (Harper et al. 2007). Efforts have been made to preserve ecosystems across the country by the creation of national parks (Appendix B). Unfortunately, deforestation continues to occur in these protected areas (Dollar 2006). The effects of this aggressive level of deforestation on many of the species in Madagascar, however, is largely unknown, especially for smaller fauna such as amphibians, reptiles, and birds. Many species in
Madagascar today are threatened or endangered, and many more are likely on “borrowed time” due to the extinction debt caused by widespread deforestation.

Humans have also introduced the Indian civet, domestic dogs, and domestic cats into Madagascar. Little is also known about the effects these species have on the native fauna, but studies have found that native Malagasy carnivores avoid dogs and cats (Gerber et al., 2012). The many ways in which these introduced species impact native species abundance and their role in spreading diseases to native Malagasy fauna is poorly understood.

The Fosa

The fosa (*Cryptoprocta ferox*) belongs to the family Eupleridae, which is comprised of seven genera and ten extant species found only in Madagascar. The phylogenetic positions of taxa in Eupleridae have historically been controversial, with genera placed in a number of different families and subfamilies (Yoder and Flynn 2004). Most recently, it was considered part of Viverridae which includes civets and genets found in Asia, Africa, and southern Europe. In 2004, DNA analysis showed that all of Madagascar’s carnivores belong to a single clade, which means that all of the extant species today came from a single herpestid ancestor that colonized the island a single time during the late Oligocene to early Miocene (Yoder and Flynn 2004).

The genus *Cryptoprocta* includes only the fosa and the giant fosa (*Cryptoprocta spelea*), which became extinct at an unknown time in recent geological history (Hoffmann and Hawkins 2015). The giant fosa appeared very similar to the fosa of today, but it was about 50% larger (Goodman et al. 2004). It is possible that the two species of
coexisted, and their size difference may have reduced potential competition for prey items (Goodman et al. 2004).

The fosa is the largest endemic carnivore in Madagascar. The mean length of an adult is 1.4m, and adult mean weight is (6.2-8.6kg) for males and (5.5-6.7kg) for females (Hawkins 1998), and fosas in Ankarafantsika fall within the same length and weight range (Dollar 2006). Their pelage is sepia brown with a cream underbelly. Notably, the underbelly of males, and to some lesser extent females, are stained with an orange secretion produced from a gland in the chest during the mating season (Hawkins 2003). The eyes are brown in color with pupils that contract vertically, and their eyes reflect orange in light. This makes them distinguishable from dogs, whose eyes reflect a cyan color in light (Hawkins 2003). The length of the tail is equal to the body reflecting their partially arboreal lifestyle (Laborde 1986). Other adaptations for arboreal locomotion are the extension of the paw pads almost to the heel, semi-retractable claws, and reversible ankles. Reversible ankles allow the fosa to grasp the trunk of a tree with both hind feet to ascend and descend as well as to jump from tree to tree (Hawkins 2003). The fosa is also a partially terrestrial species, and they have both plantigrade and digitigrade gaits, and they tend to travel on the ground more often in dry deciduous forests than in humid forests (Hawkins 2003).

This species occurs throughout Madagascar, preferring forested areas to treeless habitats (Köhnecke and Leonhardt 1986). Fosas have been documented in elevations of 2,000m in the Adringitra Mountains and on the small Isle Saint-Marie (Köhnecke and
Leonhardt 1986, Hawkins 2003), but it is absent in Madagascar’s central high plateau (Hawkins 2003). Fosa exhibit highest population densities in dry deciduous forests.

The diet of Cryptoprocta is exclusively carnivorous, with a diet mainly consisting of vertebrates including primates, birds, reptiles, and amphibians. Primates, and lemurs in particular, comprise at least 50% of the animal’s diet, but the fosa is not considered a primate specialist (Hawkins 1998).

The mating season of the fosa occurs between October and December (Hawkins 2003). Their mating is polyandrous, in which many males travel to a single “matting tree” where a female is found (Hawkins 2003, Lührs and Kappeler 2014). Hawkins also observed several females using the same tree once the previous female vacated the area (2003). This mating tree is used across years, and the dates that the fosas return to it are almost identical each year (Hawkins 2003). There is evidence that females are able to choose their mates from the group of suitors, and at times a female will mate with a specific male multiple times during one season (Hawkins 2003). After mating, gestation lasts for six to seven weeks before offspring are born in January (Hawkins 2003). The usual size of a litter is two to four (Albignac 1973), and the mother raises her offspring alone. Juvenile fosas sleep in nests that are usually hollow Commiphora trees or termite mounds (Hawkins 2003). After four months they are weaned, and after about one year they separate from their mother (Albignac 1975). Fosas reach physical maturity at the age of two and sexual maturity at three to four years (Hawkins 2003). Notably, juvenile females exhibit transient masculinization, in which they exhibit anogenital scent-marking and a proportionately larger spined clitoris (Hawkins et al 2002, Hawkins 2003). The
current belief is that transient masculinization acts as a deterrent against adult males to attempt breeding with juvenile females, as these features disappear once the female reaches sexual maturity (Hawkins et al 2002).

Compared to other tropical carnivores, the fosa occurs at abnormally low population densities (Hawkins 2003). Hawkins estimated that in the Kirindy Forest, fosa density was about 1 animal per 4km$^2$ (1998). Radio-collared females exhibited home range sizes of about 13km$^2$, whereas males occupied home ranges up to 26km$^2$ (Hawkins 1998). Males overlap home ranges with females and other males, but females’ home ranges rarely overlap with other females. During the dry season, home ranges are much larger than in the wet season. Within these home ranges, fosas rarely den or sleep in a regular location (Hawkins 2003).

The activity patterns of the fosa appear to be arrhythmic or cathemeral (Hawkins 1998). They are also described, at times, as crepuscular or exhibiting irregular activity patterns throughout both day and night (Albignac 1973, Gerber et al. 2012). Fosas tend to have short periods of rest followed by short periods of activity throughout the day. In all areas in which activity patterns have been recorded to date, fosas are active throughout morning, afternoon, evening, and night, suggesting the species is capable of a high degree of overall flexibility in activity pattern.

Fosas are generally solitary, elusive animals. There have been rare sightings of multiple fosas together outside of the mating season (Hawkins 2003). One study in particular found evidence of cooperative hunting between a group of male fosas that they had radio-tracked (Lührs and Dammhahn 2010). Except in the mating season, fosas rarely
vocalize unless they are distressed, given that gasping and yelping sounds have been documented in trapped individuals (Hawkins 2003). During the mating season they are much more vocal, especially when males compete for a mate (Hawkins 2003).

Fosa Relationship with Humans

In 2000, the fosa was listed as endangered, but in 2008 it was lowered to vulnerable status by IUCN (Hawkins and Dollar 2008). Major contributors to its vulnerability are the rapid rates of deforestation throughout the country, as well as conflict with humans due to perceived predation of livestock. Livestock losses become more prevalent near the end of the dry season, particularly for poultry (Hawkins 2003). Fosas have also been observed removing shoes and other nonfood items from research camps (Hawkins 2003), suggesting that they adjust to human presence. In general, local peoples in rural villages fear the fosa more than its size and aggression appear to warrant (Hawkins 2003).

According to studies, the fosa is not currently adequately protected. Of the 46 protected parks in Madagascar, only two are large enough to support a viable fosa population (Hawkins and Racey 2005). National laws are also inadequate due to conflicts within the legislation itself and conflicts within and among community laws (Hawkins and Dollar 2008). Conflicts in legislation as well as inadequate protection makes the future of this remarkable and understudied species appear bleak. Relatively little is known about the ecology of the fosa, and even less information is available about the species’ intricate relationships with other species within their endangered habitats.
Perhaps most importantly, very little is known about the fosa’s spatial relationships with human settlements. Several studies conducted using camera traps have demonstrated that the fosa (and their larger prey, the lemurs) avoid deforested areas of northeastern Madagascar (Farris et al. 2014) and eastern Madagascar in Ranomafana National Park (Gerber et al. 2010, 2012). These studies have focused on rural locations in rainforest ecosystems, and to date none has examined the possible overlap of fosa home ranges with human settlements.

Another understudied aspect is the possibility that fosas simply avoid temporal overlap with human activity in otherwise spatially overlapping physical habitats. Previous studies of other carnivores have shown that some species shift their peak activity times toward a more nocturnal preference in order to avoid high levels of human activity (Baker et al. 2007, Gibeau et al. 2002, Grinder and Krausman 2001). One study examined the activity patterns of fosa and other native Malagasy carnivores in deforested areas and found that fosas most often altered their activity patterns to avoid domestic dogs in the area (Gerber et al., 2012). To my knowledge, no publications have documented the activity patterns of the fosa or other carnivores in the dry deciduous habitats of western Madagascar, and none have focused on activity patterns relative to humans’ peak activity times.

A single qualitative study examined the direct relationship between fosas and human settlements by documenting reports of livestock loss due to the fosa near Ranomafana National Park (Logan et al. 2014). This study showed that according to local peoples, fosa were responsible for only 0.9% of all livestock deaths, with a substantial
percentage of livestock loss caused by feral cats. Fosas were also only seen by locals in villages less than 5km from contiguous forest. These surveys offer broad insight into the spatial relationships between fosas and human settlements, but rely on eyewitness accounts, and it is quite possible that fosas are skilled at avoiding human detection. Lack of evidence of the fosa’s spatial overlap with human settlements may be due to lack of data rather than lack of spatial overlap.

This project aims to gain a more comprehensive understanding of the range of pressures experienced by fosa in Ankarafantsika National Park. Chapter 2 explores long-term patterns in prey availability using species census records along fosa trap lines over the past two decades. Chapter 3 assesses long-term data on roadkill dangers along the major road that bisects the park, assessing the efficacy of speedbumps for mitigating wildlife roadkill events. Chapter 4 details movements and activity patterns of fosas in Ankarafantsika National Park, using GPS collar data. Together these data help to develop a clearer picture of the impact of human activities on these critical keystone predators of Madagascar.
CHAPTER 2: SPECIES ENCOUNTERS AND TRAP RATES

Introduction

The population dynamics of an ecosystem can be drastically affected by both direct and indirect human activity. As mentioned in the Introduction, direct human impacts include deforestation, population growth, poaching, and the construction of villages within or adjacent to protected areas. Humans also have an indirect impact on native species by introducing species to the environment, such as domestic cats and dogs, rats, livestock, and other fauna. These introduced fauna can interfere with natural ecosystem processes and potentially introduce deadly parasites and diseases. In this chapter, species encounter rates were collected along trap lines and compared with long term data as a proxy for understanding patterns of faunal change over time. Carnivore trap rates, for both native and introduced species, were also examined across years. Finally, prey species encounter rates and carnivore trap rates were compared to explore whether relationships could be inferred for predator/prey abundance in Ankarafantsika National Park.

Methods

Data Collection

Encounters and trap check data were collected between 1999 and 2013. A total of 11 separate field expeditions by these teams took place during this interval. Datasets gathered by these groups are dated June 1999, June to August 2000, October to December 2000, July to October 2001, July to August 2003, July to August 2004, June to July 2005, June 2006, March to July 2007, December 2009 to January 2010, and
December 2012 to January 2013. A total of 8 expeditions occurred during the dry season in Ankarafantsika, and 3 expeditions occurred during the wet season.

Encounter and trap check data collection most recently took place from June to July 2016, following the same methodology used in previous years. Tomahawk bobcat traps were placed along two trap lines and checked twice daily between the hours of 06:00 and 10:00 in the morning and 14:00 and 18:00 in the afternoon. During these checks, the time, location of the trap, the trap’s status (open or closed), and its bait status (present or absent) were documented. If any animal were captured in one of the traps, the species captured was also recorded.

When walking the trap lines, species encounter data was collected, recording time, location, height and distance from detector, bearing, method of detection, number of individuals, and current behavior of those individuals. The method of encounters, particularly for bird species, is similar to the point count method in that all individuals in the observer’s line of sight were documented whether on the path itself or in the surrounding forest; however, a fixed period of time for observations was not set as species encounter data was collected throughout the duration of the trap check process, such that encounters between trap locations were also included. All species were identified to the highest degree of specificity possible; in cases where specific/generic identification was not possible, the class was recorded and a description of the organism was documented for possible later identification.
Data Analysis

Encounter data were compared across years and between wet and dry season datasets. Encounters were compared at the level of class, family, and in some cases, species to explore for changes in wildlife encounter rates seasonally and through time. Trap check data was also examined to determine changes in capture rates of the fosa and other species, native and introduced, seasonally and through time. Because the number of field days varied across years (n=6-37 days), values were standardized when necessary to a ten-day field season, which has been the minimum field season duration since 2009.

Patterns were explored in the context of factors expected to influence encounter or trap rates. The change in species encounters was compared to carnivore trap rates to explore potential relationships among these two measures utilizing Spearman’s rank correlation. Because population density measures for carnivores or many prey items do not yet exist for Ankarafantsika National Park, capture and encounter rates serve as a first means to explore these relationships. Encounter data was also compared to roadkill data collected in corresponding years (study design for that aspect of the project detailed in Chapter 3). This offers insight into the relative encounter rate and vulnerability of Ankarafantsika fauna to roadkill mortality in crossing RN4.

Results

Species Encounters

Birds comprised the vast majority of species encounters for the duration of the long-term dataset. Figure 1 depicts the frequency of encounters for each class in both wet and dry seasons. Dry season species encounter data collection began in 1999, and
consistent wet season data collection began in 2007. Overall, the trend for proportionally high avian encounters remains the same across years and seasons in the dataset. Birds comprise the majority of encounters, followed by mammal and reptile encounters. Amphibians were very rarely encountered along the trap lines.

![Graph showing frequency of encounters by class across years and seasons.](image)

**Figure 1.** Frequency of encounters by class across years and seasons. Dry season is shown on the left and wet season on the right.

Avian species were grouped into the following categories: ground birds (ground couas, mesites, and guineafowl), raptors (falcons, hawks, eagles, and owls), and water birds (herons, egrets, grebes, and ducks). Other birds such as passerines and songbirds were analyzed separately. No general trend of increase or decrease in encounters of ground birds, raptors, or water birds was observed in the dry season dataset (Figure 2). There was, however, a significant peak in encounters for ground birds in 2007 (10.8 encounters/day) and 2008 (12.5 encounters/day). During the dry season, water bird encounters did not exceed 4.4 per day (1999), and raptor encounters did not exceed 2.8 per day (2011). During the wet season, however, water birds exhibited a large peak in
2007 at 21.3 encounters/day. Raptors were encountered less often during the wet season, with the maximum encounter rate in 2007 at 1.17 encounters/day.

Figure 2. Encounters of bird ecotypes per field season and across years. Solid lines represent the dry season dataset and dotted lines represent the wet season dataset.

Figure 3 depicts the percent of encounters per day in the remaining portion of the avian dataset. Families like Bernieridae (greenbuls), Monarchidae (paradise flycatchers), and Vangidae, which includes the common newtonia, blue vanga, sickle-billed vanga, hook-billed vanga, Van Dam’s vanga, white-headed vanga, rufous vanga, and Chabert’s vanga, remain dominant species across years in the dry season (Figure 3). Bernieridae exhibited an encounter frequency of 3 to 24%, Monarchidae from 8 to 20%, and Vangidae from 4 to 15%.
Figure 3. Frequencies of encounters of birds by family for each year in the dry season. Data were normalized by number of field season days each year.

Many families were encountered rarely (or not at all) across years. These families include Acrocephalidae (warblers), Apodidae (swifts), Coraciidae (broad-billed rollers), Motacillidae (wagtails), Numididae (guineafowl), Philepittidae (asitys), and Sturnidae (starlings). Frequency of encounters for any of these families never reached even 1% of the total avian dataset. Individuals from Motacillidae and Sturnidae were only encountered in a single year of the long-term study period (2000 and 2010 respectively).

During the wet season, two of the same families are dominant (Figure 4). Vangidae and Monarchidae are among the dominant species with encounter rates ranging from 8.7-19.9% (except for 2008, when there were 0 encounters) for Vangidae and 6.8%-33.3% for Monarchidae. Pycnonotidae and Nectariniidae were also commonly encountered during the wet season across years with encounter rates ranging from 3.4-16.4% for Pycnonotidae and 1.5-18.5% for Nectariniidae. Unlike the dry season,
however, individuals belonging to Alaudidae, Apodidae, Motacillidae, and Sturnidae were never encountered during the wet season across all years in the long-term dataset.

Figure 4. Frequencies of encounters of birds by family for each year during the wet season. Data was normalized by number of field season days per year.

Lemurs in Ankarafantsika National Park exhibited similarly interesting patterns. Species belonging to the families Indriidae (Coquerel’s sifaka, crowned sifaka, and woolly lemur), Lemuridae (brown lemur and mongoose lemur), and Lepilemuridae (Milne Edward’s sportive lemur) were encountered far more often than Cheirogaleidae (fat tailed dwarf and mouse lemurs) (Figure 5). A peak in lemur encounters in all families occurred between 2007 and 2008 during the dry season, with encounters across the other years highly variable among lemur families.
Encounter rates for Indriidae and Lemuridae, the families with multiple species in ANP, were next examined at the species level to determine the taxa comprising the majority of lemur encounters across years. Within Indriidae, Coquerel’s sifaka (*Propithecus coquereli*) comprised the majority of encounters across years. The western woolly lemur (*Avahi occidentalis*) varied in encounter numbers ranging from 0-100% of all indriid lemurs sampled (Figure 6). Just one crowned sifaka (*Propithecus coronatus*) was sighted throughout the long-term study period, in 2001. Within Lemuridae, brown lemur (*Eulemur fulvus*) comprised the vast majority of encounters throughout the study period. Encounter rates for *E. fulvus* were 86% or greater. Mongoose lemur (*Eulemur mongoz*) were less commonly seen, comprising between 0-14% of lemurid encounters over the course of the long-term dataset.
During the wet season, far less variability is observed among lemur encounters across years. Within Indriidae, Coquerel’s sifaka comprised 89-100% of the encounters, with woolly lemurs being sighted only in 2009 and 2010 with a 5-10.5% encounter frequency. Crowned sifakas were never encountered during the wet season months. Within Lemuridae, encounter frequencies during the wet season did not differ significantly from the dry season. Mongoose lemurs were sighted only during three of the wet seasons (7.5% of encounters in 2000, 3.13% of encounters in 2009, and 4.11% of encounters in 2014). Brown lemurs comprised the vast majority of encounters, in 6 of the 9 years representing 100% of lemurid sightings.

Finally, the encounter rates of different reptiles were examined across seasons and years. During the dry season, snakes and geckos were encountered most often across all years sampled (Figure 7). Skinks and chameleons were less commonly encountered, and iguanas were even more rarely encountered. The frequency of encounters among reptile groups during the wet season are generally inverse to those encountered during the dry season. Chameleons and iguanas have the highest encounter rates per day during the wet
seasons, whereas skinks and geckos are among the least often reptiles encountered (Figure 7).

Figure 7. Encounter rates of reptile groups across years in the dry (left) and wet (right) seasons. Data was normalized by number of days per field season.

Trap Rates

Trap rates were calculated as captures per number of days in each year’s field season. Figure 8 depicts mammalian carnivores that were caught throughout the study, and includes both native carnivores and introduced species. Cat capture rates were very high until 2005. It is at this point that both cat captures and fosa captures completely disappear. Anecdotal evidence of increase in dog activity inside the park between 2005-2008 suggests that the presence of dogs may impact ranging patterns for other species (Dollar, unpubl.). However, documented dog captures coincide with similar fosa capture rates (e.g. 2010 and 2016) as those in the absence of dog captures (2001, 2003, 2013, and 2014). Interestingly, fosa capture rates seem to best match the capture rate of cats.
Comparison of Trap Rates and Prey Encounters

Encounter rates for various species were then compared to the capture rates of native and introduced carnivores to explore for trends in all species encounters compared to documented predators recorded in the same areas. As trapping occurred only during the dry seasons, analysis was restricted to this portion of the dataset. A number of interesting patterns were observed among capture rates for carnivores and encounter rates for prey species. When fosa capture rates declined during the study (from 2003-2006, 2010-2011, and 2013-2014) ground bird encounters increased. For example, between 2003 to 2007, as fosa encounters declined to 0, ground bird encounters sharply increased to over 120 encounters in the field season. When fosa capture rates increase again each time (2008, 2012, and 2016), ground bird encounters begin decreasing again. Utilizing the example above to depict this, when captures of fosa resumed in 2008 the rate of ground bird encounters is reduced by more than half (Figure 9).
Figure 9. Carnivore capture rates and ground bird encounter rates in a ten-day field season.

This pattern across years corresponds more strongly with fosa captures across years ($r_s = -0.39$). The pattern of ground bird encounters and cat capture rate yielded a similar relationship, though not as prominently ($r_s = -0.23$). The other carnivore capture rates do not appear to have a relationship to species encounters of ground birds. Indeed, low ground bird encounter rates were seen in years with high overall carnivore capture rates (1999) as well as low overall carnivore capture rates (2003). In 6 of the 14 trap years (2001, 2005, 2006, 2010, 2013, and 2016), the encounter rates of ground birds appeared proportional to the number of carnivores captured (~10 encounters for every 1 carnivore captured) (Figure 9).

Another fosa prey group of interest in ANP are lemurs. For this comparison, civets (Indian civet and Malagasy civet) were excluded from the trap rates for this analysis since lemurs are not prey items for civets. Interestingly, lemurs follow the same
pattern that ground birds do in encounter rates across years. When compared to ground birds, lemur encounters correspond even more strongly to fosa captures across years ($r_s = -0.83$). Encounters with lemurs also sharply increased between 2006-2008, following the absence of fosa captures (and presumably fosa acting as predators in the study area) (Figure 10). When fosa captures resumed in 2008 (presumably reflecting their return to the study area), the encounter rates of lemurs sharply decreased again (Figure 10).

![Figure 10](image)

*Figure 10*. Projected carnivore (civets excluded) capture rates and lemur encounter rates in a ten-day field season.

Also, similar to the pattern observed in ground birds, no strong pattern is observed linking the number of lemur encounters to other carnivore capture rates. Lemur encounters do not appear to have a relationship with cat captures ($r_s = 0.03$). Encounters were similar across years with multiple cat captures (2004 and 2005) to those years with very few cat captures (2010, 2012, and 2016). Years in which more dogs were captured appear to influence lemur encounters the following year: in 2 of the 3 years that dogs
were captured, lemur encounters increased the following year (2007 and 2011). However, in 2013, following documented dog captures, lemur encounters failed to increase. This suggests that this relationship between lemurs and dogs is either weak or that perhaps the patterns are circumstantial ($r_s = -0.10$). Alternatively, lemur encounters may reflect other variables such as human activities in the study area.

Discussion

Species Encounters

Perhaps not surprisingly, birds consistently ranked the highest in species encounters across years and seasons. Birds are easily noticeable by their calls and often brightly-colored plumage. ANP has a wide variety of birds representing many different families. Some of these birds, such as the species found in Alaudidae, Apodidae, Motacillidae, and Sturnidae occupy large home ranges that sometimes extend beyond Madagascar. It is not known whether these species seasonally migrate to different regions, but it is possible that they were not encountered in the study area during wet seasons because of movements away into other habitats.

Amphibians would be expected to be absent from the trap lines due a variety of reasons. Both of the trap lines used in this study are located in forests at a higher elevation and are approximately 1-2km (JBA) and 0.5-1km (JBB) from significant water sources, which would reduce observations of stream and pond-dwelling amphibians. Additionally, traditional methods of population estimations for amphibians such as pitfall traps and night-time searches were not utilized. Very little is known about the amphibian
fauna in Ankarafantsika National Park, so it is difficult to determine potential activity patterns or life history traits that may influence encounter rates observed along trap lines.

Lemur encounter rates, however, offer more interesting patterns to explore. The mongoose lemur is a seasonally nocturnal species, meaning that during the dry season individuals are strictly nocturnal, whereas in the wet season they become diurnal (Curtis et al. 1999). Milne Edward’s sportive lemur, the western woolly lemur (Warren and Crompton 1997), and all species of mouse lemurs (Groves 2005) are regularly nocturnal. As all censuses occurred in the morning and afternoon, nocturnal species would not be expected in species encounters, except under the most unusual circumstances (active predation event, awakened by noise, visible from resting location, etc.). Coquerel’s sifaka travel in groups ranging from 3 to 10 individuals (Salmona et al. 2014), and brown lemurs travel in groups ranging from 5 to 12 (Garbutt 2007), increasing the likelihood of sightings by observers walking trap lines, and also increasing the frequency of encounters as multiple individuals were often recorded in encounter events simultaneously.

Trap Rates of Native and Introduced Carnivora

Trap rates in cats and fosa were generally proportional to each other, meaning that field seasons recording high capture rate for cats also documented high capture rates for fosa. This suggests that cats and fosa may not directly compete over the same prey items but rather the same conditions may favor success in both species. Interactions between native and introduced carnivores are difficult to compare across different habitats and species combinations. However, one study in Australia suggests that native and introduced carnivores may alter dietary preferences to minimize competition when
fundamental diets are the same (Glen et al. 2011). Cats in Ankarafantsika National Park may be capturing prey items that live in higher concentrations in close proximity to villages (namely Muridae, as well as smaller prey items such as reptiles), which would lessen competition with fosa that forage deeper in forested environments more opportunistically.

Few dog captures have been documented over the years of the long-term study. However, since the appearance of dogs in study traps, the capture rates of mesopredators have virtually dropped to 0. Indeed, Indian civets and Malagasy civets have not been captured since 2010. Dogs may be able to outcompete these smaller predators for prey, and it’s possible that civets themselves become prey for dogs. Similar negative impacts in introduced species have caused a decline of native carnivore in Europe (Kauhala and Kowalczyk 2011). Introduced carnivores in the study area may also be vectors for diseases and parasites, which can harm native predators (Kauhala and Kowalczyk 2011). Little is yet known about disease vectors for the fauna in Madagascar, or which diseases the members of Eupleridae are susceptible to. However, fosa inside Ankarafantsika National Park were found to be exposed to a number of viruses most likely introduced via cats and dogs, including canine parvovirus, canine herpesvirus, and feline caliciviruses (Pomerantz et al. 2016).

Comparison of Trap Rates and Prey Encounters

The relationship between fosa trap rates and species encounters suggests that, perhaps not surprisingly, ground birds and lemurs are indeed common prey items for fosa in Ankarafantsika National Park. The time-lag between fosa capture rates and prey
encounter rates echoes the temporal patterning seen or modeled in many studies of predator/prey relationships (Elton and Nicholson 1942; Wangersky and Cunningham 1957; Cushing et al. 1976). That the time-lag only corresponds to fosa capture rates (and not capture rates for human-introduced carnivores) for both ground birds and lemurs also suggests that neither of these groups are main prey items for the introduced carnivores in the park (cats and dogs).

Conclusions on Species Encounter Analyses

In general, species encounters remained relatively consistent across the study period. Common species, especially in birds, remained common, and amphibians remained the least encountered class. Significant variations in species encounters were not observed between the wet and dry seasons; seasonal migrations or behavioral changes may have caused some change in bird and reptile family encounter rates, but too little is known about these species’ life history traits to come to a clear conclusion on these fluctuations.

The peak in lemur and ground bird encounters between 2007 and 2008 corresponds with years in which no fosa were captured along the trap lines, suggesting that fosa presence directly impacts the subsequent encounter of prey items the following years. There is also some evidence that introduced species may not directly impact prey items in the same way that fosa do; however, if introduced species such as dogs drive away fosa, introduced carnivores then have an indirect impact on prey item encounters. Additionally, since dogs started occurring along trap lines in 2010, smaller carnivores such as Indian and Malagasy civets have no longer been seen or trapped. This suggests
that introduced species not surprisingly appear to have an impact on faunal dynamics in Ankarafantsika. The next chapter explores the impact of the major roadway running through the park on biodiversity, comparing roadkill statistics for different vertebrate groups with the data gathered in this chapter on overall species encounters in the study area.
CHAPTER 3: ROADKILL SURVEYS

Introduction

The study area in Ankarafantsika National Park is bisected by the busy roadway (RN4) that separates the park into western and eastern areas. RN4 is a major connection between Antananarivo, Madagascar’s capital, and Mahajanga, a major city in the northwest. Taxis regularly travel this road and reach highway speeds within ANP. Accidental wildlife mortalities due to vehicular traffic within parks can have a significant impact on wildlife populations (Kioko et al. 2015; Simmons et al. 2010; Laurance et al. 2009). One method of reducing number of roadkill events is the installation of speedbumps along busy roadways, designed to slow traffic to less dangerous speeds. However, the effectiveness of speedbumps in decreasing traffic speed has been widely disputed (Pau and Angius 2001; Afukaar 2003; Antic et al. 2013).

In an effort to mitigate roadway dangers for both residents in nearby villages and wildlife within the park, two speedbumps were installed by Madagascar National Parks between 2006-2007. The speedbumps are approximately only 500m apart from each other, whereas the stretch of RN4 within the park is approximately 18km. This chapter explores the long-term effectiveness of speedbump installation in reducing vehicular deaths among wildlife in Ankarafantsika National Park. Special focus was placed on species thought to be common prey items for fosa, including reptiles, amphibians, mammals, and ground birds.
Methods

Roadkill Surveying


Additional roadkill surveys were performed between June 3-24 2016, following the same methodology used by teams in previous years. Prior to data collection, existing roadkill along RN4 within Ankarafantsika National Park was removed to the side of the road. During the data collection period, the full road segment was walked each morning of the field season. When roadkill was discovered, the time, location, and identity of the roadkill to the greatest specificity possible was recorded. The specimen was then removed from the roadway to prevent duplication of data points.

Data Analysis

Data were compared across seasons and through time. Locational data was analyzed to determine whether speed bumps appear successful in mitigating the loss of wildlife to vehicle strikes, as a previous study had suggested one year after the installation of speedbumps (Schutt 2008). Data were aggregated into average number mortalities/day for each year and each season. Because the number of field days varied
across years (n=5-31 days), values were then normalized to average mortalities/day for 31 days, or one month’s worth of wildlife mortalities. The G-test was used to perform all statistical analyses.

Finally, roadkill data were compared to species encounter data collected along trap lines during corresponding years. The aim of this comparison was to explore for relationships between the species most abundantly encountered along the trap lines, and the species most abundantly impacted by road traffic.

Results

Composition of Roadkill Events

Overall, amphibians and reptiles comprised the vast majority of roadkill events in both seasons and across years of the long-term data set. In all, 7,041 amphibian and 2,053 reptile roadkill events were documented across years and seasons. Mammals and birds experienced far fewer roadkill events across years and seasons, at 437 total mammal and 69 avian roadkill events documented between 2005 and 2016. It is also notable that although mammals comprised a small minority of roadkill events, one of the GPS radio-collared fosa being tracked (M2) was also killed on the roadway by a vehicle in 2016.

The total number of roadkill events were greater during the wet season than during the dry season. Amphibians in particular experienced at least 51 deaths/day in each wet season expedition, and in three years exceeded 90 events/day (98 events/day in 2011, 211 events/day in 2010, and 212 events/day in 2009). In comparison, during the dry season amphibians experienced a greater range of roadkill events, as high as 28 events/day in 2008, and as low as just 0.18 events/day in 2005. For the four years for
which data are available in both a wet and dry field season, there roadkill events during the wet season of the corresponding year, increased by between 494-804% the values observed in the dry season.

In general, reptiles experienced more roadkill events than did amphibians during the dry seasons, and amphibians experienced more roadkill events than did reptiles during the wet seasons. In the dry seasons, reptiles comprised between 4 and 78% of all roadkill events, and representing less than 50% of all roadkill deaths in only three years (2006, 2008, and 2010) (see Figure 11). During the dry seasons, amphibians comprised a similar range (3 to 77%) of roadkill events but only two years (2006 and 2010) exceeded 50% of the total roadkill events (Figure 11). Lower roadkill mortalities were recorded for mammals and birds, with a combined range of 3 to 23% of all roadkill events.

*Figure 11. Frequency of roadkill events by class across years during the dry season.*
During the wet season, amphibians were universally the most affected species across all years, comprising between 68 and 92% of all roadkill events. Reptiles were proportionally less affected, ranging between 7 and 29% of all roadkill events. As in the dry season, mammals and birds comprised a lower percentage of roadkill mortalities, not exceeding 3% of the overall roadkill events.

Within each vertebrate class, individual families were compared to determine those taxa most impacted by the roadway. Among amphibians, mantellid frogs were hit on the road more often than any other family in both the wet season (190.34 deaths/month) and dry season (8.49 deaths/month) (Appendix E, a). Among reptiles, Lamprophiidae experienced the highest number of roadkill events in both seasons, with dry season roadkill events averaging 137.14 deaths/month, and wet season roadkill events averaging 120.83 deaths/month (Appendix E, b). Among mammals, Muridae were most represented in roadkill events during both seasons (59.16 deaths/month in dry season; 48.64 deaths/month in wet season) (Appendix E, c). Finally, avian families did not exhibit a clear trend across seasons (Appendix E, d).

**Effectiveness of Speedbumps**

The overall effectiveness of speedbumps for mitigating wildlife roadkill mortality was analyzed by vertebrate class, by comparing numbers of roadkill mortalities before and after speedbump installation. Significant differences in roadkill events associated with the presence of speedbumps were observed for amphibians (p = 1.40E-06 and 3.41E-193 in the dry and wet seasons respectively) and reptiles (p = 0.002 and 1.33E-14 respectively). However, in all four of these cases the number of vehicular deaths
significantly increased after the installation of speedbumps. Roadkill events in birds and mammals were not significantly altered in either season after speedbump installation (p>0.01). In both seasons birds saw a minor but nonsignificant decrease in mortality events, whereas mortalities in mammals slightly increased.

As the presence speedbumps generally did not appear to decrease wildlife mortality events on RN4 overall, the next step was to refine the question and determine whether roadkill mortality was reduced in close proximity to speedbump locations along RN4. The annual number of mortalities was averaged and subdivided by km marker within the park (469 – 452) (Figure 12). Mean roadkill mortality values were then compared before and after speedbump installation in both seasons.

![Figure 12](image)

*Figure 12.* Mortality counts along the RN4 segment for both seasons before and after installation of speedbumps. Vertical lines indicate the approximate locations of speedbumps in relation to the km markers.

In both seasons, the mean number of roadkill mortalities generally increased after the speedbumps were installed. Roadkill events at km markers 454 and 455 where
speedbumps were in close proximity significantly increased (p<0.01) in the dry season at km 455 and at both km markers in the wet season (p=0). Significant increases in roadkill events also occurred from 460-469 in the wet season and periodically throughout the dry season. The only locations that experienced a significant decrease in roadkill events in the dry season were km 453 (p<0.01), 464 (p=0.027), and 468 (p<0.01). Significant decreases in the wet season were found at km 457 (p=0.015) and 458 (p<0.01).

Average mortalities occurring along the road at all km markers outside of the road segment bracketed by speedbumps were compared to the average mortalities that occurred between the speedbumps after completed installation in 2008. The number of roadkill events outside the road segment bracketed by speedbumps were not significantly different from the number of events between speedbumps. For the wet season, however, significantly more deaths occurred outside of the speedbumps rather than inside (p=0).

**Do Roadkill Events Reflect Species Encounter Patterns?**

Interestingly, very little overlap occurred between the species encountered along the trap lines and those experiencing roadkill mortality. Reptiles exhibited the most overlap, although chameleons were more commonly encountered along trap lines (likely because they prefer forested habitats), and snakes were more likely to be hit by a vehicle (likely because they were sunning on the tarmac road). Birds were rarely found in roadkill surveys, but birds made up the vast majority of species encounter data. Mammals, particularly endemic fauna, were uncommonly encountered in either setting. Finally, amphibians were very rarely encountered along trap lines during either season,
but showed the highest number of roadkill deaths among the groups sampled in this study.

**Discussion**

*Composition of Roadkill Events*

The majority of roadkill events occurred in both amphibians and reptiles during the wet seasons. High mortality rates for ectotherm wildlife along roadways is to some extent, unavoidable (Ashley and Robinson 1996; Elzanowski et al. 2009; Sutherland et al. 2010) even with ambitious mitigation techniques in place. Reptiles often use roadways that have access to direct sunlight, especially in forested environments, to raise core body temperatures and maintain metabolic rates (D’Amico et al. 2015). Amphibians, as ectotherms, similarly may be attracted to the tarmac substrate to raise body temperatures, but the drastic increase in amphibian deaths during the wet season suggests a further possibility: that these species were crossing RN4 between water sources on either side of the roadway (Ashley and Robinson 1996, Glista et al. 2007).

Mammals and birds experienced the least amount of vehicular deaths, perhaps in part because they rely less on direct sunlight for thermoregulation. Most, if not all, bird species in the park are also capable of flying to avoid collisions with vehicles, and mammals occur at lower population densities compared to amphibians and reptiles. It is not surprising that the most commonly killed mammals are those species that live within villages or in close proximity to villages, such as rats (Muridae), dogs, and cats. Interestingly, birds did not exhibit a clear pattern, suggesting that roadkill events impact
avians more randomly in the study area. It is possible that ground birds avoid roads in
daily activities and in traversing home ranges.

*Effectiveness of Speedbumps*

The failure of the speedbumps in reducing roadkill events along RN4 is likely due
in part to their number and spacing. Of the 18km of road traversing Ankarafantsika
National Park, just two speedbumps have been installed, approximately one km apart
from one another.

Moreover, existing speedbumps are emplaced in areas where wildlife traffic
might naturally be lower to begin with. The substantially sized village Andranofasika is
located just beyond km 452, and a large camp for researchers as well as Malagasy shops
are located at the speedbump sites. Human traffic is already high between 452 and the
speedbumps, so although the speedbumps likely benefit humans in the area, endemic
wildlife may have already avoided those areas prior to speedbump installation, calling
into question their implementation as a coherent mitigation strategy.

Conclusions on Road Mortality Analyses

Understanding the impact of speedbumps on wildlife vehicular mortalities is an
important first step for examining the effectiveness of roadkill mitigation techniques in
Madagascar. Speedbumps are among the most feasible techniques to protect animals
along roadsides in economically developing settings because of their low cost and ease of
installation (Afukaar 2003; Forjuoh 2003). But if these measures are to be effective,
speedbumps must be more strategically placed. Future studies in ANP should examine
the effectiveness of additional techniques for mitigating roadkill biodiversity loss, such as
the installation of fencing along the roadway to divert the movement of small wildlife or the establishment of aerial trackways for arboreal species to cross. Pursuing the impact of eco-passages may also be an attractive alternative in the already highly fragmented Madagascar to facilitate movement of wildlife across roadways without coming into contact with vehicular traffic. Realistically, however, given many factors including wet and dry season fluctuations in water levels, speedbumps are likely the most feasible option for mitigating wildlife mortality due to cost and required labor for installation.

These analyses suggest that in order for speedbumps to be successful in significantly reducing wildlife mortalities along RN4 through Ankarafantsika National Park, more speedbumps should be installed, and in a more strategic fashion. Several long straight segments of road allow vehicles to reach highway speeds, and there is no posted (or enforced) speed limit. Notably, it is in one of these areas that study fosa M2 was hit by a vehicle (see next chapter). These straight segments would be excellent candidates for speedbump installation to both reduce wildlife roadkill events and to increase safety of pedestrians using the road as a walking path.
CHAPTER 4: FOSA SPATIAL AND TEMPORAL PATTERNS

Introduction

The previous chapters analyzed the impacts of prey species in Ankarafantsika National Park to human populations both directly by roadkill events and indirectly by changes in encounters over time and the trap rates of native and introduced carnivora. The final portion of this study examines the direct relationship between human populations and fosa by analyzing the spatial and activity patterns of fosa in relation to human settlements, agricultural areas, and deforested habitat.

Methods

Capturing of Fosas

Fosas were trapped within Ankarafantsika National Park using Tomahawk bobcat traps (42 x 15 x 20in), baited with beef. Forty traps were placed along two trap lines that extend a total 20km. One trap line (JBA) runs on the western side of RN4 that bisects the park. The other trap line (JBB) runs on the eastern side of RN4 (Appendix D). Traps were spaced at equal distances from each other as much as possible along the trap lines.

The traps were checked twice daily between the hours of 06:00 and 10:00 in the morning and 14:00 and 18:00 in the afternoon until candidates were captured. Candidates were healthy adults of either gender. The captured fosas were tranquilized using a dosage of telazol (0.05cc/kg). While tranquilized and physically restrained enough to handle, the animal was removed from the trap and transported directly to the central processing area. Vital signs, including blood oxygen levels, were monitored constantly to ensure that the animal did become unstable during the data collection and collaring process.
At the central processing station, the anesthetized study animal was weighed, measured, and fitted with TGW-4277-4 GPS Iridium collars. The collars have dimensions of 5.7 x 3.5 x 2.7cm and weigh 220g. Collars were only placed on animals with body masses great enough that the collars were 5% or less of their masses.

When anesthetics began to wear off, data collection on the animal stopped immediately. The fosa was placed in a dark recovery cage at the central processing area to complete recovery from the tranquilizers. After all of the anesthetics wore off, the animal was released at its original capture site.

**GPS Radio-collar Monitoring**

Collared fosas were monitored by GPS radio-tracking equipment on the TGW-4277-4 collars. The collars monitored spatial movements, mortality, and activity of the animals for the duration of the study. All parameters were measured and documented at a fixed interval of 20 minutes for at least two weeks beginning in June 2016. The date and time at which the parameters were logged was documented to track movement and activity changes over time. All data that the GPS collars document was then transmitted via satellite and emailed to a dedicated address every two days and stored for analysis.

Data for M2 (see Results) is limited because this individual was killed by a vehicle on RN4 after two weeks of data collection. The GPS collar was recovered and redeployed on F1 for the remainder of the study.

**Spatial Analysis**

Home ranges were calculated using the methodology for minimum convex polygons (MCP) (Getz and Wilmers 2004) and 50%, 90%, and 95% kernel home ranges
(Worton 1989). 90% kernel home ranges were utilized in addition to 95% kernel ranges to directly compare home range sizes to a previous GPS-collar study conducted on fosa in Kirindy Forest (Lührs and Kappeler 2013). Overlap of home ranges were also calculated across individuals.

Within the MCP home ranges, habitat selection of each individual was calculated. Landcover type for all habitat analysis was broken down into five types: grassland, forest, water, agriculture, and village. The percent of each landcover type for each home range was determined. Using compositional analysis (compana in the adehabitat R package), GPS fixes for each individual were used to analyze whether movements within home ranges were random or if individuals had a preference for certain landcover types utilizing methodology from Aebischer et al. (1993). GPS fixes within the forest habitat were additionally divided into forest interior and forest edge to explore possible movement restrictions for fosa through the forest. Finally, the range of distances traveled from each landcover type were calculated for each individual to analyze possible avoidance of certain landcover types, namely agriculture and villages.

**Activity Pattern Analysis**

Activity patterns for each individual were monitored along with GPS location data. Activity data was used to determine overall activity patterns in a 24-hour period for fosa, since there has been some disagreement on the species’ activity patterns (Hawkins 1998, Albignac 1973, Gerber et al. 2012). Activity patterns were also analyzed alongside habitat selection analysis. Activity was compared to distances from landcover types, and resting periods in the forest (where activity count = 0), were split into interior and edge
habitat as before. This was to determine whether fosa require interior forest habitat for resting, or if they are able to use edge habitat for this behavior.

Results

Home Ranges

Two males (M1 and M2) and one female (F1) were captured over the duration of the study. Each individual was tracked for a minimum of 14 days and a maximum of 88 days (Table 1). The number of successful GPS fixes (n positions) varied from 324-2634 across individuals.

Table 1 Overview of spatial data obtained for each individual

<table>
<thead>
<tr>
<th>Individual</th>
<th>N Days Tracked</th>
<th>N positions</th>
<th>MCP area (sqkm)</th>
<th>50% LoCoH kernel area (sqkm)</th>
<th>90% LoCoH kernel area (sqkm)</th>
<th>95% LoCoH kernel area (sqkm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>88</td>
<td>2634</td>
<td>141</td>
<td>49</td>
<td>128</td>
<td>154</td>
</tr>
<tr>
<td>M2</td>
<td>14</td>
<td>324</td>
<td>97</td>
<td>43</td>
<td>144</td>
<td>176</td>
</tr>
<tr>
<td>F1</td>
<td>77</td>
<td>2524</td>
<td>193</td>
<td>67</td>
<td>180</td>
<td>219</td>
</tr>
</tbody>
</table>

Home ranges for all individuals were similar to each other. MCP home ranges were 97-193 km²; however, the low number for M2 is likely due to a much lower number of positions (Table 1). 50% and 90% kernel density were similar across all individuals with a range of 43-67 km². For M1 and F1, 50% kernel areas were both 34.7% of their respective MCP areas and 37-38% of their 90% kernel areas. In all measured home range areas, F1 had the largest ranges compared to both males.
Home range overlap occurred across all individuals with a minimum of 34% overlap between any two fosa utilizing MCP home ranges. M1 and M2 overlapped in over 50% of their total home ranges. M1 shared 63% of its home range with M2, whereas M2 shared 91% of its home range with M1 (Figure 13). By comparison, F1 overlapped 59% of its total home range with M1 and 34% with M2. All three individuals were captured in trap line JBA, which is located in the area where all three home ranges overlap each other.

Figure 13. Convex hull home ranges for captured fosas.

50, 90, and 95% kernel home ranges also overlapped across individuals. 95% kernel home ranges overlapped between 54% and 95% across individuals across individuals with the least overlap occurring between M2 and F1 and the greatest overlap occurring between M1 and F1. 90% kernel home ranges had a range in overlap of 50% - 92% across individuals with the same individuals comprising the minimum and maximum overlap. 50% kernel home ranges had a minimum of 14% overlap between any
two fosa (M2 and F1) and a maximum of 74% (M1 and F1). Interestingly, M1 and M2 had less overlap in these core areas. Only 29% of M2’s core range overlapped with M1, and 33% of M1’s core range overlapped with M2.

Habitat Selection and Movement Patterns

The landcover composition of the animals’ home ranges did not differ from each other. The landcover composition for each type was as follows: 13% grassland, 25% forest, 25% water, 25% agriculture, and 12% village. Additionally, the landcover composition of the animals’ home ranges did not differ from the landcover composition of the surrounding region at a 10km radius from each home range boundary (p = 1). Within each home range, however, habitat selection was nonrandom (λ = 0, p<0.01). Over 95% of GPS fixes for all individuals fell within forest landcover (Figure 14). Fixes within grassland or agricultural lands ranged from 0 – 4%, and only M1 had a single GPS fix within the boundaries of a village.

Figure 14. Frequency of landcover types for fosa GPS fixes.
Forest landcover was then divided into interior forest and edge habitat to determine if individuals were restricted to the interior and more undisturbed patches of forest. All three individuals had a majority of fixes within 500m of the edge, with most of those fixes within 250m (Appendix F). Very few fixes beyond 800m for all three individuals, and the maximum distance from edge for all individuals was 1250m.

Compositional analysis revealed that space use was almost entirely limited to within the forest for all individuals, but there were varying amounts of avoidance of other landcover types. M1 did travel across agricultural areas and crossed into the boundaries of one village. M1’s median distance from agriculture, however, was 1.02km, and its maximum distance was 4.83km. M1’s median distance from villages was larger at 2.02km, and reached a maximum distance of 6.17km away. For the majority of the study, therefore, M1 avoided traversing agriculture and human settlements. There is no indication that M1 avoided grasslands, as almost all GPS fixes occurred within 1km distance of grassland. M1 also did not show strong dependency to water sources, as the median distance was 1.90km and ranged from .04 to 5.29km. (Appendix G)

M2 showed the same overall pattern of distances from each landcover type. The difference between distances from agriculture and villages, however, was much smaller for M2. M2’s median distance from agriculture was 1.36km and 1.76km from villages. F1 showed the greatest variation in movements of the three individuals. Distances from agriculture were similar with a median value of 1.29km, but distances from villages were the greatest with a median of 2.66km. F1’s overall range was similar to M1 and M2, being 0 - 5.07km from agriculture and 0.15 – 7.46km from villages. (Appendix G)
The combination of space use in close proximity to forest edge and avoidance of grassland habitat caused an interesting observation during the study: both M1 and F1 made use of forest patches and corridors to cross deforested areas (Appendix H). In both locations, patches were less than 1km across. Whereas forest patches were only used once by F1, solid forest corridors were used multiple times by both individuals throughout the study period.

**Activity Patterns**

All three individuals were most active from afternoon until morning. 7:00 until 12:00 was a universal resting time. Peak activity occurred at 3:00 and 15:00 for all individuals as well. Night hours (from 16:00 until 6:00) were regularly active periods for all fossa. Activity was not identical from day to day, however. Activity reached 0 for all individuals at every hour of the day, meaning that resting occurred throughout the day. Maximum activity shows that individuals were sometimes active during usual resting hours as well. (Appendix I).

There is no distinct pattern of where the highest amounts of activity occurred habitat-wise (Appendices K-M). However, there is a clear pattern for inactivity. Resting periods for all individuals was limited to within the forest (Appendix K). During the day, when all individuals were the least active, they remained exclusively within the forest. During evening and night-time hours, M1 and F1 traveled further away from the forest into other landcover types.

Periods of rest within the forest did not have a distinct pattern of distance from forest edge for any of the individuals. Resting periods occurred both within edge habitat
and greater than 750m in the forest interior (Appendix J). M1 and F1 had a greater proportion of resting periods near the forest edge than M2. In all individuals, most resting periods occurred within 500m from the edge with much variation within that range.

Although none of the fosa truly avoided villages, all individuals came the closest to villages (within 2km) just before and immediately following their inactivity period during mid-day. These events of close proximity to human settlements occurred for a maximum of one GPS fix, or 40 minutes, before the individual left the vicinity of the village.

Discussion

**Habitat Selection and Home Ranges**

The home range sizes for all three individuals were much larger than home ranges previously calculated in any other study. For example, previous studies of fosa home ranges in Kirindy Forest, another dry deciduous habitat, had home ranges between 13 and 26 sqkm in one study (Hawkins 1998) and 12.03 and 80.65 sqkm during the dry season in a more recent study (Lührs and Kappeler 2013). M1 and F1 in ANP, by comparison, have home ranges at least double these size. The difference in home range sizes may be in part due to the number of days each individual was tracked. Lührs and Kappeler (2013) had a maximum of 31 days tracked for any individual. Since M2 has such a smaller MCP area than the other two individuals and had only two weeks of tracking, it is possible that fosa take more than one month to cover the entirety of their home ranges in some cases.

It is not surprising that all individuals had very similar habitat selection and relative distances from different landcover types. All three individuals had a high degree
of overlap with each other and occupied the same area of the park. Because of their similar locations, each fosa would be potentially affected by the same number of villages, agricultural plots, deforested patches, and water sources. Individual preferences and avoidance of areas with high human impact varied slightly, but the overall pattern remained the same across individuals. This is consistent with a previous trapping field seasons conducted in Ankarafantsika National Park, where attempted captures occurred in both forest and grassland habitats. Traps in grasslands were not successful in trapping fosa (Dollar, unpubl). Camera trap studies in northeastern Madagascar discovered the same patterns of avoidance using camera traps: fosa were seen in fragmented areas, but less commonly than they were in contiguous forest (Farris et al. 2014).

The study by Farris et al. also suggests a similar pattern in the fosa’s ability to use fragmented forests and forest edges as seen with the fosa in Ankarafantsika (2014). Another study in central-eastern Madagascar revealed the use of forest fragments by fosa within 15km from contiguous forest, with similar population density in fragments close to forest compared to densities within contiguous forest (Gerber et al. 2012). Fosa in ANP did not travel beyond 100m outside of the forest, but forest patches within 2.5km were used on several occasions across individuals.

In part, the use of forest edges and fragmented habitats may be due to the fragmented nature of the entire Ankarafantsika landscape. Within the habitat selection study area, there were 2996 separate patches of forest with a mean patch size of 0.16 sqkm. The full range of patch sizes were a minimum 0.0009 sqkm to 426.04 sqkm, the largest patch being the contiguous forest that still remains. Such a highly fragmented
landscape would cause fosa to travel near the forest edge out of necessity rather than by choice. However, the presence of fosa in these fragmented areas with a great deal of edge habitat suggests that fosa are not entirely restricted to interior, contiguous forest habitats.

The close proximity of fosas to villages may also be due to the fragmentation of the habitat. Within the study area, there were 134 separate settlements scattered across the landscape. Because of their number and distribution, it is likely that the fosa were unable to avoid villages entirely. Anecdotal evidence within Ankarafantsika suggests that fosa do enter villages, however, especially to prey on poultry. Sightings by villagers supports a previous study that found at least one third of communities reported seeing fosa within 2.5km of the village (Logan et al. 2014). All individuals in Ankarafantsika either traveled into a village or came within very close proximity of a village, however. These occurrences were rare and brief, as fixes within or near villages only occurred in single intervals, meaning the individuals remained in close proximity to human settlements for a maximum of twenty minutes.

No prior study has examined the potential of forest corridors as a conservation method for fosa. Documenting movements across corridors less than 0.5km in width coupled with forest edge use suggests that, if possible, more studies should be completed on the species’ ability to use slim forest areas to cross deforested areas. A study with a greater number of individuals collared and tracked for a longer period of time would determine how often forest corridors are willingly used at a population level. Because the fosa in ANP have such large home ranges, the same areas in each individual’s home ranges were not encountered on a daily basis across the study period.
Despite the close proximity of fossa to human settlements and areas of high human activity, there was no evidence that individuals altered their activity patterns to a more nocturnal pattern in order to avoid times of high human activity. High fosa activity did occur from evening until morning overall, but both resting periods and active periods occurred at every hour across the study period. This overall pattern compared to the high flexibility in active or resting periods throughout the day sheds light on previous disagreements on the fosa’s activity cycle ranging from nocturnal, crepuscular, and cathemeral (Albignac 1973; Hawkins 1998; Gerber et al. 2012).

Although there was not a clear change in general activity patterns in fosa in relation to human settlements, there was a clear pattern with active periods and times of day that fosa traveled away from the forest. When traveling up to 100m away from the forest, fosa were always highly active, and these instances occurred during night-time hours. There was a less clear pattern on time of day that fosa came close to villages; however, these were usually during active periods as well. This suggests that though fosa are not becoming nocturnal, their activity within close proximity to villages and agricultural areas are more likely to occur during night-time hours. Therefore, the data support a pattern of avoiding human activity by altering of time of travel through human-influenced areas.

Conclusions on Spatial Analyses and Activity Patterns

The close proximity of fossa to the edge of forest habitats suggest that fossa are not completely restricted to interior habitat even if that is the species’ preference. Two
individuals readily traversed forest corridors on multiple occasions, and one individual utilized a “corridor” consisting of separate forest patches across a savannah. This means that a solid forest corridor may not be required to enable habitat connectivity for fosa populations.

The flexible activity patterns of the fosa enable individuals to avoid areas of human activity during daylight hours. Fosa in this study did not actively shift toward a nocturnal activity pattern in ANP, but did limit activity outside of the forest to evening and night-time hours when human activity was presumably lower.

In conclusion, we suggest that fosa respond to human encroachment by flexibly utilizing a wide array of forest habitats even in a fragmented landscape, and employing highly flexible activity pattern to avoid human contact. This offers hope that they can survive human encroachment at least in the short-term. Long-term viability for the species depends on maintaining connectivity among populations, and we suggest even modest forest corridors may offer promise in this regard.
CHAPTER 5: FINAL CONCLUSIONS AND IMPLICATIONS FOR CONSERVATION

Madagascar is a country of incredible biodiversity and high rates of endemism. The fosa is just one of many species found only on this island, and like many other endemic species, it has experienced precipitous population declines and currently faces serious extinction risk due to population fragmentation and other factors. Human pressures such as poaching, deforestation, and introduced species only increase the pressure placed upon species like the fosa, disrupting complex interactions between these predators and their prey species. This project explores long-term patterns in fosa ecological dynamics in the increasingly human-influenced landscape of Ankarafantsika National Park to increase understanding of fosa biology and human-wildlife interactions and provide new information to inform the conservation effort.

Chapter one of this thesis largely outlines the context of the study, providing background on the biology and previous work on the fosa. Chapter two explores species encounters and trap rates by adding to a dataset assembled over nearly two decades. Patterns reveal potential relationships between carnivore capture rates and prey species encounters, and document the disappearance of native mesopredators like the Malagasy civet subsequent to the appearance of dogs inside the park. Chapter three contributes to over ten years of roadkill surveys on major vertebrate clades to determine the efficacy of speedbumps for mitigating vehicular mortality along the major roadway bisecting the ANP. Data on roadkill revealed that high mortality rates of prey species such as reptiles and amphibians were not improved by the installation of speedbumps. The chapter directly documents the threat posed by the road to fosa in documenting the loss of one of
the study animals (M2). Reasons for the ineffectiveness of current speedbump placement for preventing roadkill events are explored. And the fourth chapter of this thesis delves into spatial and activity patterns of GPS-collared fosa to assess the habitat pressures faced by the species, seeking to document any adaptive strategies currently in play. Fosa space use and activity patterns reveal a reliance on forested habitats, utilization of forest edges and narrow forest corridors, a general avoidance of human settlements, together with a shift to more nocturnal activity when moving through areas impacted by human disturbance. Taken together, these data suggest that the species has some inherent capability to adapt to pressures caused by humans, offering some potential areas for successful conservation methods.

Overall, this project provides the first comprehensive analysis of potential predator-prey dynamics in Ankarafantsika National Park against the backdrop of ever-increasing human pressures. It provides both a foundation for understanding future changes in fosa behavior, revealing flexibilities, vulnerabilities and a host of additional questions yet to be explored in the park. Areas for future work include in-depth population density studies for endemic and introduced species in Ankarafantsika. Lemurs and carnivores are just two of many important clades that lack the detailed census data necessary to gauge population growth or decline through time. Examining the diet of introduced carnivores can provide insight on the fauna that are prey species, identifying potential areas of competition with native species. Future roadkill analyses monitoring traffic density and vehicle speeds can further assist in determining best placements for any additional speedbumps along the roadway. Finally, continuing to radio-track fosa and
other carnivore species throughout all sectors of the park (not just along the two long-term trap lines described in this project) can help determine spatial and activity patterns across native carnivore populations in the Ankarafantsika National Park ecosystem more broadly. Long-term spatial and activity pattern data should in the future be gathered during both the wet and dry seasons, and in the less-populated eastern section of the park to explore for differences further away from human populations. Such comparisons can further inform conservation efforts for this critical keystone species.

Although there remains much to be learned about the incredible dry forest ecosystems in Madagascar, patterns revealed to date offer some critical first steps that can be taken to improve existing conservation efforts in Ankarafantsika National Park. These include continuing research, communicating with residents in the surrounding settlements, and forging partnerships with both Madagascar National Parks (MNP) and local governments. Outreach to civilians can minimize human-wildlife conflict, particularly with the fosa, and joint efforts on a variety of conservation efforts with government bodies will be paramount to create long-lasting change and minimizing the disconnect between national and local governments on conservation issues.

First, educating the public on the findings in this research, particularly the fosa’s tendency to avoid villages and agricultural areas, is critical to begin shifting perceptions of the fosa from a danger to livestock to a beneficial and important species for the ecosystem. Because most livestock, namely chicken and other poultry, are free-range and roost in trees at night, reducing the predation that does occur by fosa is an important first step. A new long-term project that consists of surveys regarding perceptions toward the
fosa and the construction of chicken coops for local residents who own poultry is already underway. Disseminating results about the fosa’s general avoidance of villages in the surveys may assist in altering the negative perceptions of the species. Acknowledging peoples’ concerns about food security due to chicken predation and offering safe solutions to the problem can lessen the tension between humans and wild carnivores.

Secondly, controlling the number of feral introduced species within the park is critical to prevent the extirpation of native fauna. Capturing and sterilizing introduced species like dogs and cats can help reduce population growth in the short-term, although long-term control of domestic animals will be necessary to preserve native species in Ankarafantsika and the surrounding areas. For control of invasive species, communication with both local village residents and MNP staff is paramount. Creating a partnership with a veterinarian to perform spaying and neutering of animals that belong to village residents will reduce the number of invasive carnivores in the surrounding forest, and through this process the residents can be educated on the impacts of feral pets on the biodiversity of the very park their livelihoods rely on. Forging an agreement with MNP to sterilize invasive carnivores captured during trapping seasons can increase the success of control measures. In more extreme cases, euthanizing invasive carnivores may become necessary. Communication with MNP in this case is extremely important to monitor invasive carnivores outside the field team’s trapping season.

Thirdly, strategic installation of additional speedbumps inside the park could mitigate roadkill events and increase safety of pedestrians along the roadway. These speedbumps should be placed along long stretches of straight road between villages
where vehicles currently reach maximum speeds. As MNP was involved in the installation of the first two speedbumps, continuing a dialogue focused on effectiveness of ongoing speedbump efforts may help in the authorization of future speedbump installation. It will be important to demonstrate to MNP that the speedbumps currently in place are effective at reducing vehicle speeds, so if placed in areas of higher wildlife traffic, wildlife mortalities can be mitigated.

Finally, fosa space use suggests that forest corridors or patches may facilitate movement of individuals and increase connectivity between potentially isolated subpopulations. Expanding and connecting forest patches across grasslands would be an inexpensive method of enabling the fosa and other species to access larger swathes of habitable land in search of food and mates, counteracting human impacts by reconstructing forest connectivity throughout the park. This final suggestion will require a combination of efforts from local residents, local governments (village presidents), MNP, and future researchers to be successfully implemented. Communication with local peoples on the benefits of restoring forest habitat, for erosion control, reduction in wildfire fuel, and improvement of wildlife habitat, may spark interest among local groups to begin planting trees in deforested areas between neighboring villages that are regularly traversed by local people. Determining target areas for forest patch restoration by future researchers and communicating these results to MNP and village presidents can begin a grassroots effort in expanding forest patches without setting aside entire areas of ANP for forest corridor construction.
Each of these efforts alone will not ameliorate pressures from increased human activity faced by the fosa. Taken together, however, these measures have the potential to benefit a significant portion of wildlife species in ANP. Forging a coalition between local governing bodies, researchers, and local citizens to work in unison will increase the health of Ankarafantsika National Park not just for the fosa, but for all its species including humans living in and around its borders. Working with local stakeholders will ensure successful of conservation strategies to protect the fosa in Ankarafantsika National Park and beyond.
REFERENCES


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## APPENDIX A: ENDEMISM IN MADAGASCAR BIOMES

<table>
<thead>
<tr>
<th>Biome</th>
<th>Area (million ha)</th>
<th>Genera</th>
<th></th>
<th>Species</th>
<th>Start of biome and subsequent changes</th>
</tr>
</thead>
<tbody>
<tr>
<td>SW and &quot;spiny bush&quot;</td>
<td>5</td>
<td>15 / 31</td>
<td>48.4</td>
<td>320 / 336</td>
<td>Widespread in Paleogene, then shrinks southward</td>
</tr>
<tr>
<td>W wet-dry deciduous</td>
<td>24</td>
<td>46 / 112</td>
<td>41.2</td>
<td>1088</td>
<td>Replaces arid brush from north after mid-Paleocene</td>
</tr>
<tr>
<td>E orographic rainforest</td>
<td>14</td>
<td>38 / 102</td>
<td>37.3</td>
<td>1372</td>
<td>Eocene/Oligocene start, then permanent in east</td>
</tr>
<tr>
<td>NW monsoon rainforest</td>
<td>1</td>
<td>7 / 30</td>
<td>25.3</td>
<td>383 / 433</td>
<td>Late Miocene or Pliocene, then expands downhill</td>
</tr>
<tr>
<td>Center</td>
<td>18</td>
<td>39 / 182</td>
<td>21.4</td>
<td>2292</td>
<td>Gradually converted from arid brush during Cenozoic</td>
</tr>
</tbody>
</table>

Data from Perrier de la Bâthie (1936) and excludes taxa spanning multiple biomes. Data is outdated but consistent as assessments were made by one individual.
APPENDIX B: OVERVIEW OF MADAGASCAR PROTECTED AREAS

An overview of Madagascar’s landcover and locations of protected areas.
Overview of Ankarafantsika National Park and landcover types used to complete habitat selection analysis.
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Aerial view of trap lines JBA (west) and JBB (east). Trap locations are represented by yellow dots.
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Expected roadkill events per month by season, class, and family. From top left to bottom right: amphibians, birds, mammals, and reptiles.
From within the forest, frequencies of distance from forest edge. From top to bottom: M1, M2, F1.
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Distances from each habitat type that fosas traveled.
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Trajectories showing the use of forest patches and corridors to traverse deforested areas. M1 is shown in red and F1 is shown in pink.
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Hourly activity patterns for each individual. The center line depicts the mean, the shaded regions depict the range in maximum and minimum activity counts. From top to bottom: M1, M2, F1.
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From within the forest, frequencies of distance from forest edge during resting periods (activity count = 0). From top to bottom: M1, F1.
APPENDIX K: ACTIVITY PATTERNS BY HOUR (FOREST)

Activity Counts by hour and distances traveled from forest landcover type. From top to bottom: M1, M2, F1.
APPENDIX L: ACTIVITY PATTERNS BY HOUR (AGRICULTURE)

Activity Counts by hour and distances traveled from agriculture landcover type. From top to bottom: M1, M2, F1.
Activity Counts by hour and distances traveled from village landcover type. From top to bottom: M1, M2, F1.